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BENTHIC INVERTEBRATES AT FORAGING LOCATIONS OF NINE WATERBIRD SPECIES IN MANAGED WETLANDS OF THE NORTHERN SAN JOAQUIN VALLEY, CALIFORNIA

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Abstract: The ecologies of waterbirds are closely tied to the distribution and abundance of food resources. For many species of waterfowl and shorebirds, benthic invertebrates (especially Chironomidae) are an important dietary component that influences habitat selection. Consequently, we sampled benthic invertebrates and measured water depth at foraging locations of nine waterbird species and paired random sites in the Grasslands of the northern San Joaquin Valley, California, USA from January to April 1994 and 1995. Our resulting habitat-selection models indicate significant differences in benthic invertebrate densities or biomasses at foraging and random locations for three of nine species and significant differences in water depths between foraging and random locations for four of nine species. Additionally, we observed significant interspecific differences in water depths at foraging locations—shorebirds used shallow habitats (<10 cm), whereas most waterfowl species foraged in deep water (>20 cm). Waterfowl foraged over a wider range of water depths than shorebirds, indicating greater behavioral flexibility in habitat use. Our results indicate that selection of foraging habitat by smaller bodied waterbirds, including dowitchers, dunlin, western sandpiper, and least sandpiper is strongly influenced by water depth, which mediates the availability of benthic invertebrates. Additionally, foraging site selection of more mobile taxa that are able to forage in a wide range of water depths, including northern shoveler and american green-winged teal, is influenced by invertebrate biomass. The broad range of water depths used by waterfowl and the relatively restricted depths used by shorebirds indicate that water depth can be manipulated to benefit a multitude of waterbird species.

Key Words: benthic invertebrates, California, Chironomidae, habitat selection, Oligochaeta, shorebirds, water depth, waterfowl, wetlands

INTRODUCTION

The availability of food is of primary importance to waterbirds in the winter and spring, during which they store energy for overwinter survival and successful completion of migration (Chabreck 1979, Drent and Daan 1980). The foraging ecologies of many waterfowl (Anseriformes) and shorebirds (Charadriiformes) are coupled with the distribution of aquatic invertebrates, an important component of waterbird diets (Baldassarre and Fischer 1984, Eldridge 1992, Krapu and Reinecke 1992). Researchers have shown that benthic invertebrate populations correlate positively with waterfowl (Murkin and Kadlec 1984) and shorebird (Colwell and Landrum 1993) distributions. Moreover, waterfowl (e.g., Severson 1987, Wrubleski 1989) and especially shorebirds (e.g., Szekely and Bamberger 1992, Mercier and McNeil 1994), often deplete populations of benthic prey. Consequently, access to benthic invertebrates is a strong selective force shaping the morphology, behavior, and distribution of waterbirds, and knowledge of ecological relationships between birds and invertebrates is crucial to conservation and management of wetland habitats.

The positive correlation between distributions of birds and invertebrates suggests that foraging waterbirds select habitats based on prey abundance. This relationship has been demonstrated at a variety of spatial scales, but it is most apparent at broad scales, including entire pastures and estuaries (Goss-Custard 1970, Goss-Custard 1977, Colwell 1993, Colwell and Landrum 1993). At the individual (species) level, however, we know less about

how variation in invertebrate density and biomass influences the distribution of waterbirds.

Throughout North America, moist-soil management (Kadlec 1962, Connelly 1979, Fredrickson and 1982, Cross 1988, Payne 1992, Baldassarre and Bolen 1994) is used to manipulate wetland plant communities to benefit waterfowl. Moist-soil management entails flooding and dewatering wetlands to stimulate germination of waterfowl food plants, which also provide food and habitat for invertebrates (Severson 1987). Changes in water depth associated with moist-soil management affect waterbirds because many species are constrained morphologically to forage at specific water depths. For example, large-bodied, long-necked waterfowl forage in deeper habitats compared with smaller taxa (Poysa 1983) and shorebirds vary in the depth at which they forage based on tarsus and culmen length (Baker 1979). Consequently, we predicted that the relationship between food resources, water depth, and waterbird ecologies would be especially strong in managed wetlands where water depth is manipulated seasonally through the practice of wetland drawdowns.

