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HABITAT-RELATED FACTORS AFFECTING THE DISTRIBUTION OF NONBREEDING AMERICAN AVOCETS IN COASTAL SOUTH CAROLINA[1]

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Abstract. Changes in local environmental conditions can cause shifts in the distribution of nonbreeding shorebirds at sites that offer a wide choice of habitats. We assessed effects of water level-related variables and salinity on the distribution of nonbreeding American Avocets (*Recurvirostra americana*) among eight brackish water impoundments and two intertidal mudflats in coastal South Carolina from mid-January to mid-May, 1991 and 1992. Avocets exhibited nonrandom distribution on three spatial scales: between impoundments and natural tidal areas (impoundment use was greater), among impoundments, and within impoundments. Among all sites, avocet distribution correlated with water level-related variables ($P < 0.05$), but not salinity. Most avocets used habitats with water 10–17 cm deep and little or no exposed substrate. Furthermore, avocet numbers decreased in impoundments when the sites experienced large fluctuations in water levels ($\pm$6–10 cm). Analyses conducted at the level of one impoundment supported these results, indicating that macro- (among impoundments) and microhabitat (within impoundments) use was influenced by similar factors.

Key words: Nonbreeding; habitat use; American Avocet; Recurvirostra americana; *impoundments; intertidal mudflats; South Carolina.*

INTRODUCTION

Nonbreeding shorebirds frequently face fluctuating environmental conditions such as the availability of suitable habitat. Factors influencing habitat use include prey availability (Evans and Dugan 1984, Colwell and Landrum 1993), weather (Burger 1984), substrate types (Quammen 1982), tide cycles (Burger et al. 1977, Burger 1984), salinity (Velasquez 1992), water levels (Velasquez 1992) and morphology of individual species (Baker 1979).

One method of coping with changing local conditions is to move among a variety of habitats (Burger et al. 1977, Hartwick and Blaylock 1979, Burger 1984, Symonds et al. 1984, Davidson and Evans 1986, Velasquez and Hockey 1992). Nonbreeding shorebirds generally seek habitats where resource availability is adequate, stable, and predictable (Evans and Dugan 1984, Colwell 1993). Thus, wintering grounds that offer alternative habitats for foraging, roosting, and protection from severe environmental conditions enhance shorebird survival (Evans 1976, Connors et al. 1981, Burger 1984). In some cases, human-altered wetlands can provide a suitable alternative to natural areas. The few studies that have compared use of altered wetlands with natural tidal areas by nonbreeding shorebirds concluded that human-created wetlands were used primarily as alternative foraging sites during high tides and/or during periods of severe weather when prey availability at intertidal mudflats was low or nonexistent (Burger 1984, Davidson and Evans 1986, Velasquez and Hockey 1992).

Where both natural and human-constructed habitats are available, manipulation of water levels and salinity may play significant roles in determining which habitats shorebirds can successfully exploit (Velasquez 1992, Velasquez and Hockey 1992). Culmen and tarsus length are positively correlated with water depths in which a species forages, indicating that most shorebirds occur in a specific range of water depths (Burger et al. 1977, Baker 1979, Colwell and Oring 1988). The importance of salinity, however, is less clear. Velasquez (1992) found that birds using artificial

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saltpans responded to changes in prey composition caused by fluctuations in salinity rather than manipulation of water levels. Burger (1984) speculated that the distribution of species that forage on a narrow range of prey items are more likely to be influenced by salinity than those that have a broad prey base.

The South Carolina coast provides a variety of natural and human-created habitats for nonbreeding shorebirds. Current management of coastal impoundments includes a drawdown period whereby a mosaic of habitats is created among and within impoundments that vary in water depth, salinity, and amount of exposed substrate. The response of birds to these manipulations is poorly understood. In this study, we examine the distribution of nonbreeding American Avocets (*Recurvirostra americana*) among brackish water impoundments and intertidal mudflats. We measure differences in avocet distribution over time and among habitat conditions related to water levels and salinity to identify potential limiting factors for the species' newly-expanding range in the southeastern United States.

STUDY AREA AND METHODS

STUDY AREA AND SAMPLING REGIME

The study was conducted from mid-January to mid-May, 1991 and 1992 at the Tom Yawkey Wildlife Center on South Island in Georgetown County, South Carolina. South Island is a barrier island comprised of approximately 8,000 ha of pine and maritime forests, tidal marsh and mudflats, ocean beach, and managed brackish water impoundments (Fig. 1). During both years, a gradual draw down of impoundments began in early November. The slow release of water coupled with variation in bottom topography created a wide range of water depths (0–25 cm deep) in all drawn down impoundments from January through April. By the end of April, however, most of these sites contained expansive mudflats interspersed with sheet water (water less than 5 cm deep). All sites were reflooded (greater than 25 cm deep) during the first week of June.

Ten sites, eight impoundments, and two natural tidal mudflats (Mother Norton Shoals and the ocean front mudflat), were sampled during both years with two exceptions (Fig. 1). Santee Pond was not sampled in 1991 because it did not receive drawdown treatment, and the ocean front mudflat was not sampled in 1992 because avocets were never observed there either year. Sites were visited three times a week on randomly selected days at a randomly selected hour between sunrise and sunset. All sites were sampled in one day in random order. Rainfall precluded driving on the earthen dikes, therefore no data were collected on rainy days. Sand Creek Basin and the ocean front mudflat were the only sites where the entire area of available habitat (open water) could be viewed from one location. Therefore, viewing stations were established along dike perimeters of the remaining sites to ensure complete and systematic observation. The area within view at each station was defined as a section (see inset of Fig. 1). Landmarks such as grass islands, uprooted trees, and old pilings marked section boundaries. Because total acreage and amount of area covered by vegetation varied among sites (Table 1), number and size of sections per site also varied. Number of sections per site ranged from 1–24 and their approximate sizes ranged from 0.1 to 45 ha (the area within sections was not quantified).

