

# BEHAVIORAL PATTERNS AND NEAREST NEIGHBOR DISTANCES AMONG NONBREEDING AMERICAN AVOCETS<sup>1</sup>

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**Abstract.** We examined temporal changes in diurnal behavior among nonbreeding American Avocets (*Recurvirostra americana*) in South Carolina during 1991 and 1992. We also assessed effects of ambient temperature on foraging, and studied relationships between maintenance activities (e.g., foraging and loafing), nearest neighbor distances (NND), and microhabitat selection (individual water depth). Only foraging and resting, the two most common activities observed, exhibited temporal variation. Foraging varied significantly among all temporal variables [year:  $P < 0.02$ ; month:  $P < 0.03$ ; time of day (morning, midday, and afternoon):  $P < 0.008$ ; and interaction between month and time of day:  $P < 0.004$ ], whereas loafing differed significantly between years only ( $P < 0.02$ ). Although rising temperatures were negatively correlated with numbers of foraging avocets during both years, the relationship was significant in 1992 only ( $P < 0.004$ ). Loafing and multiple scything (a tactile foraging method) were carried out in tight, dense flocks (NND < 1 meter) whereas probing (a visual foraging method) was observed primarily in loose aggregations (NND 1–10 meters). This suggests a strong interaction between maintenance activities and NND. Overall, our study demonstrates that avocets occur in flocks throughout the nonbreeding season, suggesting that flock maintenance is selectively advantageous on the species' wintering grounds.

**Key words:** American Avocets; *Recurvirostra americana*; nonbreeding; individual water depth; nearest neighbor distance; maintenance activities.

## INTRODUCTION

Avian behavior changes throughout the annual cycle in response to environmental, social, and physiological events. Although some behaviors require more time and energy than others, the optimizing paradigm predicts that individuals perform activities at the most opportune time (Smith 1976). To understand the ecological significance of behavioral patterns, we must examine the influence of temporal and environmental factors on a species' time budget.

Behavior of nonbreeding shorebirds can change hourly, seasonally, and annually (Puttick 1979, Zwarts et al. 1990, Burger 1984, Puttick 1984, Maron and Myers 1985, Morrier and McNeil 1991, Handel and Gill 1992), but day-to-day

variation is minimal (Puttick 1984). Temporal variation has been largely attributed to seasonal differences in energy requirements (Kersten and Piersma 1987, Zwarts et al. 1990), fluctuations in prey densities and/or availability (Evans and Dugan 1984, Goss-Custard 1984, Maron and Myers 1985, Colwell and Landrum 1993), day-length (Evans 1976, Pienkowski 1982, Puttick 1984, Handel and Gill 1992), tidal influences (Connors et al. 1981, Burger 1984, Goss-Custard 1984, Puttick 1984), and ambient temperatures (Evans 1976, Burger 1984, Goss-Custard 1984). Microhabitat selection may also influence activity. Velasquez (1992) found that Pied Avocets (*Recurvirostra avocetta*) utilizing salt pans switched foraging methods when water levels were lowered. Velasquez and Navarro (1993) reported that in Whimbrels (*Numenius phaeopus*), foraging techniques in shallow water differed from those used on wet sand.

Few studies have examined the relationship between maintenance activities (e.g., foraging, loafing, preening) and spacing patterns; those that

<sup>1</sup> Received 4 March 1994. Accepted 18 July 1994.

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have focused mainly on foraging (see review Myers 1984). The first step toward understanding the relationship between nearest neighbor distances and maintenance activities is to determine whether spacing varies depending on the activity. Because individual birds continually adjust their position and activity with respect to others in the immediate vicinity, spacing sets the framework for all behavioral interactions (Myers 1983, 1984). Nearest neighbor distances are highly variable among and within species during the nonbreeding season, making it difficult to discern the role of spacing patterns (Myers 1983, 1984). This is especially true in nonbreeding areas where large numbers of shorebirds contend with limited foraging and roosting space (Recher 1966).

In this paper, we examine the following diurnal behavior patterns of nonbreeding American Avocets (*Recurvirostra americana*): maintenance activities, nearest neighbor distances among conspecifics, and microhabitat selection (individual water depth). First, we assess the effects of temporal variables on maintenance activities, nearest neighbor distances, and microhabitat selection. Second, we evaluate the effect of ambient temperature on foraging avocets. Third, we examine relationships between maintenance activities, nearest neighbor distances, and microhabitat selection. Finally, we determine whether maintenance activities vary according to nearest neighbor distance and individual water depth.

## STUDY AREA AND METHODS

The study was conducted from mid-January to mid-May 1991 and 1992 on South Island, which is part of the Tom Yawkey Wildlife Center (South and Cat Island complex) in Georgetown County, South Carolina (Fig. 1). South Island is a coastal barrier island of approximately 8,000 ha of pine and maritime forests, tidal marsh and mudflats, ocean beach, and managed brackish water impoundments. Every year, from November through late May, water is slowly released from the impoundments, which creates a mosaic of microhabitats that vary daily in water depth (0–25 cm).

## BEHAVIORAL SAMPLING

We sampled eight impoundments and two intertidal mudflats (Mother Norton Shoals and Ocean Front Mudflat; Fig. 1). Each site was 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. Because most sites were too large to view from one location, viewing stations were established along dike perimeters to ensure complete and systematic observation. The area within view at each station was defined as a section, and landmarks such as grass islands and uprooted trees served as section boundaries. In 1991, a total of 86 sections were visited each sampling day. In 1992, the number of sections increased to 91 because a new site (Santee Pond; Fig. 1) was added to the sampling scheme. For detailed descriptions of sites and sampling methodology see Boettcher (1994). Time of day was recorded when the investigator arrived at each site (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 period to account for increased daylight hours). Ambient temperature (°C) was also recorded. Scan sampling (Altmann 1974) was used to collect the following behavioral information on each individual observed: maintenance activity, water depth in relation to the avocet's legs or belly (water depth categories: no water, water below tibiotarsus, water above tibiotarsus, water belly deep, and water greater than belly deep; hereafter referred to as individual water depth or IWD); and nearest neighbor distance (NND: less than 1 m, 1–10 m, and greater than 10 m; because NND was an instantaneous visual estimate of distances between stationary or moving birds, we used broad categories to ensure accuracy). 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 individuals. Fewer than 100 individuals were scanned in 97% ( $n = 7,559$ ) of the scan samples conducted, 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 (this occurred on six different occasions during the study).

