Wilson Bull., 95(3), 1983, pp. 404–415

FEEDING HABITAT OF BLACK SKIMMERS WINTERING ON THE FLORIDA GULF COAST

BARBARA B. BLACK AND LARRY D. HARRIS

The Rynchopidae are noted for their unique bill structure and feeding method; the elongated mandible is an adaptation for skimming across the water's surface to catch fish and aquatic invertebrates. Although Zusi (1962) described in detail the morphological adaptations of the North American Black Skimmer (*Rynchops niger niger*) the species' ecological adaptations are less well understood. Earlier investigators have described Black Skimmers feeding in shallow tidal streams and pools (Chapman 1908, Pettingill 1937, Tomkins 1951, Erwin 1977) where the surface of the water was smooth (Bent 1921, Zusi 1962) and prey was concentrated (Zusi 1962). These studies suggested that skimmers occupy a narrow feeding niche as later described by Erwin (1977); however, no attempt has been made either to characterize or quantify features of Black Skimmer feeding habitat. The objectives of this study were to delineate characteristics of Black Skimmer feeding habitat, and to monitor the prey resource and the diet of wintering Black Skimmers.

MATERIALS AND METHODS

The study site was located in the tidal flats surrounding Cedar Keys (29°08′30″N, 80°02′30″W), a system of keys on the west coast of peninsular Florida roughly midway between the Suwannee and Wacassassa rivers. Study areas (Fig. 1) of 6.0 ha each were separated by at least 100 m of land or 400 m of water.

During the fall of 1979 preliminary observations of area use were made in 16 areas. In each of two trials, 12 areas were monitored in 12 time segments from 1 h before to 2 h after low tide according to a randomized block design. In the first trial skimmers were rarely or never seen in the vicinity of four areas (G, H, I, J) so the areas were dropped from observation in the second trial. Four other areas (M, N, O, P) in the skimmers' observed range were added. The measurement of area use was based on the product of a numerical response (number of birds) and a functional response (number of forages per focal bird) for all groups seen during standard 10-min observation periods. A "forage" was defined as a skimming effort in which the bird did not alter its wingbeat to change direction or lift itself from the surface of the water; the focal bird of a group was that individual whose forages were counted. The use of study areas by skimmers was analyzed using ANOVA and Duncan's multiple range test on transformed forage data.

During the winter of 1979–80 we made observations to characterize preferred feeding habitat using 12 descriptive variables (Table 1), the less obvious of which are described below. The number of other feeders was the number of birds of other species feeding in an area. The locational variable (distance from loafing site) represented the distance from the center of a study area to the nearest loafing site used by skimmers. Since loafing areas are inundated at certain tidal stages, we considered only those available at the time of observation. The distance to the mainland was measured by 500 m increments from a fixed

