FORAGING SITE SELECTION BY NONBREEDING WHITE-FACED IBIS[1]

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Abstract. We examined foraging site selection by White-faced Ibis (*Plegadis chihi*) wintering in the Grasslands Ecological Area, which contains the second largest population of nonbreeding ibis in California. We compared habitat variables at White-faced Ibis foraging sites with paired, random locations in managed wetlands of the Grasslands. We contrasted the density and biomass of benthic macroinvertebrates between a subsample of bird foraging locations and random sites. Compared to random locations, the foraging locations of White-faced Ibis were closer to emergent vegetation > 10 cm in height. Moreover, ibis selected foraging locations with significantly higher chironomid and lower oligochaete biomasses relative to random sites. These findings suggest that ibis foraged close to vegetation where prey abundance may be greater and illustrate the importance of maintaining the presence of emergent vegetation in freshwater wetlands.

Key words: foraging ecology, nonbreeding waterbirds, Plegadis chihi, San Joaquin Valley, water depth, wetland management, White-faced Ibis.

Currently less than 6% of an historic two million hectares of wetlands remain in the Central Valley of California (Frayer et al. 1989). Approximately 30% (~47,000 ha) of these wetlands are within the Grasslands Ecological Area (hereafter, the Grasslands), and the majority of these wetlands are highly managed systems (Fredrickson and Taylor 1982). Because the relationship between water depth and food availability for waterbirds is strong (Safran et al. 1997) and due to the significant reduction of freshwater wetlands and the seasonal manipulation of modified wetlands in the Grasslands, management plans that target groups of organisms are of critical importance. A species of special concern both in California and at the federal level (United States Fish and Wildlife Service [USFWS] 1995), the White-faced Ibis (*Plegadis chihi*) may serve as a target species for wetland management plans that also provide habitat for other waders and dabbling ducks (Safran et al. 1997).

The purpose of this study was to elucidate attributes of White-faced Ibis foraging site-selection in wetlands of the Grasslands during winter which, in contrast to summer habitat use, has been little studied. We ex-

amined the hypothesis that ibis choose to forage in microhabitats that differ from randomly selected locations in the Grasslands. We had two primary objectives: (1) to compare habitat characteristics between White-faced Ibis foraging sites and paired, random locations, and (2) to contrast the density and biomass of benthic macroinvertebrates between ibis foraging locations and random sites. The goal of this study is to provide information on White-faced Ibis wintering ecology which may assist in making conservation and management decisions for this and other waterbird species.

METHODS

STUDY AREA

The Grasslands is located in the northern San Joaquin Valley and has been an important and consistently used site for nonbreeding White-faced Ibis in California, even during dramatic ibis population declines in the 1960s and 1970s (Shuford et al. 1996). Presently, the Grasslands accommodates the second largest wintering population (~12,000, or ~45%) of White-faced Ibis in California (Shuford et al. 1996). Humans regulate wetland hydrology through canals and other water control structures, developed for irrigation purposes in the late 1800s (Ogden 1988). Managers manipulate water depth seasonally and flood wetlands prior to the hunting season in late fall. This practice provides abundant waterfowl habitat which may not accommodate the diversity of waterbirds that winter or stopover in the Grasslands.

FIELD METHODS

We studied White-faced Ibis in the Grasslands from 16 January to 30 March 1995. We examined habitat characteristics at foraging locations of White-faced Ibis in wetlands at 13 duck-hunting clubs (hereafter, duck clubs) within the Grasslands and in managed wetlands throughout the Los Banos Wildlife Management Area (hereafter, LBWA). We used a tripod-mounted rifle scope (9×) to observe each ibis ($n = 60$) for 4 min and randomly chose one bird within each flock to minimize dependence of samples. If an ibis foraged consistently throughout the observation, we recorded the last behavior (probe, or peck) at the end of 4 min. We defined "probe" when an ibis foraged by inserting its bill in the benthos, and "peck" when an ibis picked up items from the surface without inserting its bill into the substrate. We recorded these foraging behaviors in order to ascertain the extent to which ibis foraged in the benthos (probe).

We marked ibis foraging locations by aligning the intersection of the crosshairs of the rifle scope with the

location of the bird when it last probed or pecked. We used hand signals to direct a field assistant to place a wooden stake at the bird location, indicated by crosshairs of the scope. Due to depth perception distortion and scope error at far distances, this method is accurate up to 100 m (Colwell et al. 1994). Thus, we only sampled birds that were less than 100 m (measured in paces from scope to bird site) from our observation point. For each ibis foraging location, we measured habitat data at a paired site, determined by a random compass direction and a random distance within 5–100 m.