Avocets' maintenance activities (hereafter referred to as activity) were divided into the following categories: (1) *probing*—capturing of sighted prey from the water column, substrate surface, or sediment with a quick jab of the bill

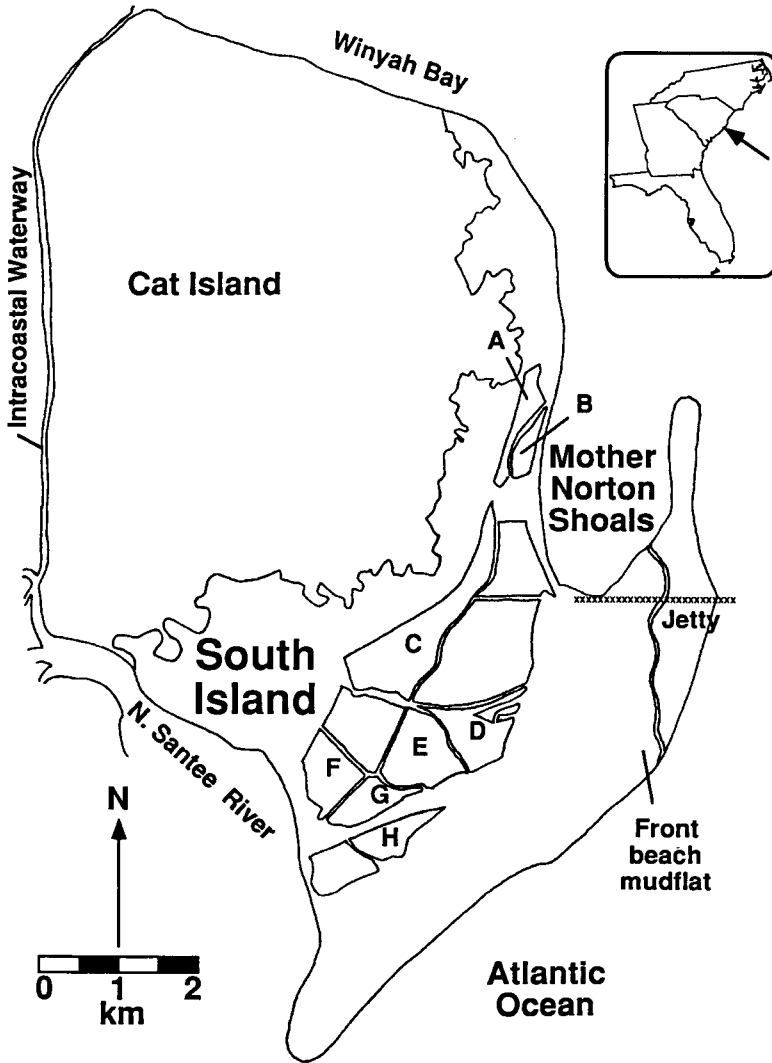


FIGURE 1. Impoundments and tidal mudflats on South Island, Georgetown County, South Carolina. (A) Upper Reserve; (B) Lady Pond; (C) Lower Reserve; (D) Sand Creek Basin; (E) Wheeler Basin; (F) Santee Pond; (G) Gibson Pond; (H) Upper Pine Ridge.

while standing still or walking slowly; (2) *multiple scything*—tactile feeding method that involved sweeping the slightly opened (less than one cm) distal portion of the bill through the water column or on the substrate's surface without pause while walking rapidly forward (Hamilton 1975); (3) *single scything*—tactile feeding method similar to multiple scything except that a pause and swallow followed each back and forth sweep of

the bill as the bird progressed forward one step at a time (Hamilton 1975); (4) *loafing*—resting position; bill tucked under wing or standing motionless with head and neck drawn close to the body; (5) *comfort movements*—preening (manipulation of feathers with the bill), bathing, stretching, and scratching; and (6) *miscellaneous*—wading or swimming (locomotion without feeding) and intraspecific aggression (interspecific aggres-

sion was never observed); together, these comprise 1% of the total observations collected during the study.

## STATISTICAL ANALYSES

All impoundments were censused weekly during high tide. These data were used to estimate the size of the study population and to serve as an index to weekly fluctuations in avocet numbers. Regression analysis was used to assess effects of mean daily temperature on daily percentage of foraging avocets during both years. Foraging percentages were arcsine transformed for analysis. General linear models for unbalanced ANOVAs were used to measure temporal effects on activity, NND, and IWD. Similar models were developed to examine relationships between activity, NND, and IWD. Count data used in the models were square-root transformed for analysis (Sokal and Rohlf 1981). Sampling days served as independent replicates in all analyses. The dependent variable, total avocets (T), represents the number of avocets observed within categories of activity, NND, or IWD. The following is a description of each model:

*Temporal model:*  $T = \text{grand mean} + \text{year} + \text{month}(\text{year}) + \text{time of day}(\text{year}) + \text{month} \times \text{time of day}(\text{year}) + \text{random error}$ . This model examined the effect of year on T and assessed within year differences of T among months, time-of-day categories, and time-of-day categories within months. Within-year model terms were nested in year to account for significant annual differences among activity and NND categories. An ANOVA was conducted on individual categories of activity, NND, and IWD, whereby T represented total number of avocets in each class. Probing, multiple scything, and single scything were combined to form a single feeding category to measure effects of time on foraging regardless of method (when analyzed separately, temporal effects were not significant among individual foraging methods). Results from this model identify which temporal variables, if any, had significant effects on avocet behavior.

*NND model:*  $T = \text{grand mean} + \text{activity} + \text{NND} + \text{day} + \text{NND} \times \text{activity} + \text{random error}$ . This model examined main and interaction effects of activity and NND on T. The variable day was included in the model to account for day-to-day variation in number of birds scanned, which in turn, reduced the degrees of freedom

for error. Subsequent pairwise comparisons were made with least square means derived from the model's interaction terms to identify which activities differed significantly within categories of NND. To ensure protection of experimentwise multiple comparison error rates, we used the Bonferroni technique to establish an adjusted level of significance for each pairwise comparison. This involved dividing the overall probability level of 0.05 by the total number of comparisons. Preliminary tests revealed significant interaction effects between year, activity, and NND, therefore separate analyses were performed for each year.