Modified scan sampling (Altmann 1974) was used to count the number of avocets in sections and to record individual water depth (IWD) in relation to the legs of each bird observed: no water, water above the foot, water below the tibiotarsus, water above the tibiotarsus, water belly deep, and water greater than belly deep. One scan per section (per sampling day) was conducted from a stationary vehicle at each viewing station using a 15×–60× spotting scope. Duration of scans depended on the number of avocets present in a section, which ranged from 0–349

TABLE 1. Total area, open water, and percentage of open water among impoundments and natural tidal mudflats sampled on South Island, SC, January–May 1991–1992 (see Figure 1 for locations).

Sites	Total area (ha)	Open water (ha)	%
Gibson Pond (G)	35.4	19.8	5
Lady Pond (B)	14.8	9.4	3
Lower Reserve (C)	124.0	99.0	26
Mother Norton Shoals	110.5	110.5	30
Ocean front mudflat	8.8	8.8	2
Sand Creek Basin (D)	57.1	35.7	10
Santee Pond (F)	44.3	15.9	4
Upper Pine Ridge (H)	40.0	13.1	3
Upper Reserve (A)	24.6	16.4	4
Wheeler Basin (E)	82.6	48.1	13

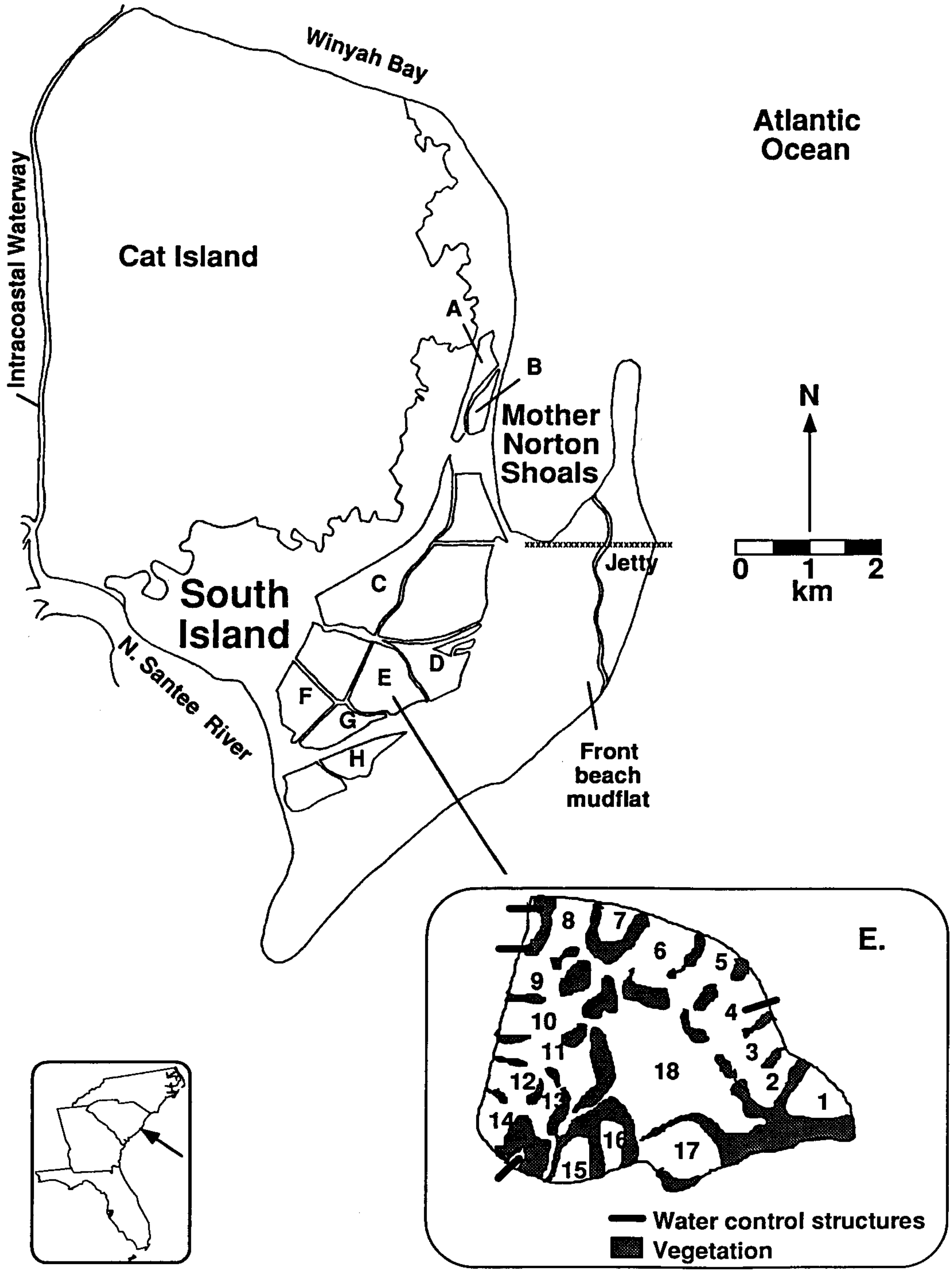

FIGURE 1. Impoundments and natural tidal mudflats sampled on South Island, Georgetown County, SC. (A) Upper Reserve; (B) Lady Pond; (C) Lower Reserve; (D) Sand Creek Basin; (E) Wheeler Basin; (F) Santee Pond; (G) Gibson Pond; (H) Upper Pine Ridge. Numbers in inset (E) represent sections of Wheeler Basin.

individuals. Of the total scans conducted during the study (n = 7,793), 97% (n = 7,559) had fewer than 100 birds present, thus most scans took less than five minutes to complete. If avocets were observed moving among sections while scanning, sampling was terminated to avoid counting individuals twice at a given site. Data collected prior to termination were not used for analyses. Daily site totals were calculated by summing the number of birds observed in each section.

Weather data, tide stage (number of hours preceding high and low tide), impoundment water levels (gross measure of water depth obtained from one sampling point in each impoundment; 1992 only), Julian day, and time were recorded when the investigator arrived at each site. Because avocets appeared to use sections with little or no exposed substrate in 1991, an estimate of the percentage of exposed mudflat in section was recorded after each scan in 1992. A refractometer was used to measure salinity levels weekly at each site during both years. All impoundments were censused once a week to determine size of the study population.