HABITAT VARIABLES

We sampled 11 habitat variables using a 1×1 m^2 quadrat frame subdivided into 25 subplots (each subplot = 400 cm^2). To measure the surface of the foraging and random locations, we estimated the percent cover of the quadrat using five variables: emergent vegetation, floating vegetation, open water, mudflat, and vegetative detritus. In 10 randomly determined subplots of the quadrat, we measured water depth (cm) and vegetation height (cm). We also recorded maximum vegetation height (cm), the tallest pieces of emergent vegetation, anywhere within the 10 random subplots of the sampling grid. We measured all vegetation heights ($\pm$ 1 cm) from the water or mudflat surface by placing a sampling rod vertically in the center of each subplot. Additionally, we estimated distance to the aquatic/terrestrial interface (m), distance to vegetation (m) > 10 cm in height, and distance to continuous vegetation (m) from the center of the sampling grid. We recorded the species of emergent vegetation in association with the distance to vegetation and the distance to continuous vegetation variables. We estimated distance from the sampling plot using the following categories (m), 0–1, >1–5, >5–10, >10–20, >20–50, >50–100, and >100. For all categories, we used negative values to indicate distance from mudflat to water and positive values to indicate distance from water to the nearest non-aquatic interface.

BENTHIC INVERTEBRATES

We sampled benthic invertebrates at 20 pairs of ibis foraging locations and random sites using a 5-cm diameter core sampler. We pushed the core sampler 10 cm into the benthos to extract a sample in one randomly selected subplot within the 1-m^2 grid. We immediately placed cores in labeled plastic bags and processed (using water and a fine mesh sieve) and fixed invertebrates in 70% ethanol within several hours of sampling. We extracted and processed a total of 20 benthic invertebrate samples at both random and bird locations.

We sorted and identified invertebrates based on Pennak (1978) and Merritt and Cummins (1984). Data generated included order or family, abundance (converted to density m^{-2}), and dry biomass (converted to mg m^{-2}). We estimated biomass by calculating mass differences of weighing tins alone and tins with samples after 17 hr drying at 60°C.

STATISTICAL ANALYSES

We calculated averages ($\pm$ SD) for the water depths and vegetation heights recorded in 10 subplots for each

bird and random location. We used the median value of the distance categories in our statistical analyses.

We used matched-pairs logistic regression (MPLR) to compare 11 habitat variables between the foraging and random locations. Additionally, we compared chironomid biomass and density and oligochaete biomass and density between bird and random locations. In MPLR, the sample size is defined as the number of matched pairs (bird and random locations), the dependent variable consists of "1"s, the model does not contain an intercept, and the differences between paired locations are used as independent variables or covariates (Hosmer and Lemeshow 1989). MPLR enabled us to pair bird and random locations within each wetland, following our sampling methodology, and thereby reduce variability in the data derived from differences among wetlands. Moreover, one can use MPLR for multiple independent variables.

For each paired observation, we subtracted random location data from bird data, which created 11 covariates corresponding to the 11 habitat variables, and 4 benthic invertebrate variables. Because of the manner in which we calculated the covariates, negative and positive coefficients indicated that random locations had greater and lesser values, respectively.

We examined univariate MPLR results using the Wald Chi-square (χ^2) test statistic and included each covariate with a P-value < 0.25 in a multivariate MPLR model, as suggested by Hosmer and Lemeshow (1989). We conducted backwards elimination multivariate MPLR and based model selection on the Akaike Information Criterion (AIC) (Lebreton et al. 1992). The AIC adjusts the −2 log likelihood statistic (or deviance), which is analogous to sums of squares error in linear regression) for the number of terms and observations used in the model. AIC is calculated by adding the deviance to (2 × P), where P = the number of parameter estimates contained in the model (Lebreton et al. 1992). Generally, one selects the model with the lowest AIC value ±1 unit (Lebreton et al. 1992). Additionally, we performed stepwise multivariate MPLR to compare model selection using the above described method. We also examined coefficients of both the univariate and multivariate models, which should be similar when colinearity is not a problem (Hosmer and Lemeshow 1989).

We used F-max tests (Sokal and Rohlf 1981), which test for heteroscedasticity, to compare the variation of covariates measured at random sites and bird locations.

We analyzed habitat and benthic invertebrates separately because of large differences in sample sizes (n = 60 for habitat variables, n = 20 for benthic invertebrate variables). We performed all statistical analyses using SAS version 6.11 (SAS Institute 1989). We used the LOGISTIC procedure to perform MPLR analyses. We report MPLR parameter estimates and mean differences between bird and random locations with standard error values. We report all other data as mean values $\pm$ SD.