Specifically, the objectives of this study were to determine the influences of benthic invertebrates and water depth on foraging site selection of four waterfowl species and five shorebird species in wetlands of the Grasslands during the nonbreeding season. In this paper, we examine differences in benthic invertebrate densities and biomasses between the foraging locations of nine waterbird species and paired, random sites in managed wetlands of the northern San Joaquin Valley, California, USA.

STUDY SITE

We studied waterbirds and benthic invertebrates from mid-January to mid-April 1994 and 1995 in ten wetlands within the Grasslands Ecological Area (hereafter, the Grasslands) of the northern San Joaquin Valley, California (Figure 1). The Grasslands encompasses the largest (~47,000 ha) block of palustrine wetlands in California. This landscape of private and public lands is a mosaic of native uplands and highly modified wetlands, which historically received seasonal flood waters from the San Joaquin River and smaller watersheds of the coastal range. Now, wetlands within the Grasslands receive water by canals, and wetland hydrology is almost entirely manipulated by humans. Most (85%) private wetlands are managed using moist-soil practices—they are flooded each fall prior to the waterfowl hunting season and dewatered in late winter and early spring to promote growth of waterfowl food plants (Fredrickson and Taylor 1982, Heitmeyer et al. 1989). Because of its size, the Grasslands is recognized as important nonbreeding habitat for wa-

terfowl (Heitmeyer et al. 1989) and shorebirds (Hunter et al. 1991). Soils within the Grasslands are derived from a mixed alluvium dominated by river sediments and are poorly drained (Fredrickson and Laubhan 1995). Water salinities vary greatly (750–5000+ μmhos) among wetlands within the Grasslands (Colwell et al. 1994). See Fredrickson and Laubhan (1995) for a more thorough description of the study area.

METHODS

We collected benthic invertebrates and measured water depth (± 1 cm) at foraging locations of nine species of waterbirds and paired random sites (Table 1) within ten wetlands of the North and South Grasslands (Figure 1). Each of the ten wetlands is managed for germination of swamp timothy, *Heleochloa schoenoides* (L.) Host.; these ponds are dewatered in late March through early April to facilitate propagation of this waterfowl food plant.

To sample benthic invertebrates at waterbird foraging sites, we randomly located and observed an individual bird for a period of two minutes through a tripod-mounted rifle scope (9X). We marked the waterbird foraging location using the rifle scope by aligning the intersection of the crosshairs of the scope with the surface of the water or mudflat at the location of the last foraging behavior (e.g., probe, peck for shorebirds; dabble, head-under for waterfowl). To mark the location of each waterbird in the wetland, we used hand signals to direct a field assistant to place a wooden stake at the bird location, indicated by crosshairs of the scope. We placed a 1 × 1 m sampling quadrat at each shorebird foraging location and three 1 × 1 m sampling quadrats at waterfowl foraging locations. The sampling quadrat was divided into twenty-five 400-cm² subplots. For each foraging sample, we collected benthic invertebrates in one randomly determined subplot within the quadrat; we sampled invertebrates in the center quadrat (of three) at waterfowl locations. We also collected one benthic invertebrate sample at one paired, random site based on a random compass direction and distance within 5 to 100 m of the foraging location.

We sampled benthic invertebrates with a 5-cm-diameter cylindrical core sampler pushed 10 cm into the substrate and immediately placed cores in labeled plastic bags. Within several hours of sampling, we washed invertebrates using water and a fine mesh sieve, then fixed invertebrates in a 70% ethanol solution. We sampled the benthos to a depth of 10 cm in order to compare invertebrates accessible to the range of waterbirds based on variation in morphology related to foraging (e.g., tarsus and culmen length).