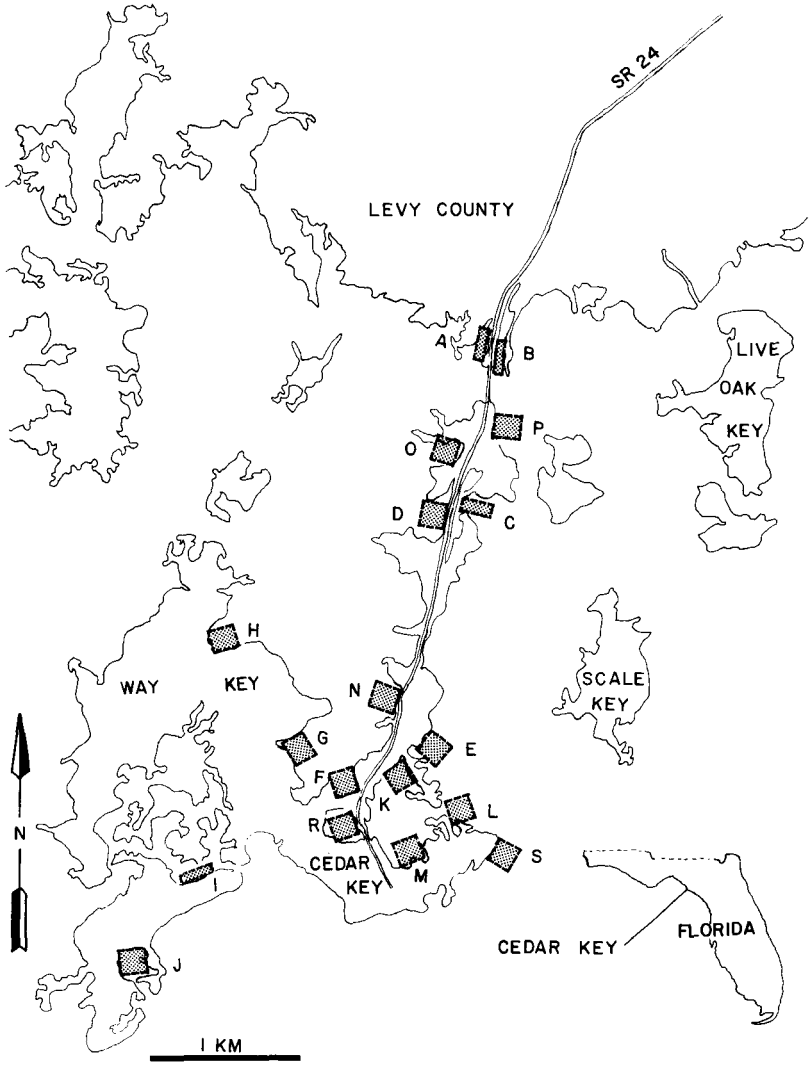

FIG. 1. Locations of the study areas at Cedar Key, Levy Co., Florida.

reference point on the mainland to the feeding site. The six physiognomic variables were recorded as follows. The tidal stage was classified as 1 of 12 one-h increments beginning with the previous high tide. Water depth was measured with a water depth marker at the deepest non-canal location in each study area. Patchiness was designated by one of four classes ranging from 1 = minimal land-water interspersion to 4 = maximal land-water interspersion. Shelter by land was scored from 1–10 (each integer representing 50 m of land)

TABLE 1
VARIABLES RECORDED DURING 10-MIN OBSERVATION PERIODS

Variables	Acronym	Unit
Temporal		
Min to sunset	(MTS)	min
Physical		
Wind direction	(WID)	degree
Wind speed	(WIS)	km/h
Social		
Number of other feeders	(FED)	bird
Locational		
Distance from loafing site	(DFL)	m
Distance to mainland	(DTM)	m
Physiognomic		
Tidal stage	(TIS)	h
Water depth	(WAD)	cm
Patchiness	(PAT)	classes
Shelter by land	(SBL)	m
Open water	(OPW)	percentage
Land	(LND)	percentage

depending on the amount of land adjacent to an area in the direction of the prevailing wind during the observation. The percentages of open water and land (mudflat or sandbar) in an area were estimated from 25 point readings taken in a standard pattern with a cross-wire ocular scope (Winkworth and Goodall 1962) and converted to percentage values. Ten-min observation periods were assigned randomly to six used areas for 20 h in each of the 12 tidal stages. If no feeding was observed during an observation period, then the observer moved to the next designated area. If feeding was observed, then the observer remained in the area until no feeding had occurred for 10 min. In this way 89 skimmer-feeding observations were recorded with accompanying environmental measurements. A principal factor analysis (procedure FACTOR, Statistical Analysis Systems, Helwig and Council [1979]) was used to analyze these data.

To further study feeding areas, we noted the number of forages in two zones: "edge," a 2-m zone to either side of a land-water interface and "open water," a zone including all other water in the area. The relative abundance of these zones was estimated from point samples converted to percentage values. Skimmer use was compared to feeding zone availability using a Chi-square test for goodness-of-fit. The prey resource was sampled in four areas during peak feeding by skimmers, low to incoming tide (Black and Harris 1981), and adjacent to land-water interfaces. In each area eight seine hauls were made on each of 8 days for a total of 64 seine hauls per area. The number of prey sampled were compared between days (random variable) and between areas (fixed variable) using ANOVA. Additionally, the stom-