*IWD model:*  $T = \text{grand mean} + \text{activity} + \text{IWD} + \text{day} + \text{activity} \times \text{IWD} + \text{random error}$ . This model assessed main and interaction effects of activity and IWD on T. The variable day was included in the model for the same reason stated above. To identify which activities differed significantly within categories of IWD, we compared the interaction terms' least square means in the same manner described for the NND model. Because of significant interaction effects between year, activity and IWD, data from both years were analyzed separately. Independent variables in all analyses, except for pairwise comparisons were considered significant if their probability levels were  $\leq 0.05$ . All statistical procedures were performed with the Statistical Analysis System (SAS Institute 1990).

## RESULTS

### BEHAVIOR SUMMARY

South Island American Avocet population averaged 321.5 (SD = 107.4, range = 42–470) birds in 1991 and 393.1 (SD = 101.6, range = 40–495) birds in 1992. A total of 7,793 scans (88 sampling days) were conducted during the study, which resulted in the collection of 29,571 behavioral observations. Because birds were not marked, it was impossible to ascertain the mean number of observations per avocet. Intra-seasonal distribution among sites was nonrandom and predictable (certain sites consistently received greater use than others; Boettcher 1994), therefore we assumed that within-day, movements among sites were minimal. Comparisons made between total number of birds scanned per sampling day and weekly census totals revealed that 76% ( $n = 67$  sampling days) of the daily totals were less than the corresponding weekly census total during both

TABLE 1. Results from temporal models (analysis of square-root transformed data) that measured annual and intraseasonal variation in behavior patterns of nonbreeding American Avocets on South Island, SC (January–May, 1991–1992).

Behavior	Category	Year		Month		TOD <sup>a</sup>		Month × TOD	
		df	F	df	F	df	F	df	F
Activity	Comfort movements	1	2.1	7	1.6	4	2.3	12	0.9
	Foraging	1	5.6*	7	2.3*	4	3.6*	14	2.4*
	Loafing	1	5.8*	7	1.8	4	0.9	14	1.4
	Miscellaneous	1	0.9	7	1.1	4	0.3	6	0.9
NND <sup>b</sup>	<1 meter	1	2.3	7	2.3*	4	2.7*	13	2.4*
	1–10 meters	1	5.0*	7	1.5	4	2.4	14	1.5
	>10 meters	1	11.4*	7	4.5*	4	0.9	13	1.5
IWD <sup>c</sup>	No water	1	2.4	5	0.0	3	0.7	4	0.9
	Below tibiotarsus	1	0.8	7	1.7	4	1.7	12	1.8
	Above tibiotarsus	1	0.0	7	1.5	4	1.8	13	1.1
	Belly deep	1	0.0	7	2.1	4	2.3	12	1.8
	>belly deep	— <sup>d</sup>	—	2	0.6	2	0.3	2	0.4

<sup>a</sup> Time of day.

<sup>b</sup> Nearest neighbor distance.

<sup>c</sup> Individual water depth.

<sup>d</sup> Between-year comparison was not possible because avocets were observed in water >belly deep during 1991 only.

\*  $P \leq 0.05$ .

years. This, along with the fact that scans were conducted at different location (sites and sections) throughout the day, indicates that the frequency of multiple observations collected on the same individual was probably not extensive.

Of the total number of behavioral observations ( $n = 29,571$ ), foraging comprised 58% ( $n = 17,070$ ), loafing 35% ( $n = 10,468$ ), comfort movements 6% ( $n = 1,702$ ), and miscellaneous activities 1% ( $n = 331$ ). Probing, the most commonly observed feeding method, constituted 75% ( $n = 12,703$ ) of the total foraging observations, whereas multiple scything comprised 24% ( $n = 4,168$ ) and single scything 1% ( $n = 102$ ). Probing was used mainly to extract invertebrates from the substrate (on numerous occasions, probing avocets were observed capturing and swallowing large polychaete worms from soft sediment areas of the impoundments), whereas multiple and single scything were used primarily to capture organisms in the water column (e.g., small fish).

Among NND categories, 55% ( $n = 16,415$ ) of all observations were of birds less than 1 m apart, 43% ( $n = 12,603$ ) were of birds 1–10 m apart, and 2% ( $n = 553$ ) were of birds more than 10 m apart. Distribution of observations among categories of IWD were as follows: less than 1% ( $n = 87$ ) in no water (on wet mud), 17% ( $n = 4,957$ ) in water below the tibiotarsus, 49% ( $n = 14,560$ ) in water above the tibiotarsus, 33% ( $n = 9,898$ ) in water belly deep, and less than 1% ( $n = 69$ ) in water greater than belly deep.

## MODEL RESULTS

*Temporal model: activity.* Loafing and foraging were the only activities that varied significantly with time. Avocets were observed loafing significantly more often in 1992 than in 1991 ( $P < 0.02$ ; Table 1, Figs. 2A, 3A). Foraging numbers varied significantly between years (more birds were observed foraging in 1991;  $P < 0.02$ , Figs. 2B, 3B), among months ( $P < 0.03$ ), among time-of-day categories ( $P < 0.008$ ), and among time-of-day categories within months ( $P < 0.004$ ), suggesting that feeding varied among all measures of time. Because fewer number of days were sampled in January (1991:  $n = 3$ , 1992:  $n = 6$ ) and May (1991:  $n = 2$ , 1992:  $n = 0$ ) relative to other months ( $n = 12$ ), loafing and foraging numbers (and percentages; Fig. 2A, 2B) were low during these months.

*Temporal model: NND.* Temporal variation was found among all NND categories, indicating that spacing patterns fluctuated with time. Number of avocets less than 1 m apart differed significantly among months ( $P < 0.03$ ), among time-of-day categories ( $P < 0.03$ ), and among time-of-day categories within months ( $P < 0.005$ , Table 1). Birds that were 1–10 m apart differed significantly between years only ( $P < 0.03$ ). Despite low number of observations, there were significant differences in number of birds more than 10 m apart between years ( $P < 0.001$ ) and among months ( $P < 0.0002$ ).