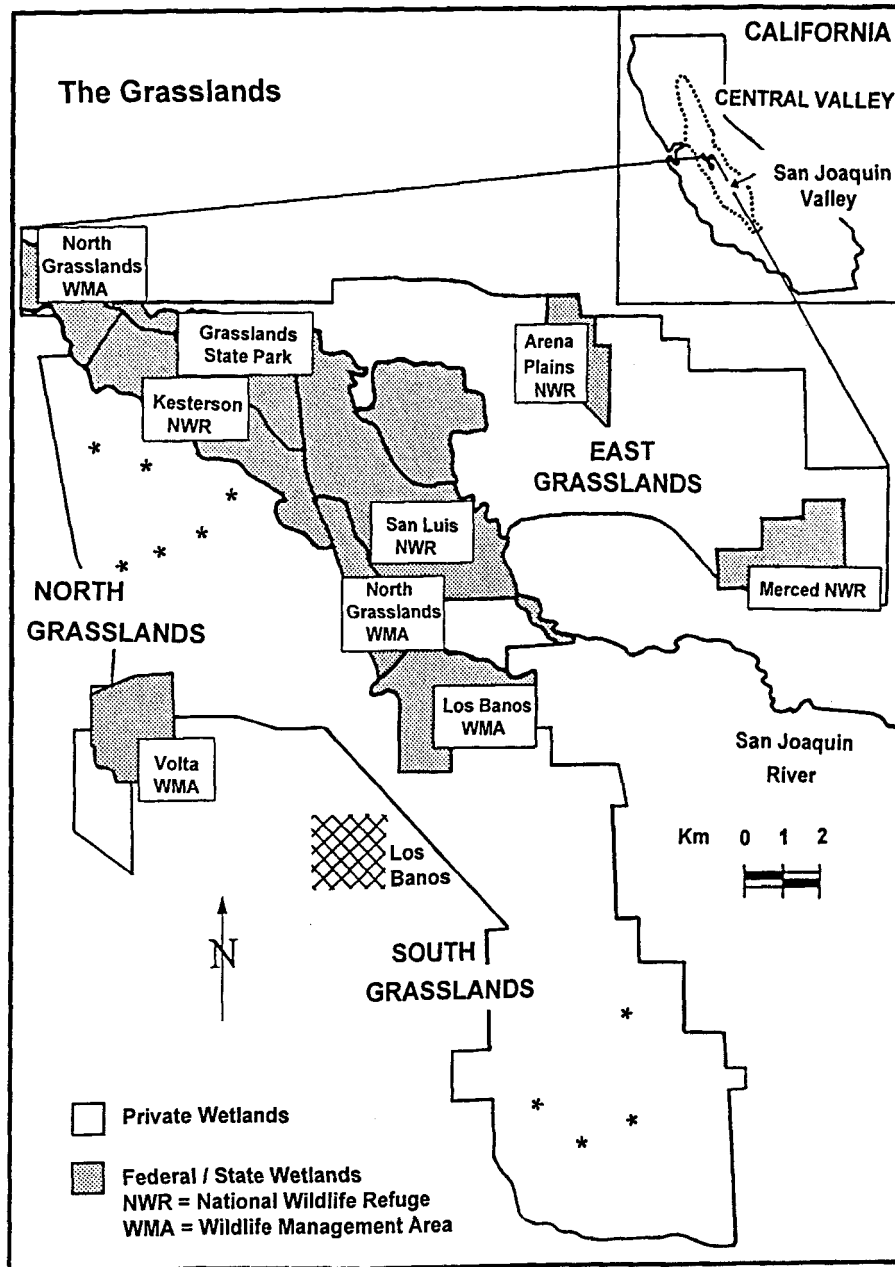We used dissecting (3–7X zoom) and compound (10X) microscopes to sort and identify invertebrates

Figure 1. Location of ten wetlands in the Grasslands (*), Merced County, CA, USA where we sampled benthic invertebrates at foraging locations and paired random sites of nine waterbird species from January to April, 1994 and 1995.

based on Pennak (1978) and Merrit and Cummins (1984). Data generated from this procedure included 1) taxonomic group at the level of order (Oligochaeta) or family (Chironomidae), 2) abundance (converted to density per m²), and 3) dry biomass (converted to mg per m²). We estimated biomass by calculating mass differences of weighing empty tins and tins with samples subsequent to 17 hrs drying at 60°C. We weighed samples to the nearest 0.0001 g using a Mettler balance.

Data Summary and Analysis

We compared density and biomass of invertebrates and water depth between foraging and random loca-

tions using univariate matched pairs logistic regression (Hosmer and Lemeshow 1989). The advantage of using this analysis is the ability to pair the foraging and random locations following our sampling methodology, and thereby reducing the variation derived from differences among wetlands. In matched pairs logistic regression, the sample size is defined as the number of matched pairs (foraging and random locations), the intercept term is removed from the model, and the differences between paired locations are used as independent variables or covariates (Hosmer and Lemeshow 1989). Moreover, one can use matched pairs logistic regression for multiple independent variables.