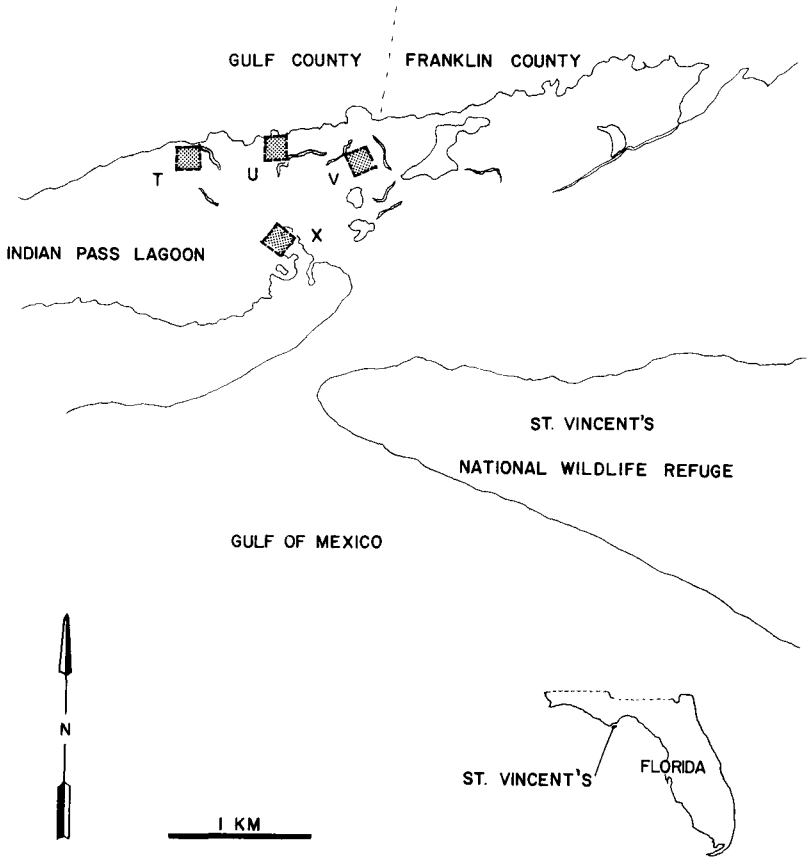

FIG. 2. Locations of the study areas at St. Vincent National Wildlife Refuge, Franklin Co., Florida. Areas V and X were presumed "suitable" and areas T and U were presumed "unsuitable."

ach contents of 13 skimmers collected while feeding were analyzed to determine the frequencies of occurrence, relative weights, and relative volumes of prey species captured.

In the winter of 1980–81 we used the 12 descriptive variables to compare two highly-used and two unused feeding areas at Cedar Key. This completed the identification, delineation, and quantification of preferred feeding areas at Cedar Key. To test these results in an independent location, we selected an area 175 km to the northwest. At this second location, St. Vincent National Wildlife Refuge, Franklin Co., Florida, study sites were compared using selected variables based on the results of the Cedar Key study and were assigned to a "suitable" or "unsuitable" status (Fig. 2). Observations of skimmer use then were conducted to test the null hypothesis of equal use by feeding skimmers.

TABLE 2

AVERAGE NUMBER OF BLACK SKIMMER FORAGES IN STUDY AREAS DURING TWO TRIALS AS SHOWN BY DUNCAN'S MULTIPLE RANGE TEST[a] ON TRANSFORMED FORAGE DATA[b]

Trial one		Trial two	
Area[c]	Mean	Area	Mean
C	4.7	C	3.7
A	4.5	A	2.8
K	2.6	M	1.5
L	2.5	K	1.3
E	1.8	L	1.3
B	1.7	P	1.2
G	1.4	E	1.1
F	1.2	B	1.0
D	1.0	D	1.0
H	1.0	F	1.0
I	1.0	O	1.0
J	1.0	N	1.0

[a] Means joined by a single line do not differ significantly ($P > 0.05$).
[b] Data were transformed using a square-root transformation of (a + 1).
[c] See Fig. 1 for location of areas.

RESULTS

Habitat characteristics.—In two trials Black Skimmers used some feeding areas more frequently ($F = 5.91$, df = 11, $P < 0.01$) ($F = 2.44$, df = 11, $P < 0.01$) than others and in both trials used areas A and C significantly more ($P < 0.05$) than most other areas (Table 2). Skimmers fed intermittently in eight areas (B, E, F, G, K, L, M, P), but were not observed feeding in six other areas (D, O, H, N, J, I).

Within areas skimmers fed more often near certain topographic features. Of the total forages recorded in the winter of 1979–80 (N = 5461) 71% were within 2 m of a land-water interface. Thus, skimmers foraged significantly more ($\chi^2 = 40.8$, df = 1, $P < 0.0001$) along the water's edge than in areas of open water.