STATISTICAL ANALYSES

Variables were grouped into two categories: temporal and habitat. Temporal variables consisted of month, week, Julian day, and time of day (morning = dawn–09:59, midday = 10:00–13:59, and afternoon = 14:00–dusk; during April and May an hour was added to each time block to account for increased daylight hours). Habitat variables included tide stage, salinity, and the following water depth-related variables: individual water depth; percentage of exposed mudflat (1992 only); and impoundment water levels (1992 only).

Three general linear models (GLM) were used to examine relationships between temporal variables, habitat variables, and number of avocets (T) that occurred at sites and/or sections. Analysis of variance (ANOVA) was used to analyze all GLMs. Because the dependent variable T represented count data, it was square-root transformed for analysis (Sokal and Rohlf 1981). Habitat variables, which served as treatments, were not controlled in an experimental fashion. This resulted in very few observations among rare values of the variables, thus precluding the use of interaction terms in the models. Tide stage was excluded from all models because preliminary analyses, which specifically examined effects of tide, indicated that it had no effect on avocet numbers among sites. Preliminary analyses also revealed significant annual differences in site use by avocets and among habitat variables; therefore separate analyses were performed for each year. Prolonged draw downs during the study period resulted in day-to-day variation in habitat conditions among and within impoundments. Furthermore, in 1992, we established that avocets departed from South Island at dusk and returned just before dawn the following day. Based on the assumption that the birds encountered new microhabitats upon their return each morning, we chose to use sampling days as independent replicates for all models. In the first model, habitat variables were treated as numeric. In two subsequent models, habitat measurements were transformed into class variables by combining ranges of sequential numeric data to form categorical values as described below and in Table 2. This helped to increase the number of observations among habitat values.

Salinity. Water with salt concentrations of 0.5–30 ppt (parts per thousand) is generally considered brackish (Remane and Schlieper 1971). Salinity levels in this study ranged from 3–28 ppt. Thus, the continuum was divided into three classes of brackish water.

Percent exposed mudflat (1992 only). Percentage of exposed mudflat (PEM) in sections was estimated in increments of 10 ranging from 0–100% exposed substrate and grouped into three classes of mudflat. A fourth class, "flood," represented sections that were entirely submerged by water estimated to be greater than 25 cm deep.

Mean individual water depth (MIWD; 1992 only). MIWD is the daily average water depth of areas in sections where avocets were observed; it does not reflect conditions in areas where they did not occur. The purpose of this measure was to determine whether avocets, when presented with a wide range of water depths, occurred in similar depths over time. With IWD data, the following categories were created based on measurements from museum skins: (1) bottom of foot to top of foot (1 cm); (2) tarsometatarsus length (bottom of foot to tibiotarsus; 10 cm); and (3) tibia length (tibiotarsus to belly; 7 cm). MIWD was calculated by dividing the sum of daily numeric IWDs by the corresponding number of

TABLE 2. Categorization of habitat variables.

Variable	Range	Classes
Salinity (ppt)	≤10	Low
	11–20	Medium
	>20	High
% Exposed mudflat	Deep water	Flood
	0–30	≤30%
	40–70	40–70%
	80–100	>70%
Mean ind. water depth (cm)	0	No water
	1–5	Above foot to mid-tarsometatarsus
	5–10	Mid-tarsometatarsus to tibiotarsus
	10–13.5	Tibiotarsus to mid-tibia
	13.5–17	Mid-tibia to belly
	>17	> belly deep
DVIWL (cm)[a]	0	none
	1–5	Small Increase
	6–10	Large Increase
	−1–−5	Small Decrease
	−6–−10	Large Decrease

[a] Daily variation in impoundment water levels.

avocets in each section. This yielded a large continuum of values across sections and days that was divided into six classes.

Daily variation in impoundment water levels (DVIWL; 1992 only). With impoundment water-level data, day-to-day water level fluctuations were calculated by subtracting the previous day's water level from the current level. Daily variation ranged from 0 to 10 cm.

Models. Model I assessed the effects of time (month, week, and time of day) and location (site and section) on both T and habitat variables. The form of the model was Y = *grand mean* + *month* + *week* + *time of day* + *site* + *section* + *random error* where Y was either T or one of the habitat variables. A separate ANOVA was conducted for each dependent variable. Results from this model indicate whether time and location terms would be important components of subsequent models involving T.

Model II examined the effects of habitat variables on avocet numbers across sites and sections. The form of this model was T = *grand mean* + *habitat variable* + *site* + *section* + *day (or week)* + *random error.* Because interaction effects between habitat variables and time and location factors could not be assessed, the terms site, section, and day or week (depending on how often the habitat variable was measured) were entered in the model as main effects. This reduced variation in the model not attributed to the habitat variable. The variable *site* accounted for differences between section means among sites (n = number of sections within a given site multiplied by the number of days the site was sampled). The variable *section* accounted for differences among section means in a given site (n = number of days each section was sampled per site). Finally, day or week was incorporated into the model to account for differences between daily or weekly section means (n = total number of sections sampled per day or week). A separate ANOVA was conducted for each habitat variable.

Model III measured the effects of individual water depth and percentage of exposed mudflat on T within sections of the most extensively used site (Wheeler Basin). The form of this model was T = *grand mean* + *habitat variable* + *section* + *day* + *random error.* As in Model II, the terms section and day were included in Model III to reduce variation that would otherwise be attributed to error. *Section* accounted for differences between section means (n = number of days each section was sampled), and *day* accounted for daily differences between section means (n = number of sections sampled per day). Salinity and DVIWL were excluded from this analysis because they were not section-specific. A separate ANOVA was conducted for each habitat variable.

To determine whether avocets used impoundments more than intertidal mudflats, we used two chi-square tests, each useful in assessing resource selection (Alldredge and Ratti 1992). The first test compared habitat use (total number of birds observed in each habitat type) to availability (total area of open water among impoundments and mudflats sampled), and the second compared the number of days avocets were present in each habitat. In both comparisons, data from impoundments were pooled and treated as a single unit. Model terms and chi-square comparisons were considered significant if their probability levels were ≤ 0.05. All calculations were performed using Statistical Analysis System (SAS Institute 1990).