We subtracted random-centered location data from

Table 1. Mean ± SE differences between foraging and random locations for nine waterbird species in managed wetlands of the Grasslands, Merced County, CA, 1994–1995. Negative numbers indicate greater values at random locations. Sample Size = 20 for all observations.

Species	Acronym	Scientific Name[c]	Water Depth cm	Density/m² Chironomid	Density/m² Oligochaete	Biomass mg/m² Chironomid	Biomass mg/m² Oligochaete
Gadwall	GADW	Anas strepera	2.62 ± 1.97*	50.93 ± 408.14	3580.38 ± 3017.44*	-33.08 ± 223.64	175.26 ± 119.77*
Northern Pintail	NOPI	Anas acuta	0.68 ± 1.26	203.72 ± 631.03	4838.35 ± 5032.66	285.21 ± 178.07*	211.35 ± 209.68
Northern Shoveler[a]	NOSH	Anas clypeata	1.71 ± 2.14	428.88 ± 480.47	-2037.20 ± 3275.46	482.49 ± 220.35*	-53.61 ± 164.53
American Green-winged Teal[b]	AGWT	Anas crecca carolinensis	-3.55 ± 1.92*	-107.22 ± 551.45	3319.12 ± 2218.47*	225.17 ± 114.61*	292.18 ± 138.04*
American Avocet	AMAV	Recurvirostra americana	2.12 ± 1.26*	-101.86 ± 433.39	2088.13 ± 2677.85	290.31 ± 166.47*	96.77 ± 98.76
Dowitcher	DOWI	Limnodromus spp.	-3.03 ± 0.99**	-713.03 ± 872.74	7894.15 ± 8075.84	-348.88 ± 222.88*	170.62 ± 242.13
Dunlin	DUNL	Calidris alpina	-1.99 ± 0.81**	25.46 ± 744.36	-585.70 ± 4210.51	66.21 ± 158.36	119.70 ± 175.20
Western Sandpiper	WESA	Calidris mauri	-1.02 ± 0.45*	-933.14 ± 890.62	8530.77 ± 5168.46*	-253.74 ± 108.07*	371.77 ± 255.60*
Least Sandpiper	LESA	Calidris minutilla	-2.64 ± 0.84**	254.65 ± 453.50	1018.60 ± 5868.0	-109.30 ± 126.54	137.52 ± 238.83

[a] Sample size = 19.
[b] Sample size for biomass data = 19.
[c] American Ornithological Union.
* = P value for univariate matched pairs logistic regression ≤ 0.25; the value for inclusion in multivariate matched pairs logistic regression models.
** = P value for univariate matched pairs logistic regression ≤ 0.05.

foraging-centered location data and created five covariates for each species: water depth, chironomid density, oligochaete density, chironomid biomass, and oligochaete biomass. As a result of the manner in which we calculated the covariates, a negative coefficient indicates larger values (water depth, densities, or biomass) at random locations compared to foraging locations.

We examined univariate matched pairs logistic regression results using the Wald Chi-Square (χ^2) test statistic. We included each covariate with a P value of ≤0.25 in a multivariate model, as suggested by Hosmer and Lemeshow (1989) and conducted backwards elimination matched pairs logistic regression using the significance of the -2 log likelihood χ^2 and Akaike's Information Criterion (AIC). The AIC adjusts the -2 log likelihood statistic (often referred to as deviance, which is analogous to sums of squares error in linear regression) for the number of terms and observations used in the model, and generally, we selected the model with the lowest AIC value ±1 unit (Lebreton et al. 1992). We also used stepwise model selection techniques to compare the results of our model selection methodology.

We analyzed interspecific differences using one-way ANOVA with species as treatment. When ANOVA detected significant results among groups of species ($P \leq 0.05$), we used the Tukey multiple comparison test to identify differences between species (Day and Quinn 1989, Zar 1996). All statistical analyses were performed using SAS version 6.11 (SAS Institute 1990).