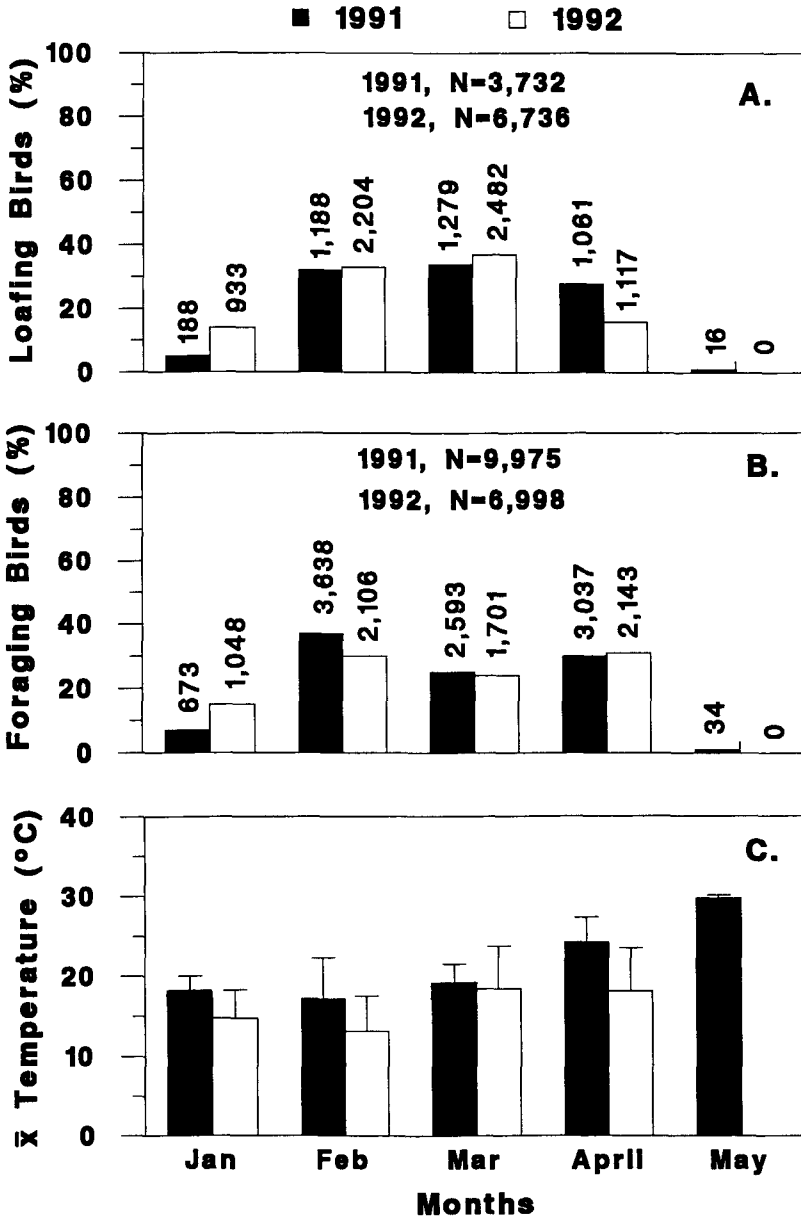


FIGURE 2. Monthly percentage of loafing (A) and (B) foraging avocets observed in 1991, 1992. N = annual number of loafing and foraging observations from which monthly proportions were calculated. Sample sizes above the bars represent actual loafing and foraging numbers. Bottom graph (C) illustrates annual comparisons of monthly average temperatures ( $\bar{x} \pm SD$ ).

*Temporal model: IWD.* Number of avocets within categories of IWD did not differ significantly with time, suggesting that they consistently selected similar water depths during the course of the study (Table 1).

*Ambient temperature effect.* Although rising

temperatures were negatively correlated with daily percentages of foraging birds during both years, ambient temperature effect was significant in 1992 only ( $R^2 = 0.17, P < 0.004$ ; Fig. 4). Temperature did not vary significantly between years.