RESULTS

AVOCET DISTRIBUTION

American Avocet population on South Island averaged 321.5 (SD = 107.4, range = 42–470) birds in 1991 and 393.1 (SD = 101.6, range = 40–495) birds in 1992. Each year, avocets used seven of nine sites, six of which were impoundments (Table 3). In 1991, tidal mudflats (Mother Norton Shoals + ocean front mudflat) comprised approximately 32% of the total area of available habitat sampled (Table 1), yet only 6% (n = 865) of the avocets observed occurred there (Table 3; χ^2 = 4,812; df = 1; $P < 0.05$). In 1992, only 3% (n = 420) of all observed birds were at Mother Norton Shoals (ocean front mudflat was not sampled the second year), despite the fact that the mudflat encompassed approximately 30% of the total area of available habitat sampled (χ^2 = 5,048; df = 1; $P < 0.05$). Furthermore, avocets were observed significantly more often in the impoundments than at the tidal mudflats (1991: χ^2 = 15.49; df = 1; $P < 0.05$, 1992: χ^2 = 9.09; df = 1; $P < 0.05$).

In 1991, avocets did not use the Sand Creek Basin impoundment, even though it was drawn down (Table 3). In 1992, they did not use impoundments that remained flooded (Lady Pond and Upper Pine Ridge). During both years, at least 60% of the total avocets observed occurred at Wheeler Basin. Some sites were used with greater regularity than others. In 1991, avocets used Gibson Pond, Lady Pond, and Wheeler Basin over 75% of the days each site was sampled (Table 3). In 1992, high-use sites included Gibson Pond, Santee Pond, and Wheeler Basin. Despite random sampling, high-use sites were sampled more often during low tide in both years (over 55% of the sampling days), when one would

TABLE 3. Distribution and abundance of nonbreeding American Avocets on South Island, SC, January–May 1991–1992 (n = number of days sites were scan sampled).

Sites	1991 $\bar{x}$ (±SD) birds per day	1991 n	1991 Days present (%)[a]	1991 Annual total	1991 %[b]	1992 $\bar{x}$ (±SD) birds per day	1992 n	1992 Days present (%)	1992 Annual total	1992 %
Gibson Pond (G)[c]	29.4 ± 45.9	43	41 (95)*	1,279	8	9.6 ± 11.0	45	34 (76)*	433	3
Lady Pond (B)	64.5 ± 54.5	23	18 (78)*	1,483	10	0	45	0 (0)	0	0
Lower Reserve (C)	20.0 ± 71.4	43	8 (19)	860	6	12.4 ± 34.5	45	16 (36)	556	4
Mother Norton Shoals	20.1 ± 58.1	43	11 (26)	865	6	9.3 ± 29.4	45	5 (11)	420	3
Ocean front mudflat	0	40	0 (0)	0	0	—	—	—	—	—
Sand Creek Basin (D)	0	42	0 (0)	0	0	73.2 ± 60.8	44	16 (36)	1,047	7
Santee Pond (F)	—	—	—	—	—	23.8 ± 104.8	45	36 (82)*	3,294	23
Upper Pine Rdg. (H)	0.6 ± 1.4	17	4 (24)	11	0	0	45	0 (0)	0	0
Upper Reserve (A)	4.4 ± 18.3	41	8 (20)	180	1	0.02 ± 0.2	44	1 (0.02)	1	0
Wheeler Basin (E)	243.5 ± 122.4	43	43 (100)*	10,472	69	181.1 ± 137.2	46	40 (87)*	8,692	60

[a] Number of days avocets were present at each site (percentages of n are given in parentheses).
[b] Percent of total observations collected from all sites.
[c] Refer to Figure 1 for locations.
* High-use sites (birds present at least 75% of the days sites were scan sampled).

TABLE 4. Effects of time and location on nonbreeding avocet numbers (T) and habitat conditions on South Island, SC, from January to May, 1991–1992.

	1991						1992					
Y	R^2	Month	Week	TD[a]	Site	Sect	R^2	Month	Week	TD	Site	Sect
T	0.52	***	***	***	***	***	0.35	ns	**	***	***	***
% Exposed mudflat	—	—	—	—	—	—	0.48	*	**	***	ns	***
MIWD[b]	0.68	***	***	***	***	***	0.65	***	***	***	***	***
Salinity	0.86	***	***	ns	***	ns	0.94	***	***	ns	***	ns
DVIWL[c]	—	—	—	—	—	—	0.01	ns	ns	ns	ns	ns

[a] Time of day.
[b] Mean individual water depth (numeric values).
[c] Daily variation in impoundment water levels.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.

expect to see a decrease in impoundment use and an increase in intertidal mudflat use.

RESULTS FROM MODELS

Model I. This model, which examined effects of time and location on avocet numbers and habitat variables, indicated that time and location explained a large portion of the variability in the data as evidenced by the model's high R^2 values (Table 4). During both years, avocet numbers (T) varied significantly over time and among sites and sections, indicating nonrandom distribution at both spatial scales. All habitat variables, except daily variation in impoundment water levels (DVIWL) varied significantly over time as well as among sites and sections. Based on these results, time and location were accounted for in subsequent models to avoid their confounding effects.

Model II. This model examined effects of habitat variables on T across all sites and sections (Table 5). During both years, mean individual water depth (MIWD) had a significant effect (1991: $P < 0.0001$, 1992: $P < 0.0001$) on the distribution of birds among sections; at least 75% were observed in sections with water 10–17 cm deep (Fig. 2B). Avocet numbers did not vary significantly among salinity levels either year. In 1992, percent of exposed mudflat (PEM) had a significant effect ($P < 0.0001$) on T. Over 90% of the avocets occurred in sections that had 30% or less exposed mudflat (Fig. 2A). Furthermore, avocet numbers decreased significantly (DVIWL: $P < 0.0002$) in impoundments when sites experienced large fluctuations in water levels (±6 –10 cm; Fig. 3).

Model III. This model examined the effects of IWD and PEM on T across sections of Wheeler Basin. Results obtained from Model III (Table 6) concurred with those derived from Model II

TABLE 5. Effects of daily variation in impoundment water levels (DVIWL), percent exposed mudflat, mean individual water depth (MIWD), and salinity on the distribution of nonbreeding American Avocets on South Island, SC, from January to May, 1991–1992.