RESULTS

Intraspecific Patterns

The results of univariate analyses identified several variables for inclusion in multivariate models (Table 1); however, most of these variables did not contribute to final habitat selection models. The tremendous amount of variation present in nearly all foraging and random density and biomass values, owing to the characteristic patchy distribution of benthic invertebrates, is likely a reason for these results (Figures 2 and 3). Nevertheless, the descriptive data (Figures 2, 3, and 4) illustrate several patterns of habitat selection. Compared to random sites, oligochaete densities and biomasses were greater at seven and eight waterbird foraging locations, respectively (Table 1, Figure 2). Also compared to random sites, chironomid biomasses were greater or nearly equivalent at waterfowl locations, while the opposite was the case for smaller shorebirds (Table 1, Figure 3). The importance of shallow water depths to all four species of small bodied shorebirds and American green-winged teal is apparent (see Table 1 for scientific names). Interestingly, the larger and more mobile waterfowl (gadwall, northern pintail, and northern shoveler) and shorebird (American avocets)
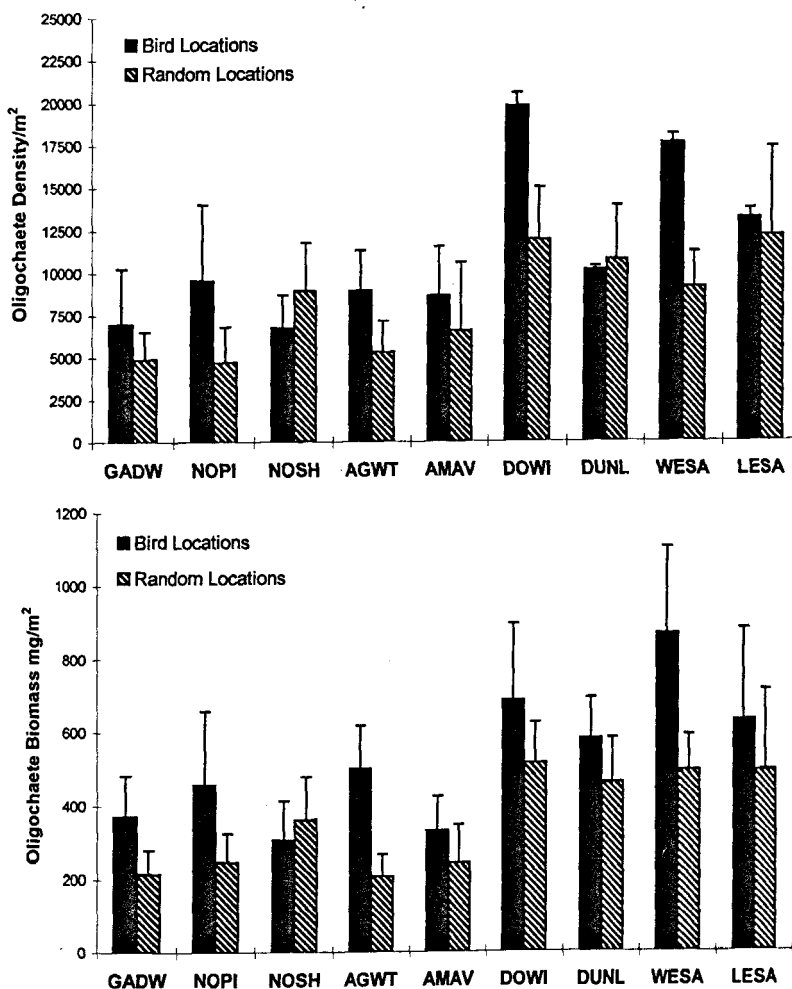
Figure 2. Average (±SE) Oligochaete Density and Biomass at foraging locations and paired random sites of nine waterbird species in the Grasslands, Merced Co., CA, USA, 1994–1995. Table 1 presents species' acronyms and sample sizes.

species foraged in deeper water compared to random sites. Moreover, waterfowl and avocets foraged at a wider range of water depths, whereas shorebirds, particularly small sandpipers, foraged in narrower ranges of shallow water (Figure 4).

We obtained significant habitat selection models for six species (Table 2). These models indicate that water depth was an important attribute of habitat selection for four smaller bodied shorebird species; dowitchers, dunlin, western sandpipers, and least sandpipers foraged in water shallower than random locations (Table 1, Figure 4). Additionally, benthic invertebrates seemed to influence the site selection of three species examined in this study: northern shoveler, American green-winged teal, and western sandpiper. The habitat selection model for western sandpiper included water depth and chironomid and oligochaete densities as independent variables. Although the univariate P value of differences in chironomid density at western sandpiper foraging sites and random locations was slightly above the criteria for multivariate inclusion of this variable ($P = 0.28$), this variable was found to be important using stepwise model tech-

niques and AIC; thus we retained differences in chironomid density in the final model for western sandpiper.