Measurements of environmental variables recorded during skimmer feeding were used to identify the key factors of intermittently and frequently used habitat (Table 3). The first three factors accounted for 83% of the variation in the original data: factor 1, factor 2, and factor 3 accounted for 50%, 20%, and 13% of the variation, respectively. The four variables with high loadings on factor 1 describe the structure of skimmer feeding habitat. These variables were water depth, patchiness, amount of open water, and amount of land (mudflat and sandbar). Factor 2 was com-

TABLE 3

THE FIRST THREE "FACTORS[a]" (STRUCTURE, LOCATION, AND WIND SPEED) CREATED BY THE FACTOR ANALYSIS

Variables	Factor pattern		
	Factor 1 "structure"	Factor 2 "location"	Factor 3 "wind speed"
TIS	−0.24	−0.30	−0.16
WAD	−0.85	−0.16	0.05
PAT	0.90	−0.09	0.04
DFL	−0.36	0.48	0.25
DTM	−0.25	−0.52	−0.53
MTS	0.58	−0.38	0.09
SBL	0.24	0.46	−0.11
WID	−0.10	0.45	−0.29
WIS	0.32	−0.26	0.65
FED	0.05	0.49	−0.03
P[b]	−0.85	−0.22	0.19
L[c]	0.85	−0.06	−0.21
Percentage of total variance accounted for	49.5	20.7	13.0
Cumulative percentage of total variance accounted for	49.5	70.2	83.2

[a] These factors accounted for 83% of the variation in the original data describing skimmer feeding habitat.
[b] P represents the arcsine transformation of the percentage of open water.
[c] L represents the arcsine transformation of the percentage of land (mudflat or sandbar).

prised of variables primarily associated with the location of the feeding area. These variables were distance from loafing site, distance to mainland, shelter by surrounding land, wind direction, and number of other feeders. Two variables, wind speed and distance to the mainland, had high loadings on factor 3 and were related to wind speed.

When highly-used and unused feeding areas at Cedar Key were compared, no significant differences were found for any climatic variables (wind speed, wind direction) or temporal variables (minutes to sunset, tidal stage) (Table 4). Significant differences did occur between area types for some social, locational, and physiognomic variables. Used areas were characterized by more feeding birds of other species, as well as proximity to loafing sites and the mainland. Used areas were also typified by shallower water with more shelter provided by surrounding land, less open water, more land-water interspersion, and more mudflat.

At St. Vincent National Wildlife Refuge variables important in the iden-

TABLE 4

MEANS ± SE AND RESULTS OF STATISTICAL ANALYSES COMPARING VARIABLES IN USED AND UNUSED FEEDING HABITAT IN THE CEDAR KEY AREA

Variable	Used habitat N = 49[d]	Unused habitat N = 70	*P*
Temporal			
Min to sunset[a]	266.7 ± 26.8	321.8 ± 24.1	NS
Physical			
Wind direction[b]	240.1 ± 14.3	201.6 ± 16.0	NS
Wind speed[a]	7.6 ± 0.7	6.6 ± 0.5	NS
Social			
Number of other feeders[b]	18.7 ± 6.5	2.1 ± 0.3	<0.05
Locational			
Distance from loafing site[b]	5.9 ± 0.5	13.4 ± 0.2	<0.0001
Distance to the mainland[b]	2.8 ± 0.2	3.5 ± 0.1	<0.01
Physiognomic			
Tidal stage[a]	7.8 ± 0.1	7.8 ± 0.1	NS
Water depth[b]	13.4 ± 1.1	31.9 ± 1.5	<0.0001
Patchiness[c,e]	4.0	2.0	<0.0001
Shelter by land[b]	5.8 ± 0.5	1.9 ± 0.3	<0.0001
Mudflat or land[a]	43.8 ± 2.8	8.2 ± 1.5	<0.0001
Open water[a]	22.7 ± 2.6	62.2 ± 1.6	<0.0001

[a] Student's *t*-test (homogeneous variance).
[b] Approximate *t*-test (heterogeneous variance) (Steel and Torrie 1960:81).
[c] Wilcoxon's rank sum test.
[d] N equals the number of 10-min observations.
[e] Median value replaces mean.

tification of structure (water depth, patchiness, percentage of land, and percentage of open water) were the principal criteria for our selection of "suitable" and "unsuitable" sites. Selection based on the second factor, location, was more difficult since the only areas with structural features similar to the non-used areas of Cedar Key were located close to, rather than far from, the mainland and were more sheltered by land. The other locational variable associated with factor 2 (distance from loafing site) was, thus, the secondary basis for area selection. The third factor, wind speed, did not vary significantly between area types at Cedar Key or St. Vincent and was, therefore, not heavily considered in study area selection at St. Vincent.