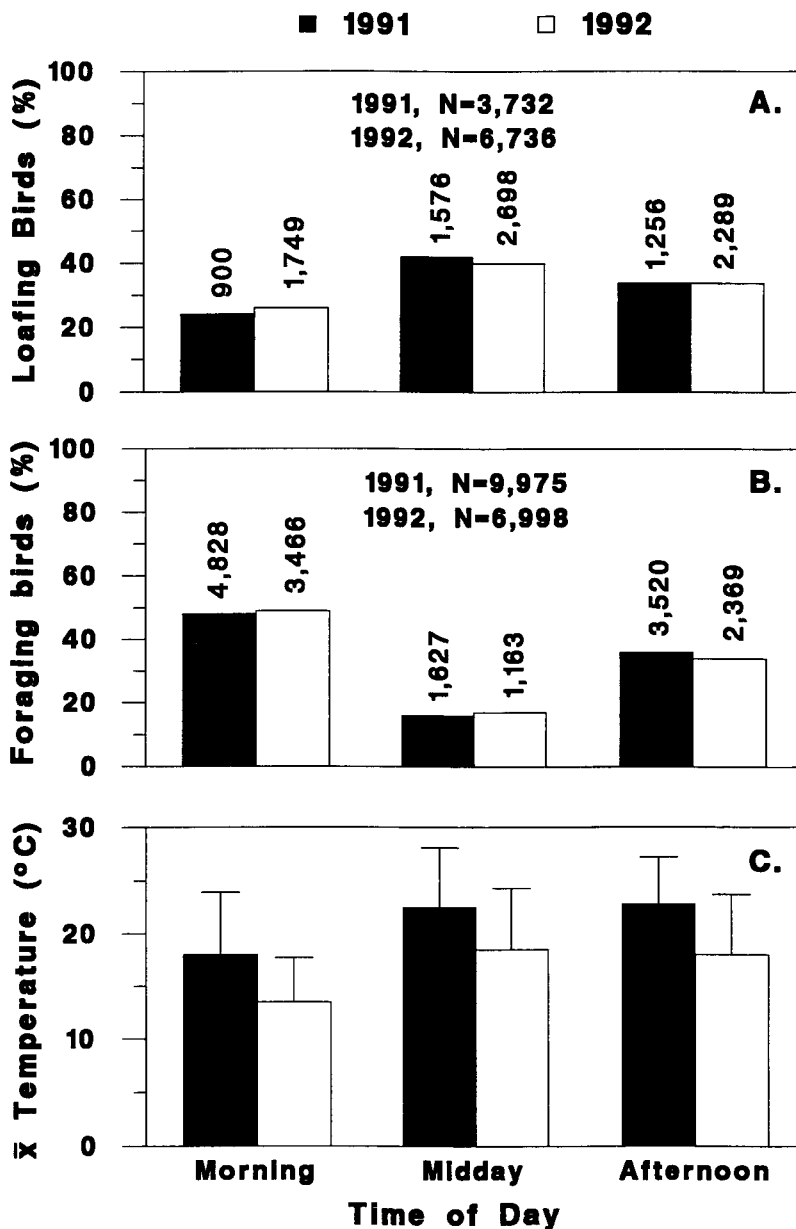


FIGURE 3. Percentage of avocets observed loafing (A) and foraging (B) within each time-of-day category. N = annual number of loafing and foraging observations from which time-of-day proportions were calculated. Sample sizes above bars represent actual loafing and foraging numbers. Bottom graph (C) compares annual mean temperatures ( $\bar{x} \pm SD$ ) recorded within time-of-day categories.

*NND model.* Avocet numbers differed among categories of activity and NND. Furthermore, the model demonstrated a strong interaction effect between both variables, suggesting that activities differed among levels of NND. Loafing and multiple scything were the most common

activities observed among birds less than 1 m apart, whereas probing was the most frequently observed activity among birds 1–10 m apart (Fig. 5).

In 1991, activity ( $P < 0.0001$ ; Table 2), NND ( $P < 0.0001$ ), and the interaction between activ-

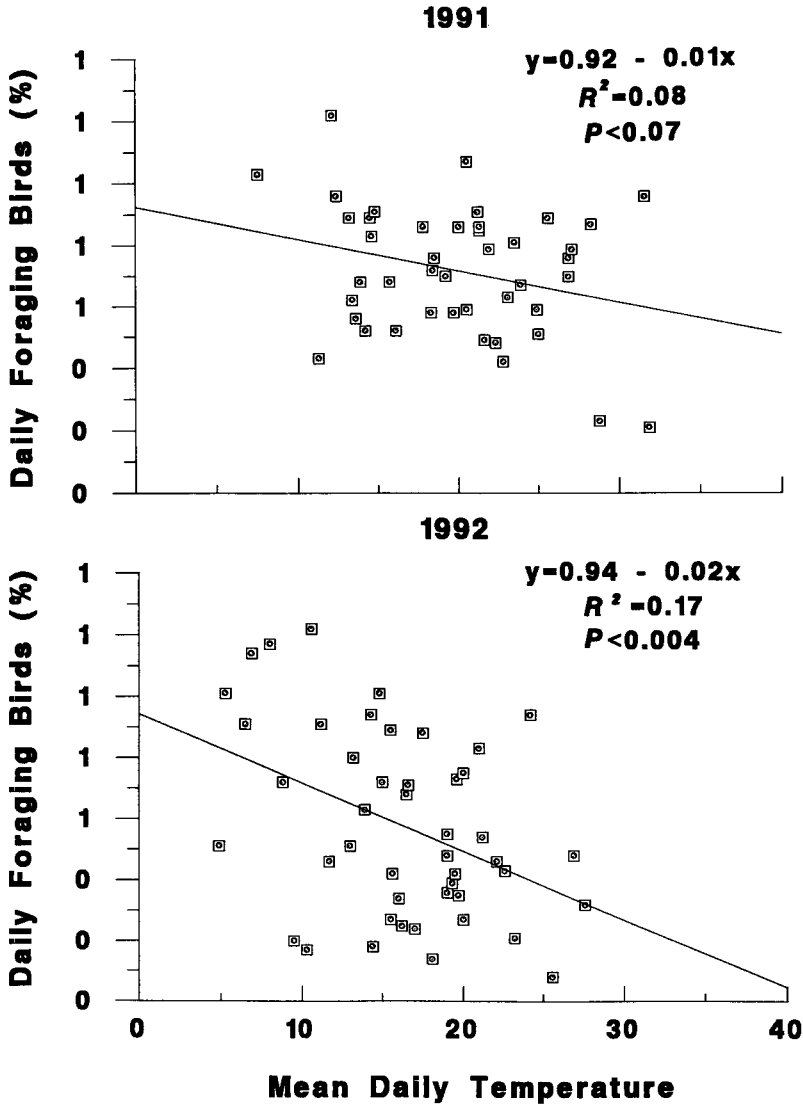


FIGURE 4. Relationship between mean daily temperature and daily percentage of foraging avocets (arcsine-transformed data) in 1991, 1992.

ity and NND ( $P < 0.0001$ ) had a significant effect on T, despite the fact a significant source of variation (day,  $P < 0.0001$ ) was accounted for in the model. Using least square means derived from the model's interaction terms, pairwise comparisons among the six activity categories were conducted within each level of NND. This resulted in a total of 45 pairwise comparisons (15 comparisons per level of NND) and a significance level of  $\leq 0.001$ . These comparisons revealed the following: among birds that were less than one meter apart, there was no significant difference

between the number observed loafing and multiple scything, however, both were significantly greater than the number of birds engaged in other activities ( $P \leq 0.001$ ; Fig. 5); among birds 1–10 m apart, probing was observed significantly more often than any other category of activity ( $P \leq 0.001$ ); no significant differences were detected among activities performed by birds more than 10 m apart.