RESULTS

Ibis foraged using both nonvisual tactile probing and surface pecking. Based on our observations of foraging behavior associated with feeding locations (n = 48),

TABLE 1.   Average habitat characteristics ($\pm$ SD; n = 60) and benthic invertebrate densities and biomasses ($\pm$ SD; n = 20) at White-faced Ibis foraging sites and paired, random sites.

Variable	White-faced Ibis foraging sites	Random sites
Emergent vegetation (%)	13.1 $\pm$ 18.9	10.2 $\pm$ 20.3
Floating vegetation (%)	2.5 $\pm$ 10.6	2.2 $\pm$ 12.2
Open water (%)	82.0 $\pm$ 24.4	84.1 $\pm$ 27.4
Mudflat (%)	0	1.9 $\pm$ 9.7
Vegetative detritus (%)	2.4 $\pm$ 11.9	1.6 $\pm$ 6.6
Water depth (cm)	10.9 $\pm$ 4.3	14.5 $\pm$ 11.5
Vegetation height (cm)	3.1 $\pm$ 4.3	4.6 $\pm$ 14.7
Maximum vegetation height (cm)	5.4 $\pm$ 7.5	6.9 $\pm$ 18.2
Distance to vegetation (m)	2.1 $\pm$ 4.7	6.1 $\pm$ 12.1
Distance to continuous vegetation (m)	10.0 $\pm$ 11.7	11.8 $\pm$ 15.0
Distance to aquatic/terrestrial (m)	12.2 $\pm$ 12.6	15.4 $\pm$ 23.8
Chironomid density m^{-2}	3,641.5 $\pm$ 2,746.5	2,215.5 $\pm$ 2,193.9
Oligochaete density m^{-2}	2,877.6 $\pm$ 4,403.8	7,653.1 $\pm$ 1,439.9
Chironomid biomass mg m^{-2}	1,909.9 $\pm$ 1,373.3	1,196.9 $\pm$ 1,215.1
Oligochaete biomass mg m^{-2}	636.6 $\pm$ 661.9	1,652.7 $\pm$ 2,363.4

ibis predominantly probed (92%) the benthos in wetland habitats.

Univariate analyses detected marginal differences in water depth and distance to nearest vegetation between bird and random locations after we applied corrections for multiple comparisons (Table 1). Compared to random locations, White-faced Ibis foraged in shallower water depths (χ^2 = 4.2, P < 0.04) and closer to emergent vegetation >10 cm in height (χ^2 = 3.8, P = 0.05). In the final model, the difference in distance to vegetation significantly discriminated between bird and random locations (χ^2 = 7.7, P < 0.01). A model containing both the distance to vegetation and water depth parameters significantly discriminated between bird and random locations (χ^2 = 9.4, P < 0.01); however the AIC of this model was slightly higher than the final model which contains the single parameter.

Although the average distance to emergent vegetation at bird foraging locations was 2.1 $\pm$ 4.7 m, 68% of ibis foraging locations were within 0.5 m of emergent vegetation where there were equal proportions of short (50%) and medium-tall (50%) vegetation types (Safran 1997). Moreover, in another study we found that White-faced Ibis foraged close to emergent vegetation regardless of vegetation height, and that proximity to emergent vegetation is not confounded by a relationship with vegetation height (Safran 1997). Percent cover did not differ between bird and random locations.

BENTHIC INVERTEBRATES

White-faced Ibis foraged in areas with a greater density and biomass of midge larvae (Order Diptera, Family Chironomidae) than random locations. But, ibis foraged at locations with lower density and biomass of oligochaetes (Oligochaeta) than random locations (Table 1). We retained chironomid biomass and oligochaete biomass in the multivariate MPLR model to explain differences between White-faced Ibis foraging locations and random sites (χ^2 = 10.6, P < 0.005).

VARIATION BETWEEN RANDOM AND BIRD LOCATIONS

Results of the F-max tests indicated that there was significantly greater variation (P < 0.05) present at random sites compared to bird locations for the following variables: water depth, vegetation height, maximum vegetation height, distance to vegetation, distance to continuous vegetation, distance to aquatic/terrestrial interface, and oligochaete biomass.

DISCUSSION

In managed wetlands of the Grasslands, distance to emergent vegetation and benthic invertebrates are principal factors influencing White-faced Ibis habitat selection. Moreover, although not included in the final habitat selection model, we believe that intermediate water depths are an important attribute of ibis foraging locations.