When "suitable" and "unsuitable" areas at St. Vincent were compared, no significant differences ($P > 0.05$) were found in climatic variables (wind

TABLE 5

MEANS ± SE, AND RESULTS OF STATISTICAL ANALYSES COMPARING VARIABLES IN SUITABLE AND UNSUITABLE FEEDING HABITAT IN THE ST. VINCENT'S AREA

Variable	Suitable habitat N = 41[d]	Unsuitable habitat N = 39	*P*
Temporal			
Min to sunset[a]	293.6 ± 22.6	310.6 ± 20.8	NS
Physical			
Wind direction[a]	104.1 ± 15.1	108.9 ± 17.5	NS
Wind speed[a]	8.2 ± 0.6	7.6 ± 0.5	NS
Social			
Number of other feeders[b]	10.2 ± 1.3	2.7 ± 0.4	<0.0001
Locational			
Distance from loafing site[b]	4.1 ± 0.4	19.1 ± 0.2	<0.0001
Distance to the mainland[b]	1.4 ± 0.1	1.0 ± 0.0	<0.0001
Physiognomic			
Tidal stage[a]	7.7 ± 0.1	7.8 ± 0.1	NS
Water depth[a]	21.0 ± 2.2	43.6 ± 2.5	<0.0001
Patchiness[c,e]	4.0	2.0	<0.0001
Shelter by land[b]	4.4 ± 0.4	7.2 ± 0.7	<0.01
Mudflat or land[b]	33.6 ± 3.2	0.7 ± 0.2	<0.0001
Open water[b]	19.7 ± 2.0	65.9 ± 1.2	<0.0001

[a] Student's *t*-test (homogeneous variance).
[b] Approximate *t*-test (heterogeneous variance) (Steel and Torrie 1960:81).
[c] Wilcoxon's rank sum test.
[d] N equals the number of 10-min observations.
[e] Median value replaces mean.

speed, wind direction) or temporal variables (minutes to sunset, tidal stage) (Table 5). As expected, significant differences were found for all structural variables (water depth, patchiness, percentage of mudflat, percentage of open water) and the locational variable (distance from loafing site) by which the area types were selected. In addition, "suitable" areas had more feeders of other species, but were less sheltered by land and were farther from the mainland than "unsuitable" areas. Allowing for these two differences, the area types at Cedar Key and St. Vincent were similar for all other variables tested.

At St. Vincent, Black Skimmers used "suitable" areas 2.5 times more frequently (obs. = 105) than they used "unsuitable" areas (obs. = 39); thus, a significantly unequal distribution of forages ($\chi^2 = 15.1$, df = 1, $P < 0.01$) was recorded in the two area types. These results indicate that feeding habitat selection of St. Vincent's Black Skimmers was consistent

TABLE 6

MEANS ± SE, AND RESULTS OF DUNCAN'S MULTIPLE RANGE TEST FOR THE NUMBER OF FISH AND SHRIMP PER SEINE HAUL IN TWO HIGHLY USED AREAS (A AND C) AND TWO UNUSED AREAS (D AND O) AT CEDAR KEY

Area	Preference class	Number of seine hauls	$\bar{x}$ ± SE
C	high	64	293.5 ± 44.2
D	non	64	195.2 ± 73.7
A	high	64	124.1 ± 38.6
O	non	64	66.4 ± 8.9

with that of Cedar Key Black Skimmers and predictable from the factor analysis of Cedar Key habitats.

Prey resource and diet.—At Cedar Key prey abundance did not differ significantly ($F = 0.82$, df = 7, $P > 0.5$) between days but did vary significantly ($F = 4.63$, df = 3, $P < 0.01$) between areas. Area differences, however, were not consistent with skimmer use since some highly used and unused areas did not differ significantly in prey numbers (Table 6). Prey levels were not necessarily higher in preferred feeding areas nor consistently lower in non-preferred areas. Additionally, prey composition was similar in all areas (Fig. 3); shrimp and members of the Sciaenidae (Perciformes) made up at least 87% of the total catch in each area.