In 1992, all model terms had a significant effect on T (activity:  $P < 0.0001$ ; NND:  $P < 0.0001$ ; activity  $\times$  NND:  $P < 0.0001$ ) except for the



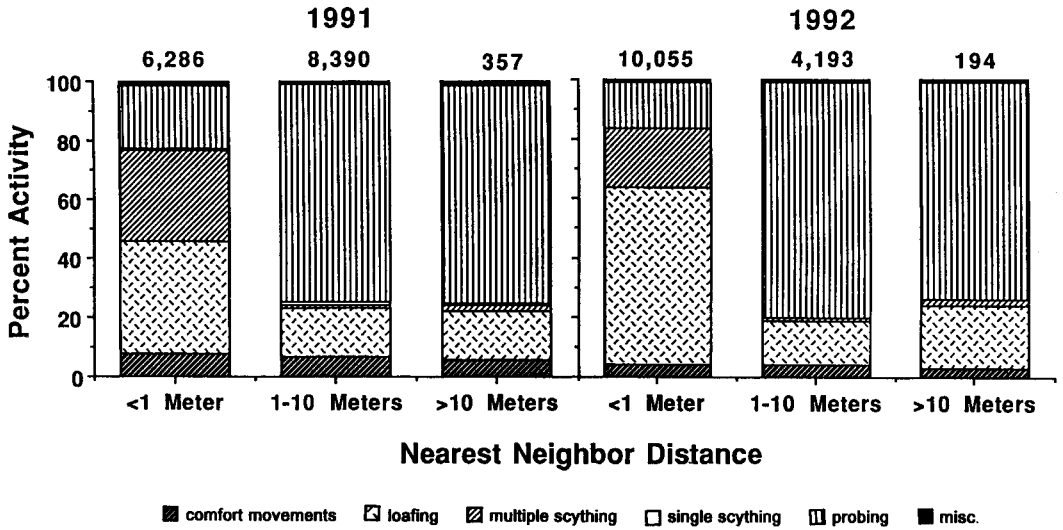


FIGURE 5. Percentage of maintenance activities within categories of nearest neighbor distances (NND). Sample sizes above bars indicate actual number of observations per NND category.

variable day (Table 2), which indicates that daily variation in number of birds scanned was considerably less than the year before. Results from the least square comparisons ( $n = 45$ ) were similar to those obtained from the 1991 analysis. Among birds less than 1 m apart, loafing and multiple scything were observed significantly more often than any of the other activities ( $P \leq 0.001$ ; Fig. 5). Furthermore, loafing numbers were significantly greater than multiple scything numbers ( $P \leq 0.001$ ). This difference may be attributed to the fact that more birds were observed loafing in 1992 than in 1991 (see Table 1 and Figure 2a). Among birds 1–10 m apart, number observed probing was significantly higher than all other categories of activity ( $P \leq 0.001$ ). There were no significant differences in activity among birds more than 10 m apart.

*IWD model.* Avocet numbers differed significantly among categories of activity and IWD. Despite significant interaction effects, relationships between both variables were difficult to interpret because of annual discrepancies among least square mean comparisons. Results indicate that all activities were observed at each water depth except for water greater than belly deep (Fig. 6). Significant differences were detected primarily among common activities (probing, multiple scything, and loafing), and mostly at depths where the majority of avocets occurred (water above the tibiotarsus and water belly deep). Because these differences were not consistent from

year to year, we were unable to establish a causal relationship between IWD and activity.

In 1991, avocet numbers differed significantly among categories of activity ( $P < 0.0001$ ; Table 3) and IWD ( $P < 0.0001$ ). Interaction between activity and IWD also had a significant effect on T ( $P < 0.0001$ ). As in the 1991 NND model, day was a significant source of variation in this model as well ( $P < 0.0002$ ). Fifteen pairwise comparisons were made between activity least square means within all but one level of IWD. Among birds that occurred in *water greater than belly deep*, swimming (miscellaneous category) was the only activity observed, therefore no comparisons could be made. This resulted in a total of 60 pairwise comparisons and a probability level of  $\leq 0.0008$ . Trends revealed by these com-

TABLE 2. Results from nearest neighbor distance (NND) model (analysis of square-root transformed data), which examined main and interaction effects of maintenance activities and NND on nonbreeding American Avocets on South Island, SC (January–May, 1991–1992).

Independent variables	1991		1992	
	df	F	df	F
Activity	5	63.2*	5	14.9*
NND	2	32.1*	2	21.3*
Day	42	2.6*	44	1.3
Activity × NND	10	35.5*	9	23.1*

\*  $P < 0.0001$ .

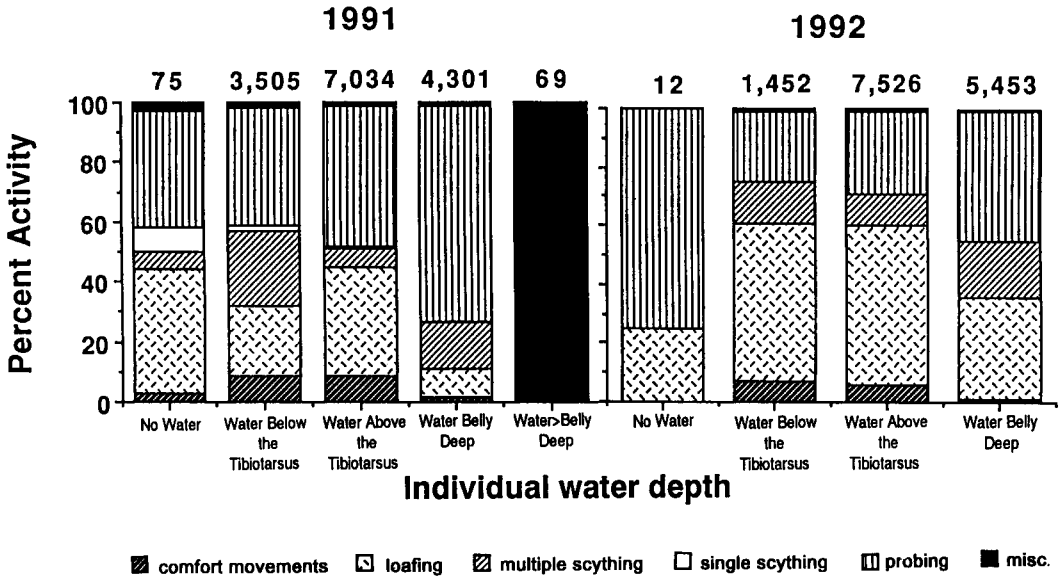


FIGURE 6. Percentage of maintenance activities within categories of individual water depth (IWD). Sample sizes above the bars indicate actual number of observations per IWD category.

parisons were as follows: in the categories of *no water* there were no significant differences among activities; in the category of *water below the tibiotarsus* observations of probing birds were significantly greater than observations of comfort movements, single scything, and miscellaneous activities; in the category of *water above the tibiotarsus*, loafing and probing numbers were significantly greater than all other categories of activities ( $P \leq 0.0008$ ), but were not significantly different from each other; in the category of *water belly deep*, probing observations were significantly higher than all other activities ( $P \leq 0.0008$ ).