			Habitat variable		Site		Section		Day (or week)	
Habitat variable	Y	R^2	df	F	df	F	df	F	df	F
DVIWL	T[a]									
1991		—	—	—	—	—	—	—	—	—
1992		0.35	4	5.67**	8	89.80***	84	13.38***	44	1.71*
% Exposed mudflat[b]	T									
1991		—	—	—	—	—	—	—	—	—
1992		0.36	3	45.54***	8	90.81***	84	13.81***	44	1.47*
MIWD	T									
1991		0.75	5	596.72***	8	16.40***	80	6.90***	42	1.53*
1992		0.62	4	743.95***	8	13.42***	84	7.77***	44	0.88
Salinity	T									
1991		0.29	2	1.38	8	170.43***	80	15.39***	14	9.03***
1992		0.23	2	1.02	8	92.19***	84	13.34***	15	2.98***

[a] Number of avocets in the form of square-root transformed data.
[b] Percent exposed mudflat.
* $P \leq 0.05$, ** $P \leq 0.001$, *** $P \leq 0.0001$.

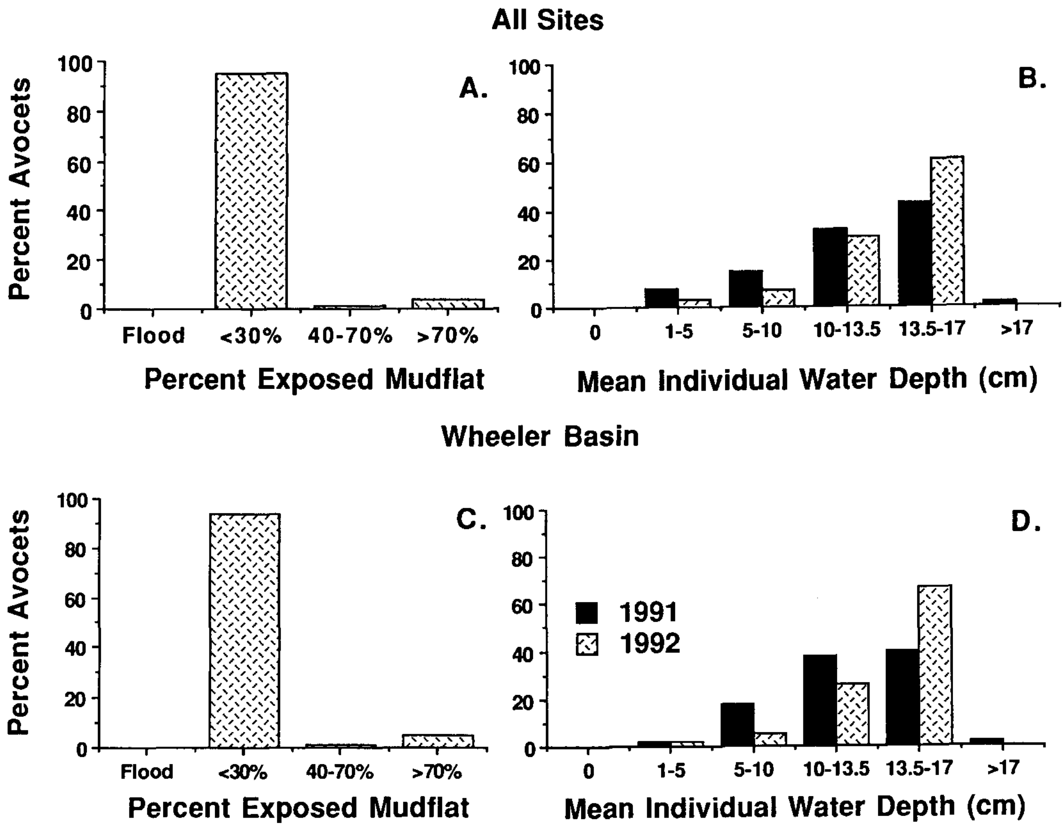

FIGURE 2. Percentage of avocets among classes of percent exposed mudflat and mean individual water depth across all sites (A) and (B) and at Wheeler Basin (C) and (D) on South Island, SC.

(Table 5). In both years, MIWD had a significant effect on avocet numbers among sections of Wheeler Basin (1991: $P < 0.0001$, 1992: $P < 0.0001$). Over 75% of the birds at the site occurred in sections with water 10–17 cm deep (Fig. 2D). In 1992, PEM also had a significant effect ($P < 0.05$) on the distribution of avocets in Wheeler Basin. Over 90% occurred in sections with less than 30% exposed mudflat (Fig. 2C).

DISCUSSION

Results from this study demonstrate that nonbreeding avocets exhibited nonrandom distribution on South Island during 1991 and 1992.

TABLE 6. Effects of mean individual water depth (MIWD) and percent exposed mudflat on the distribution of nonbreeding American Avocets in Wheeler Basin on South Island, SC, from January to May, 1991–1992.

			Habitat variable		Section		Day (or week)	
Habitat variable	*Y*	R^2	df	*F*	df	*F*	df	*F*
MIWD	T^a							
1991		0.76	5	124.68**	18	13.24**	42	1.46*
1992		0.40	4	82.53**	18	9.43**	44	0.79
% Exposed mudflat	*T*							
1991		—	—	—	—	—	—	—
1992		0.40	2	3.10*	18	20.86**	44	2.24**

[a] Number of avocets in the form of square-root transformed data.
* $P \le 0.05$, ** $P \le 0.0001$.