Interspecific Patterns

We observed significant interspecific differences between the foraging water depths of all waterbirds included in this study (Table 3, Figure 4). Sandpipers foraged in water <5 cm; dowitchers and avocets used habitats 5–10 cm. American green-winged teal foraged at water depths within 10–15 cm; other dabblers foraged in water >20 cm. Across species, variation in habitat use increased with average water depth—waterfowl foraged over a broader range of water depths compared with shorebirds. We observed no interspecific differences in density and biomass of benthic invertebrates (Table 3, Figures 2 and 3).

DISCUSSION

Intraspecific Patterns

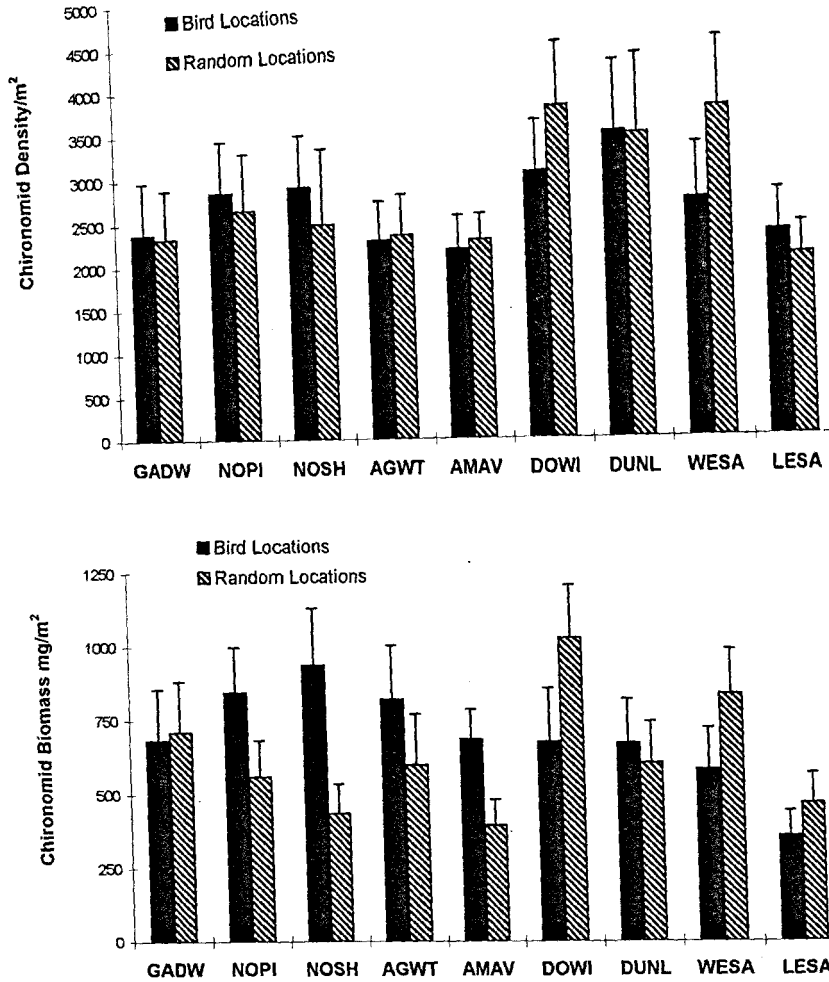We detected significant differences in benthic invertebrate biomass and density between random sites and

Figure 3. Average (±SE) Chironomid Density and Biomass at foraging locations and paired random sites of nine waterbird species in the Grasslands, Merced Co., CA, USA, 1994–1995. Table 1 presents species' acronyms and sample sizes.
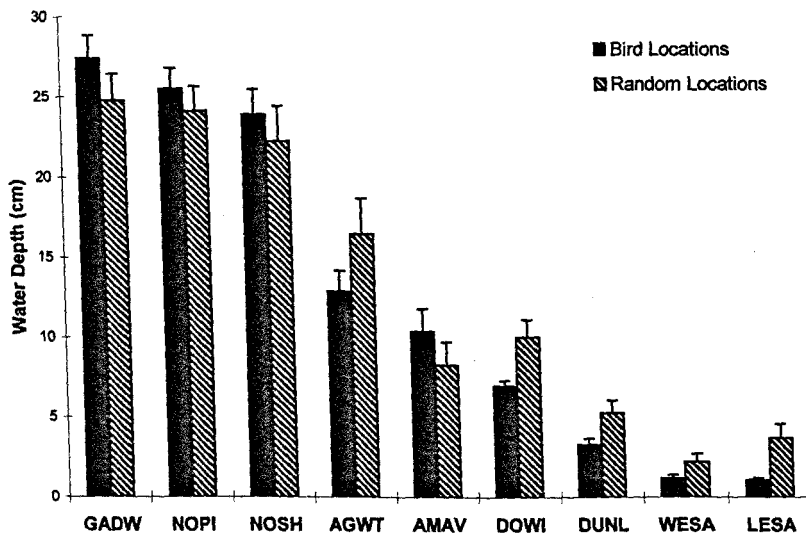