In 1992, all model terms had a significant effect on T (activity:  $P < 0.0001$ ; IWD:  $P < 0.0001$ ;

activity  $\times$  IWD:  $P < 0.0001$ , Table 3) except for day. A probability level of 0.001 was used to detect significant differences between a total of 41 pairwise comparisons. A decrease in the number of activities observed within categories of IWD led to reduction in overall number of comparisons. In the category of *no water*, loafing and probing were the only two activities observed, thus only one comparison was made. Among *water below the tibiotarsus* and *water above the tibiotarsus*, all activities were represented, generating 15 comparisons within each category. In *water belly deep*, five activities were observed (single scything was the only activity not observed), which resulted in 10 comparisons. No comparisons were made within the category *water greater than belly deep* because in 1992, avocets were not observed at that depth, even though it was available to the birds. The following trends were uncovered by these comparisons: in the categories of *no water* and *water below the tibiotarsus*, differences among activity least square means were not significant; among birds that occurred in *water above the tibiotarsus*, loafing numbers were significantly higher than all other activities ( $P \leq 0.001$ ) except for probing, which did not differ significantly from any activity; in the category of *water belly deep*, occurrences of comfort movements were significantly less than those of

TABLE 3. Results from individual water depth (IWD) model (analysis of square-root transformed data), which examined main and interaction effects of maintenance activities and IWD on nonbreeding American Avocets on South Island, SC (January–May, 1991–1992).

Independent variable	1991		1992	
	df	F	df	F
Activity	5	17.4**	5	24.1**
IWD	4	12.4**	3	8.5**
Day	42	2.1*	44	0.7
Activity $\times$ IWD	17	7.3**	10	4.5**

\*  $P \leq 0.001$ .  
 \*\*  $P \leq 0.0001$ .

multiple scything, probing, and loafing ( $P \leq 0.001$ ). All three were not significantly different from each other.

## DISCUSSION

### TEMPORAL VARIATION IN ACTIVITY PATTERNS

Avocets fed more and rested less in 1991 than in 1992 (Figs. 2, 3) despite the fact that temperatures did not vary significantly between years. This suggests that other factors were responsible for annual differences in foraging and resting. Birds in Wheeler Basin, the most extensively used site (Boettcher 1994), exhibited the greatest annual difference in number of feeding and loafing birds. Of the total birds observed at the site in 1991, 68% ( $n = 6,450$ ) foraged; 28% ( $n = 2,870$ ) rested. In 1992, only 41% ( $n = 3,550$ ) foraged, and 55% ( $n = 4,793$ ) rested. During March and April, Wheeler Basin's invertebrate density was lower in 1992 than in 1991 (Weber 1994), which may have contributed to the 1992 reduction in foraging numbers. However, invertebrate densities in Wheeler Basin alone are not likely to account for all variation in annual foraging numbers since densities were high (or higher) in other impoundments that were not used as extensively (Weber 1994), and avocets did not feed exclusively on invertebrates.

Night feeding may be an effective way to meet increased energy demands (Evans 1976, Pienkowski 1982, Puttick 1984), particularly among shorebirds wintering in temperate latitudes where shorter daylight hours and adverse weather conditions may cause diurnal energy deficits (Evans 1976). Even though many species forage partly or mainly at night, little is known about the effect of nocturnality on diurnal behavior (McNeil et al. 1992). Because avocets feed diurnally as well as nocturnally during the nonbreeding season (Evans and Harris 1994), our study population may have fed more intensively at night during the second year, thus reducing the need to forage diurnally (Morrier and McNeil 1991). In 1992, we discovered that avocets departed from South Island at dusk and returned just before dawn the following day (their nocturnal destination was not found, despite our searching). It is possible they left the island to forage at another location.

Factors affecting intraseasonal variation in foraging effort among shorebirds include fluctuating temperatures (Kersten and Piersma 1987) and

pre-migratory hyperphagia (Zwarts et al. 1990). Overall, rising temperatures resulted in lower numbers of avocets foraging on South Island (Fig. 4). Relative to other months, a high percentage of avocets were observed feeding in February, the coldest month during both years (Fig. 2). Foraging also increased from March to April, perhaps in response to the need to increase body mass for spring migration.

In marine environments, within-day variation in foraging patterns is often related to tidal cycles (Burger 1984, Goss-Custard 1984, Puttick 1984). Evans and Harris (1994) reported that avocets at their study site fed primarily during low tide and rested during high tide, even in nontidal feeding areas. This trend did not occur on South Island. During both years, a smaller percentage of avocets foraged during midday while a greater percentage rested (Fig. 3). Furthermore, over 94% ( $n = 15,961$ ) fed in nontidal impoundments versus on the intertidal mudflats, indicating that they were not responding to tidal influences. Thus, the decrease in feeding and the increase in loafing may have been a response to rising midday temperatures (Fig. 3; McLachlan et al. 1980). Alternatively, midday light conditions may have created glare, thereby reducing the foraging efficiency of birds that rely on visual cues.

Our failure to detect temporal differences among comfort movements, which comprised only 6% of all observations, may have been due to the fact that scan sampling was conducted only during daylight hours. Anecdotal evidence suggests that these activities may have been more intensive during crepuscular periods. Just before sunset, avocets routinely gathered in tight flocks (NND less than one meter apart) and engaged in vigorous preening, bathing, and wing stretching up to the time of their evening departure. Handel and Gill (1992) reported similar increases in preening among Dunlin (*Calidris alpina*) traveling between roosting and foraging sites.