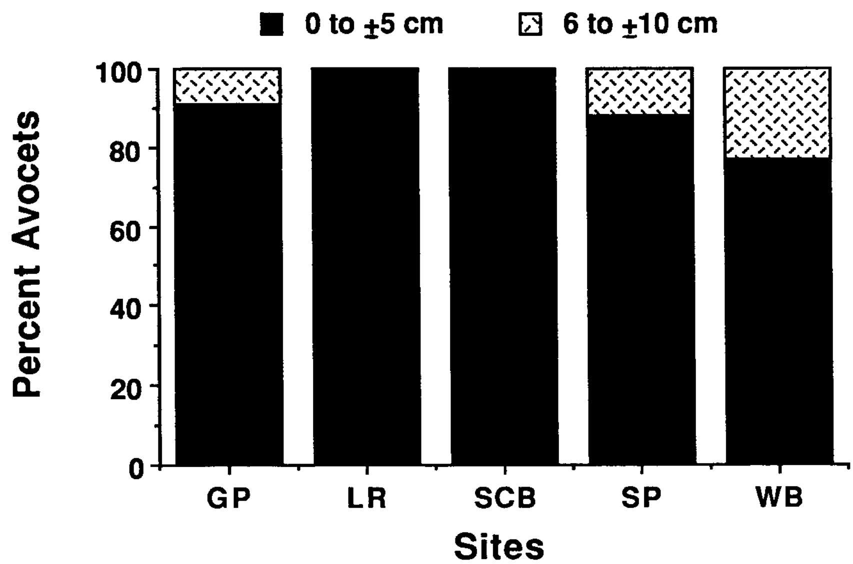

FIGURE 3. Percentage of avocets observed among sites as a function of water level fluctuations. Small increases (dark shading) = daily changes in water levels ranging from ± 0 to 5 cm. Large increases (hatched shading) = daily changes in water levels ranging from ± 6 to 10 cm. (GP) Gibson Pond; (LR) Lower Reserve; (SCB) Sand Creek Basin; (SP) Santee Pond; (WB) Wheeler Basin.

This was apparent on three different spatial scales: impoundments versus natural tidal areas; among impoundments; and within impoundments (among sections).

IMPOUNDMENTS VERSUS NATURAL TIDAL AREAS

Our study revealed that impoundment use was far greater than intertidal mudflat use. The rare presence of avocets at Mother Norton Shoals was in direct contrast with other shorebirds that occurred on South Island. Dunlin (*Calidris alpina*), Long and Short-billed Dowitchers (*Limnodromus scolopaceus* and *L. griseus*), Willets (*Catoptrophorus semipalmatus*), Greater and Lesser Yellowlegs (*Tringa melanoleuca* and *T. flavipes*), and various sandpipers (*Calidris* spp.) were regularly at the mudflat during low tide. Evans and Harris (1994) speculated that construction of oxidation ponds and creation of islands in a nearby lake contributed to the establishment of distribution patterns exhibited by nonbreeding avocets at North Humboldt Bay, California. Furthermore, they reported that avocets, who normally foraged at intertidal mudflats during low tide, occasionally fed exclusively at the oxidation ponds. They speculated that the birds were taking advantage of large, but variable concentrations of *Daphne magna*. Impoundments may have had a similar effect on South Island avocets.

Avocets feed on myriad of prey items including those that occur in the sediment and in the water column (Wetmore 1925, Gibson 1971, Hamilton 1975, Quammen 1984). In the impoundments, avocets were observed foraging for infaunal and nektonic organisms (avocets frequently captured and swallowed large polychaetes (*Laeonereis culveri*) and small fishes). At Mother Norton Shoals, the birds fed exclusively in the water column, suggesting that nektonic organisms were the primary prey items at the mudflat (Boettcher et al. 1994). Sediment samples collected from high-use impoundments (Table 3), at water depths where avocets typically foraged (5–17 cm deep; Boettcher et al. 1994) contained a multitude of invertebrates, many of which were *Laeonereis culveri* (unpubl. data). In contrast, sediment samples collected from Mother Norton Shoals at similar water depths contained few invertebrates and no *Laeonereis culveri* (unpubl. data), despite the fact that the mudflat's substrate was similar to substrate found in high-use impoundments. Water column samples revealed that nektonic species collected in the impoundments did not differ greatly from those collected at Mother Norton Shoals (unpubl. data). However, tide, water temperature, currents, and fluctuations in salinity (Moyle and Cech 1982) may have influenced the presence of water dwelling organisms at the mudflat and thereby created a highly variable foraging environment (Boettcher et al. 1994). Conversely, nektonic organisms that entered impoundments from adjacent bays (including Mother Norton Shoals), creeks, and rivers via water control structures, were trapped and could not escape. Because they were confined to a relatively small area, opportunities for locating and capturing these organisms may have been greater in the impoundments than at Mother Norton Shoals.

Withers and Chapman (1993) found that habitat breadths (an index for measuring habitat specialization) calculated for nonbreeding avocets that occurred on tidal mudflats in Texas were generally smaller than those for Dunlin, small sandpipers, and dowitchers. The same appeared to be true for avocets on South Island. Variation in bottom topography, wind effects (high winds redistributed shallow water in impoundments, which resulted in decreased water depths in some sections and increased water depths in other sections; Boettcher et al. 1994) and the slow release of water, created a wide range of microhabitats in the impoundments. Despite this, avocets invariably used areas that were covered by shallow water (5–17 cm deep) with little or no exposed substrate (Fig. 2). The birds' use of these areas may have reduced competition for resources with short-legged shorebirds who prefer shallower water and/or exposed substrate (Recher 1966, Baker 1979). Because impoundments were not influenced by daily tidal cycles, they provided sufficient foraging and roosting space for avocets throughout the day and minimized the amount of habitat overlap with other shorebirds (Withers and Chapman 1993).

AVOCET DISTRIBUTION IN IMPOUNDMENTS

Impoundments used by avocets consisted of a mosaic of dense emergent vegetation and open water. Avocets occurred exclusively in open water areas. Amount of open water (Table 1) varied among high-sites indicating that quantity of available habitat did not have a direct influence on whether a site was used. However, it may have had a limiting effect on the number of avocets observed at high-use sites (Recher 1966). Of the total birds observed on South Island, less than 25% occurred at Gibson Pond, Lady Pond, and Santee Pond, whereas over 59% occurred at Wheeler Basin (Table 3). Wheeler Basin, which encompassed more than twice as much open water habitat as the other high-use sites, may have been able to support larger numbers of birds because there was more area to exploit. Among impoundments that received less use, area of open water did not have much of an effect on bird abundances. Lower Reserve, which contained the greatest amount of open water habitat among all impoundments (Table 1), comprised less than 10% of the annual totals during both years (Table 3). Furthermore, birds were present less that 40% of the days the site was sampled. This suggests that the amount of open water does not explain all the differences observed in the distribution and abundance of avocets among impoundments.