Some wader species avoid foraging close to emergent vegetation possibly to reduce the risk of predation (Metcalfe 1984, Cresswell 1994). In this study, 68% of ibis foraged very close (<1 m) to emergent vegetation; differences between bird foraging locations and random sites were not based on specific vegetation types or heights (Safran 1997). Hence, the possible relationship between proximity to vegetation and predator avoidance is not clear. Although we did not witness predation, we did observe ibis to be extremely sensitive to low levels of disturbance in both open and relatively closed habitats (screened by emergent vegetation). Moreover, ibis have been shown to exhibit increased levels of vigilance in tall vegetation in agricultural fields (Bray and Klebenow 1988).

Several researchers have noted the positive correlation between benthic macroinvertebrates, including oligochaetes and chironomids, and emergent wetland vegetation (Merritt and Cummins 1984, Streever et al. 1995). Given this relationship and the significantly greater chironomid biomasses at bird locations, we speculate that ibis chose foraging sites close to emer-

gent vegetation where prey abundance is likely greater. However, this does not explain why ibis foraged at locations with significantly lower oligochaete biomasses.

Lower oligochaete biomasses at ibis foraging locations could indicate that birds had been foraging consistently in the area and thus, reduced the number of prey items. This follows from results of several avian exclosure studies that have demonstrated prey reduction by foraging waterbirds (Szekely and Bamburger 1992, Mercier and McNeil 1994). However, there is more evidence to conclude that chironomids are a more important food item to White-faced Ibis than smaller oligochaetes (Ryder and Manry 1994). We were unable to visually determine small prey items taken by White-faced Ibis, but several studies list the presence of benthic insect larvae, including chironomids, in the stomach contents (Ryder and Manry 1994), esophagi (Bray and Klebenow 1988), and at feeding sites (Taylor et al. 1989) of White-faced Ibis. No information exists about the dietary importance of oligochaetes to White-faced Ibis, although in pastures, earthworms (Lumbricidae) are a primary component of ibis diets (Ryder 1967, Bray and Klebenow 1988). Nevertheless, the significant differences in benthic invertebrate biomasses and water depths between bird foraging and random sites support the speculation that White-faced Ibis select feeding locations, within accessible water depths, based on invertebrate prey. But, do higher chironomid biomasses alone at feeding sites translate into higher quality habitat? We have not addressed this question in this study, but the significant differences between random sites and bird locations suggest that prey distributions may influence ibis foraging site-selection in the Grasslands.

There appears to be greater variation at random locations compared to ibis foraging sites for most of the habitat and benthic invertebrate variables we measured in this study. Interestingly, the F-max tests results suggest that White-faced Ibis foraged within a narrower range of habitat than what was available in each wetland.

IMPLICATIONS OF THIS STUDY

Water depth is the primary manipulative component of moist-soil management practices (Fredrickson and Taylor 1982), and water depth strongly influences the availability of waterbird habitat. As part of an experimental study in the Grasslands, Williams (1996) demonstrated greater densities of larger-bodied waterbirds (primarily diving and dabbling waterfowl) in deeper water and greater numbers of smaller-bodied shorebirds in shallower water. This relationship was strongest in the winter, when fewer wetlands were undergoing drawdowns (Williams 1996) and therefore, less shallow water habitat was available. Additionally, a fine-scale examination of waterfowl and shorebird foraging habitat selection in the Grasslands indicated similar relationships between morphology and foraging water-depth ranges (Safran et al. 1997). These findings and other studies (White and James 1978, Baker 1979, Pöysä 1983) support the supposition that waterbird habitat selection is largely constrained by avian morphology (e.g., tarsus and culmen length in shorebirds; Baker 1979).

Food availability and the acquisition of lipid and protein reserves are of primary importance to non-breeding waterbirds (Drent and Daan 1980). Several studies illustrate the positive correlation between waterbird distribution and benthic invertebrate densities at a variety of spatial scales (Goss-Custard 1970, Goss-Custard 1977, Colwell and Landrum 1993). Yet, an examination of benthic invertebrates at waterbird foraging sites in the Grasslands indicate that invertebrates influ `nced the site selection of only three of nine waterbird species (Safran et al. 1997). Interestingly, larger-bodied waterbirds, including ibis, Northern Shovelers (*Anas clypeata*), and American Green-winged Teal (*Anas crecca*) that foraged in a variable range of water depths appeared to choose foraging sites based on invertebrates, whereas smaller bodied birds were constrained to forage in water depths in which they had access to forage in the benthos (Safran et al. 1997). Again, this implies that water depth mediates availability of benthic invertebrates and underscores the importance of providing shallower water depths that accommodate both small and large bodied waterbirds.

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