*Relationship between activity and NND.* Our study demonstrates that avocets maintain cohesive flock structures during the nonbreeding season. Furthermore, a strong relationship appears to exist between NND and activity as evidenced by the fact that activities differed according to NND (i.e., loafing and multiple scything were observed primarily among birds less than 1 m apart, whereas probing was the most common activity among birds 1–10 m apart; Fig. 5).

Flocking is often described as a predator avoidance behavior because individual risk within flocks is likely to be lower than risk to solitary birds (Hamilton 1971, Stinson 1980, Myers 1984). Birds engaged in activities that reduce their ability to watch for predators may be more inclined to form tight flocks. Conversely, behaviors that allow a greater degree of vigilance may be performed solitarily or in loose flocks (Blick 1980). Although we did not observe any predation attempts on avocets during our study, evidence suggests that they do not have to be frequent for flocking to be selectively advantageous (Stinson 1980).

Loose aggregations of probing avocets seemed to exhibit continuous vigilance by raising their heads in what appeared to be an alert position; usually after every probe. Resting individuals in tight flocks intermittently opened one or both eyes, suggesting that they maintained a more relaxed form of vigilance. Multiple scything birds, who also formed tight flocks, occasionally stopped in unison, held their heads up in an alert position for several seconds, and then resumed feeding with their heads down. Based on this anecdotal evidence, we speculate that individuals within loose flocks may have maintained a relatively high degree of vigilance, whereas cohesive flocking may have reduced the need for high vigilance among individuals because overall flock vigilance was high.

Intraspecific aggression among avocets was rarely recorded via scan sampling. Instead, it was seen more often during periods of casual observation (longer than 15 min), and primarily among probing birds. Two types were noted: supplanting, a mild form of aggression whereby the aggressor flew or ran to the position of another bird (Hamilton 1975); and violent intraspecific aggression, which involved physical contact with the opponent (Hamilton 1975). Both types of interactions usually ended when the intruding individual was displaced several meters from the area.

Aggression may be an important spacing mechanism among shorebirds (Recher and Recher 1969, Burger et al. 1979; but see Myers 1984). The most intense encounters are usually linked to territoriality (Myers et al. 1979, Myers 1984). According to our anecdotal observations, the avocets' displays of aggression were too sporadic and infrequent to suggest that they were

actively defending territories. Young (1989) indicated that the intensity, not frequency, of intraspecific aggression is high among visually feeding shorebirds. Furthermore, visual feeders tend to occur solitarily or in loose flocks (Recher and Recher 1969, Myers 1984) because they may be more sensitive to foraging interference than tactile feeders (Goss-Custard 1970, 1980; Vines 1980). The infrequent, yet sometimes violent aggression may explain greater spacing among probing avocets, thus minimized foraging interference.

It has been suggested that the costs of tight flocking (i.e., foraging interference) may outweigh its benefits (i.e., increased vigilance; Goss-Custard 1980, Myers 1984; but see Rands and Barkham 1981). We offer an alternative hypothesis regarding the advantages of flock foraging. Rather than simply enhancing predator detection, we speculate that multiple scything may represent a form of cooperative foraging, whereby large numbers of closely spaced avocets served to flush or herd nektonic prey items, thereby making them easily attainable by flock members as well as other opportunistic species. Götmark et al. (1986) found that fishing success among individual Black-headed Gulls (*Larus ridibundus*) increased with flock size. They attributed this rise in foraging success to schooling fish becoming more dispersed when hunted by flocks, which increased their vulnerability to subsequent attacks. They further suggested that conspicuous white upper parts in gulls served to attract other birds to the flock, which also improved hunting success. A similar situation may occur among avocets. Flocks of avocets were observed multiple scything amid dense schools of small fish; many of which were captured and swallowed. Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), Common Terns (*Sterna hirundo*), and Laughing Gulls (*Larus atricilla*) often foraged among the avocets during these periods. Because avocets did not attempt to chase the opportunistic birds away, suggests that they did not reduce the avocets foraging success, but rather may have improved it. Myers (1984) argued that cooperative hunting by flushing cannot benefit shorebirds because they feed primarily on invertebrates which are not capable of being flushed; instead they are likely to withdraw beneath the surface of the substrate when approached by a large flock of birds. His argument

did not consider that a few species, such as the avocet, feed on nektonic prey items, which are easily flushed.

## CONCLUSIONS

This study increases our understanding of diurnal behavior patterns exhibited by nonbreeding avocets. Furthermore, it provides new information regarding the association between maintenance activities and flocking. However, further data are required to identify specific causal mechanisms that help to explain the observed behavior patterns. Below are several suggestions for future work.

First, the entire 24-hr period should be sampled in order to fully understand how avocets allocate time and energy to activities in relation to changing environmental and biological events (McNeil et al. 1992, McNeil et al. 1993). Second, frequencies of aggressive encounters and vigilance should be quantified and compared among resting, probing, and multiple scything individuals to determine their influence on NND. Finally, in order to accurately compare the costs (i.e., increased interference) and benefits (i.e., decreased vulnerability to predation and increased foraging success through cooperative foraging) of foraging in tight flocks, it is necessary to first determine which foraging method (probing or multiple scything) is more effective in meeting the avocets' energy demands. That is, if caloric intake is higher among probing birds, then the benefits of increased foraging success in loose flocks may outweigh the costs of decreased protection from predators. By addressing these issues, we may gain new insight into the relative importance of maintenance activities and establish causal relationships between activities and spacing patterns for nonbreeding avocets.

## ACKNOWLEDGMENTS

The study was funded by the South Carolina Cooperative Fish and Wildlife Research Unit. We especially thank the Tom Yawkey Foundation for access to the study area and housing during the field seasons. R. Joyner, the staff of the Tom Yawkey Wildlife Center, and M. Spinks provided invaluable logistical and technical support. L. Weber furnished 1991 weekly census data. W. Shaw and C. Roy assisted with fieldwork. S. Gauthreaux, D. Otis, and C. Marsh reviewed several drafts of the manuscript and made many helpful suggestions. Additional thanks to S. Gauthreaux, who provided use of his image intensifier, to C. Marsh for valuable information about the study area, and to L.

Weber and J. Lyons for their encouragement and stimulating discussion during the analyses and preparation of the manuscript.

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