Figure 4. Average (±SE) water depth at foraging locations and paired random sites of nine waterbird species sampled in managed wetlands of the Grasslands, Merced Co., CA, USA, 1994–1995. Lines below acronyms connect species with similar water depth ranges based on results of a Tukey Multiple Comparison Test. See Table 1 for species' acronyms and sample sizes.

Table 2. Results of backwards elimination matched pairs logistic regression using water depth and four benthic invertebrate variables to compare waterbird foraging locations and random sites in managed wetlands of the Grasslands, Merced County, CA, 1994–1995. See Table 1 for sample sizes.

Species[a]	Independent Variable	Significance of Variable			Significance of Model		
		Parameter Estimate ± SE	Wald χ^2	P Value	Model χ^2	DF[b]	P Value
Northern Shoveler	Chironomid Biomass	0.0014 ± 0.0008	2.78	0.10	4.98	1	0.03
American Green-winged Teal	Chironomid Biomass	0.0055 ± 0.0028	3.72	0.05	12.55	2	0.002
	Oligochaete Biomass	0.0047 ± 0.0023	4.24	0.04			
Dowitcher spp.	Water Depth	−0.4646 ± 0.2196	4.48	0.03	9.56	1	0.002
Dunlin	Water Depth	−0.2914 ± 0.1446	4.06	0.04	5.30	1	0.02
Western Sandpiper	Water Depth	−0.4757 ± 0.3813	1.55	0.21	11.75	3	0.008
	Chironomid Density	−0.0005 ± 0.0003	2.40	0.12			
	Oligochaete Density	0.0001 ± 0.0001	1.76	0.18			
Least Sandpiper	Water Depth	−0.7490 ± 0.3533	4.49	0.03	11.30	1	0.0008

[a] No significant models for Gadwall, Northern Pintail, and American Avocet.
[b] Degrees of freedom.

the foraging locations of three waterbird species in this study (Table 2, Figures 2 and 3). These findings were surprising, given that spatial distribution of foraging waterbirds has been correlated with abundance of benthic invertebrates in other habitats (Goss-Custard 1970, Colwell and Landrum 1993). Chironomids are important components of waterfowl diets, especially during the pre-breeding period encompassed by our study (Euliss and Harris 1987, Dubowy 1988, Krapu and Reinecke 1992). In addition, shorebird diets often consist largely of chironomid larvae (Baldassarre and Fischer 1984, Eldridge 1992). By contrast, less is known about the importance of small aquatic oligochaetes (Aelosomatidae and Naididae) to the waterbirds we examined in this study during the nonbreeding season (Krapu 1974, Baldassarre and Fischer 1984, Euliss and Harris 1987, Dubowy 1988, Krapu and Reinecke 1992). The oligochaetes we encountered in the Grasslands were tiny and fragile, and these organisms are presumably difficult to detect in the stomach contents once ingested.

We are not able to conclude that greater densities and biomasses of benthic invertebrates at foraging locations simply translates into higher quality feeding sites. For example, western sandpipers foraged in lo-

cations with significantly lower chironomid densities than random sites. These results complement the conclusions of a waterbird exclosure experiment conducted in the Grasslands that detected benthic prey reduction, primarily by shorebirds, in shallow water depths as wetlands were dewatered (Colwell pers. comm.). Hence, these lower chironomid densities at western sandpiper foraging locations could indicate that prey items, accessible to these birds at shallow water depths, are being depleted. Interestingly, similar trends, although not statistically significant, are apparent for the other smaller bodied shorebirds we examined in this study; lower chironomid densities and biomasses were detected at dowitcher foraging locations, lower oligochaete densities were found at dunlin foraging locations, and lower chironomid biomasses were present at least sandpiper foraging sites (Table 1, Figures 2 and 3). In contrast, the omnipresent pattern of higher oligochaete densities and biomasses, (although significant for only two species) at the foraging locations for nearly all the species examined in this study is difficult to ignore. Do these higher values suggest the importance of oligochaetes to foraging waterbirds?