Avocets forage for benthic invertebrates in soft sediments rather than on sandy or hard substrate (Tjallingii 1972; Quammen 1982; Raey 1988, 1992), suggesting the bird's slender, recurved bill may be limited to probing in sediments that are easily penetrated. Probing was the most common foraging method used by avocets on South Island (Boettcher et al. 1994). Because much of the high-use sites' substrate was comprised of soft, silty sediment that sustained abundant populations of polychaete worms throughout the study period (Weber 1994), we speculate that sediment type may have contributed to the consistent use of these sites. Because avocets fed in the water column and in the sediment, they were not necessarily confined to soft sediment habitats (Quammen 1982). Impoundments with firm substrate were used infrequently by avocets (Lower Reserve, Sand Creek Basin, and Upper Pine; Table 3). At these sites, the birds fed mostly in the water column and almost exclusively in large flocks (>50 birds), indicating that nektonic organisms were the primary prey (Boettcher et al. 1994). Despite the fact that water dwelling prey were trapped in the impoundments, they were still able to avoid predators by remaining in water depths that were out of the predator's reach or by hiding in dense vegetation. Therefore, prey availability in hard-sediment impoundments may have been less predictable than in soft-sediment impoundments where an abundance of relatively sedentary infaunal prey resided.

Results indicate that avocet numbers decreased considerably when impoundments experienced large fluctuations (6–10 cm) in water levels (Fig. 3). Abrupt shifts in avocet distribution among impoundments may have been driven in part by extreme fluctuations (>10 cm) in water levels. From mid-January through mid-February 1992, the drawdown of Wheeler Basin

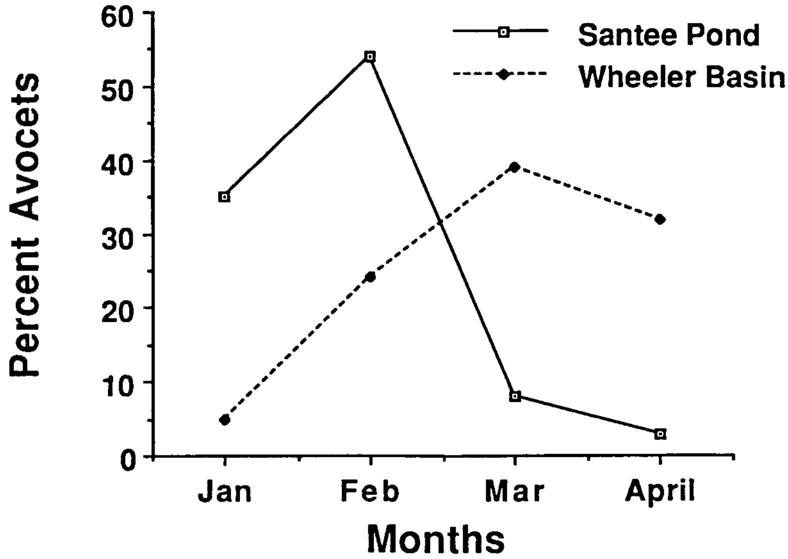

FIGURE 4. Monthly percentage of avocets observed at Santee Pond and Wheeler Basin in 1992.

was interrupted on several occasions. Water levels went from shallow conditions down to sheet water (<5 cm deep). As water re-entered the site via the water control structure, heavy rains fell causing water levels to rise to near flood stage (>25 cm). It was during this period that Santee Pond was used extensively by avocets (Fig. 4). When normal water levels were restored, avocet numbers increased dramatically in Wheeler Basin and dropped substantially in Santee Pond. The lack of significant differences in DVIWL over time and among sites generated by Model I (Table 4) suggests that the remaining impoundments were drawn down slowly and at relatively similar rates during the course of the season. This may explain why avocets did not exhibit such sudden shifts in site use among other impoundments.

DISTRIBUTION OF AVOCETS IN WHEELER BASIN

Avocets consistently used sections in Wheeler Basin that were covered by shallow water (5–17 cm deep) with little or no exposed substrate (Fig. 2). Temporal variability in numbers among sections may have been related to slow decreases in water levels over time and to the slope of the impoundment. Figure 5 illustrates monthly variation within four randomly chosen sections of Wheeler Basin. Elevated sections (2 and 6) received heavy use from January–March and declined in use during April. In contrast, low lying sections (12 and 14) with few birds initially had increased avocet use during March and April. Elevated sections experienced decreases in water depths and increases in exposed mudflat at a faster rate than low lying sections. Consequently, as shallow water receded from elevated areas, more avocets began to use low lying sections.

Other factors such as hardness of substrate and prey abundance (Quammen 1982, Evans and Dugan 1984, Goss-Custard 1984, Colwell and Landrum 1993) may have also been important predictors of habitat selection at finer spatial scales. Sections 1, 7, 15, 16, and 17 of Wheeler Basin received little or no avocet use during both years (Fig. 6). All five had firm substrate with few polychaete worms (Boettcher, unpubl. data). Because probing was the primary foraging behavior performed in Wheeler Basin, sections with firm sediment may have offered avocets fewer foraging opportunities than those with soft sediment.

CONCLUSIONS

Findings from our study indicate that impoundments do provide important habitat for nonbreeding avocets in South Carolina. These human-altered wetlands may help mitigate, but not