Table 3. Results of One-Way ANOVAs testing interspecific differences between 9 waterbird species with respect to chironomid density, chironomid biomass, oligochaete density, oligochaete biomass and water depth. Source of variation = 9 waterbird species (See Table 1 for sample sizes), degrees of freedom = 8.

Dependent Variable	Sums of Squares	Mean Square	F Value	P Value	Model R^2
Chironomid Density	26494481.57	3311810.19	0.52	0.84	0.02
Chironomid Biomass	4213713.75	526714.22	1.12	0.35	0.05
Oligochaete Density	3440439175.14	430054896.89	1.11	0.36	0.05
Oligochaete Biomass	5259562.49	657445.31	1.13	0.34	0.05
Water Depth	17514.98	2189.37	100.45	0.0001	0.82

Or, conversely, do these larger biomasses and densities indicate that birds do not feed on these invertebrates?

We did not examine the possible impact of waterbird foraging activities on invertebrates by collecting data on foraging rates, densities of waterbirds at each wetland, nor the length in which birds foraged in one site. Therefore, it is difficult to interpret the direction of trends and significant differences in benthic invertebrates between bird foraging locations and random sites detected in this study. Nonetheless, the nearly ubiquitous pattern of greater oligochaete densities and biomasses at bird foraging locations, in addition to the significant differences included in habitat selection models, suggest that benthic invertebrates do influence foraging site selection. More information about the importance of small, aquatic oligochaetes to waterbird diets is needed to evaluate this conjecture.

For four of five shorebird species, we observed strong patterns of habitat selection based on water depth (Table 2, Figure 4), which suggests that availability, rather than abundance, of benthic invertebrates is an important determinant of habitat use. These results are supported by additional research conducted in this region, which demonstrated that communities and densities of waterbirds varied strongly with water depth (Williams 1996). Shorebirds are more limited by water depth than waterfowl; this is demonstrated by the wider ranges of water depths used by waterfowl, while smaller shorebirds are constrained morphologically to have access to narrower ranges of shallow water (Figure 4). Hence, we expected that the more mobile species should choose foraging sites based on food abundances. The results of our study hint at that. Northern shovelers, which foraged across the greatest range of water depths compared to other waterbirds (Colwell et al. 1994), seemed to select feeding locations based on chironomid biomass (Table 2). Additionally, American green-winged teal, which foraged across a variable range of medium water depths (Figure 4), also showed differences in site selection based on invertebrate biomass (Table 2, Figure 2 and 3). Results of a study of nonbreeding White-faced Ibis, a large wading bird that forages in medium water depths of 6–16 cm, also supports this conclusion. While ibis foraged in a range of water depths shallower than random sites, fine-scale habitat selection in the Grasslands was also influenced by chironomid and oligochaete biomass (Safran 1997).

Interspecific Patterns

Among species, we observed no significant differences in benthic invertebrate density and biomass (Table 3, Figures 2 and 3), but species segregated strongly in their use of habitats based on water depth (Table 3,

Figure 4). Our findings support the widely held view (Helmers 1992) that differences among waterbirds in habitat use is largely a function of water depth (Baker 1979, Poysa 1983, Colwell and Oring 1988, Dubowy 1988, Velasquez 1992, Weber and Haig 1996). Thus, we believe that our data suggest that waterbirds are constrained by morphology (Baker 1979, Poysa 1983, Weber and Haig 1996) to use zones of water depth within which they forage at random with respect to invertebrates.

Wetland managers have focused recent attention on integrated management techniques that provide habitat for a greater diversity and abundance of waterbird species (Helmers 1992, Laubhan and Fredrickson 1993). The results of our study clearly indicate that wetland managers should focus on water depth as the primary variable affecting waterbird habitat use within wetlands in the Grasslands (see Williams 1996).

ACKNOWLEDGMENTS

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