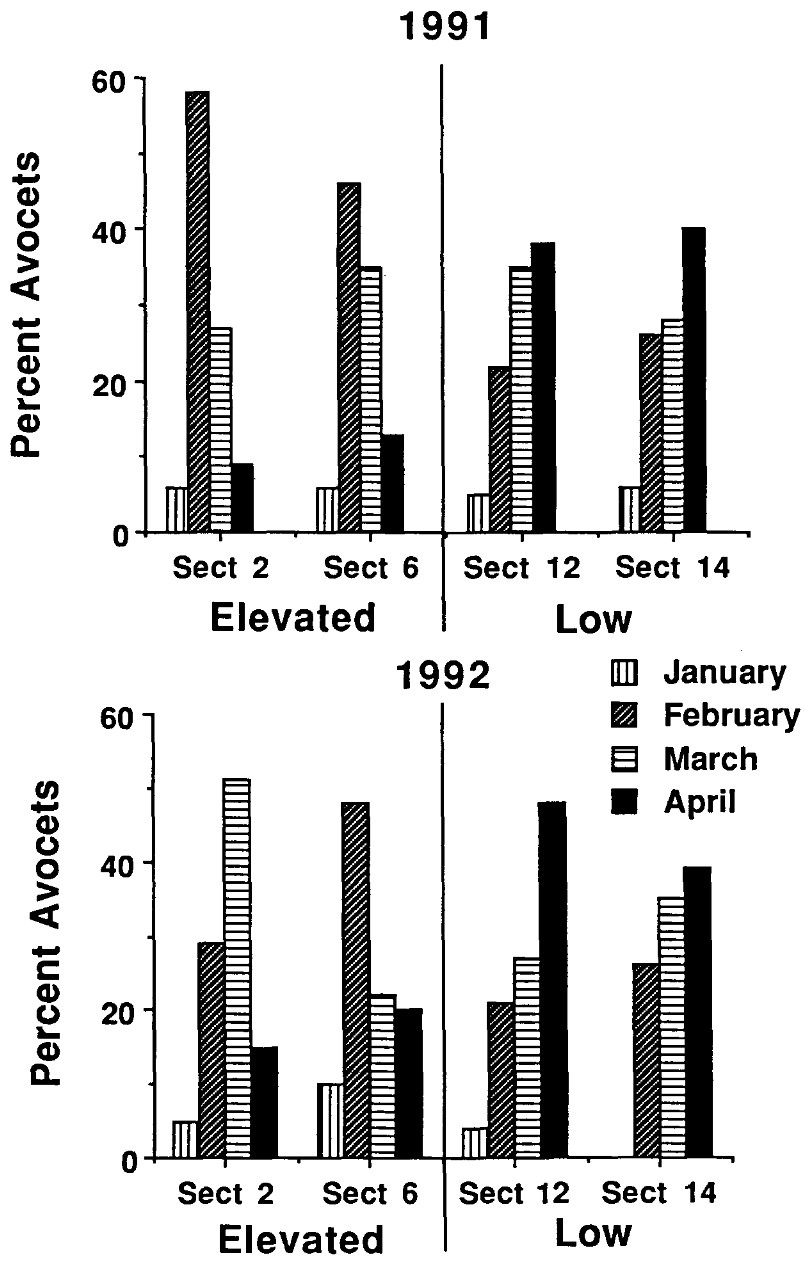

FIGURE 5. Monthly variation in percentage of avocets observed among four sections of Wheeler Basin. A comparison of avocet numbers is made between sections located in low-lying areas (denoted as low) and elevated areas (denoted as elevated).

eliminate the negative impact of wetland loss (Davidson and Evans 1986, Velasquez 1992, Velasquez and Hockey 1992). Evans and Harris (1994) suggested that the establishment and increase of wintering avocet populations in North Humboldt Bay, California may be attributed, in part, to the construction of oxidation ponds in the area. The creation of altered wetlands in South

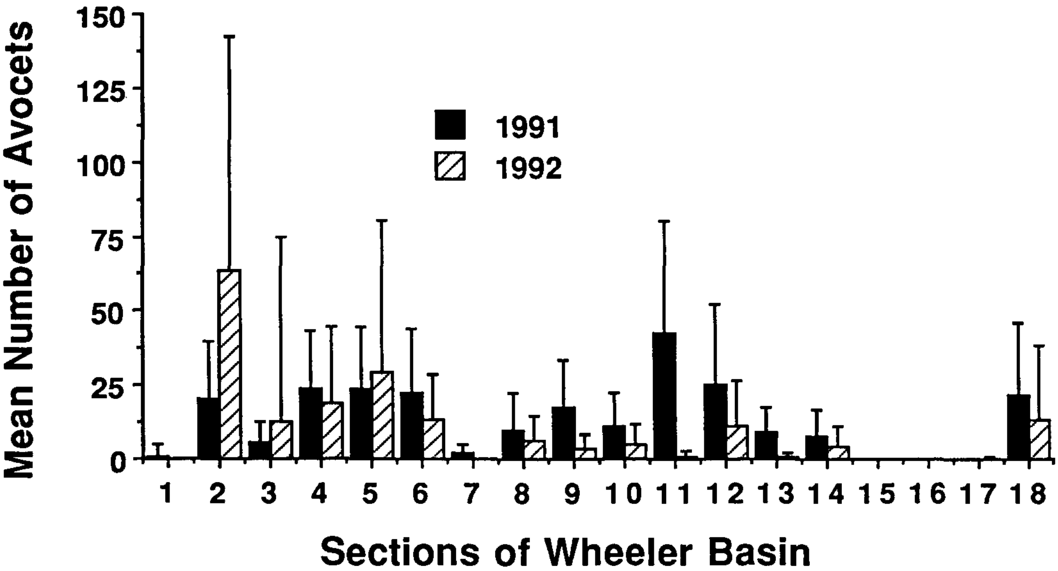

FIGURE 6. Mean (±SD) number of avocets that occurred among sections of Wheeler Basin (1991–1992).

Carolina may have also contributed to the growth of this state's nonbreeding avocet population. Sightings prior to the mid 1940s were rare and usually consisted of only 1–2 individuals (Sprunt and Chamberlain 1949). In 1946, however, 50 avocets were observed in newly constructed impoundments on South Island (Sprunt and Chamberlain 1949). Since then, observations have increased during the nonbreeding season, particularly on South Island where as many as 1,000 individuals were observed in a single sighting (Sprunt and Chamberlain 1970). Large numbers of avocets (>300) have also been observed at two spoil sites: one located near the mouth of the Cooper River in Charleston, South Carolina and the other near the mouth of the Savannah River, which borders Georgia and South Carolina (Anonymous 1981; T. Murphy, pers. comm.). Very few avocets in the state have been sighted in natural habitats (Marsh and Wilkinson 1991; T. Murphy, pers. comm.). Increasing numbers may be attributed to better management of altered wetlands. Further work is necessary to determine how these areas are contributing to expansion of American Avocet wintering range along the southeastern seaboard.

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