From the skimmer stomachs examined, a total of 63 identifiable items were recovered of which 60% were shrimp and 40% were fish. However, fish were the predominant prey taken by both weight and volume (81% and 77%, respectively). In order of frequency the fishes recovered were: eight longnose killifish (*Fundulus similis*); seven striped mullet (*Mugil cephalus*); three Gulf killifish (*F. grandis*); two unidentified larvae (*Sciaenidae*); one diamond killifish (*Adenia xenica*); one Atlantic thread herring (*Opisthonema oglinum*); one tidewater silverside (*Menidia beryllina*); one needlenose fish (Belonidae); one unidentified larvae (Clupeiformes). The three most frequently captured fish were also the largest types of prey being eaten.

Although shrimp were the most abundant prey recovered, they represented only 7% of the weight and 9% of the volume of the stomach contents examined. Shrimp species identified from whole specimens included: four *Palaemonetes pugio*; two *P. intermedius*; and one *P. vulgaris*. Finely digested material accounted for 12% of the weight and 14% of the volume of the stomach contents analyzed.

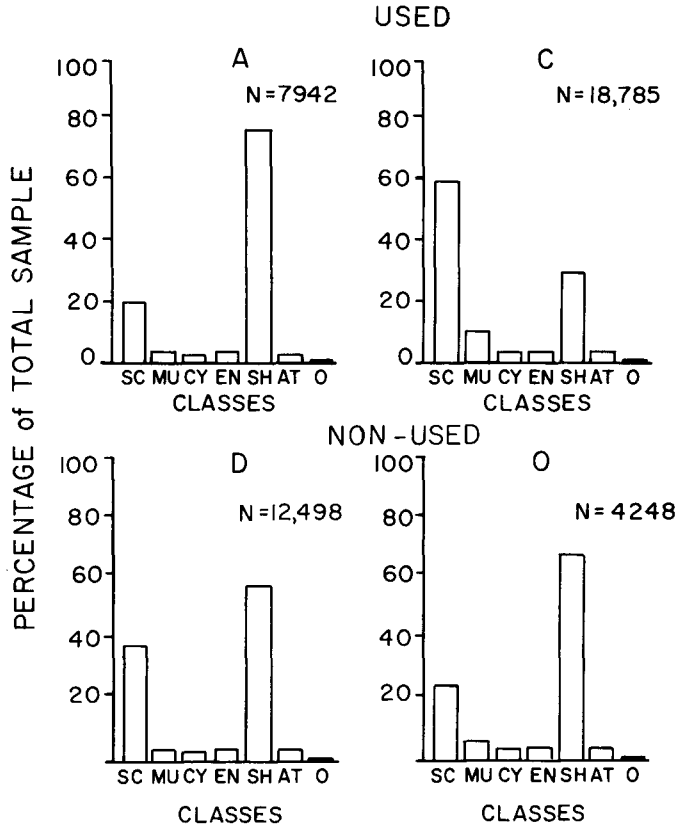

FIG. 3. Frequency histograms of fish and shrimp sampled in 256 seine hauls in two highly used areas, A and C, and two non-used areas, D and O. SC = Sciaenidae, MU = Mugilidae, CY = Cyprinodontidae, EN = Engraudidae, AT = Atherinidae, SH = shrimp, O = other.

DISCUSSION

A premise underlying this study is that a species with stereotyped feeding behavior (Morse 1980) will be specific rather than plastic in feeding habitat choice. Erwin (1977) reported on the foraging zone use of three species of seabirds (Common Tern [*Sterna hirundo*], Royal Tern [*Sterna maxima*], and Black Skimmer) and found that skimmers were the most restricted in their habitat use. Among open bay, beach/inlet, tidal creek and marsh/tidal pool habitats, Erwin (1977) found that skimmers fed almost exclusively in marsh/tidal pools. In our study, which looked at feeding

only within the marsh/tidal-flat habitat, microhabitats were not used equally since skimmers fed in some areas frequently, in some intermittently, and in some not at all. Although some of the unused areas (J, I, H) were outside of the observed feeding range of the skimmers, other areas (D, N, O) were traversed frequently by foraging birds but were not used as feeding sites. Apparently, then, skimmers were selecting specific patches of habitat in which to feed within a single habitat type.

Skimmers should select feeding areas where they are either most successful or consistently successful in capturing prey. If one assumes that no other factor or factors affect skimmer feeding, then skimmers should feed most often in those areas of high prey abundance. However, this has been shown not to be the case since areas of high use and non-use did not differ significantly in prey abundance. In addition, prey composition was similar among all areas sampled and skimmer diets consisted of species of similar abundance in all areas. Other factors must, therefore, be involved in the selection of feeding areas.

The "structure" of feeding areas was found to account for the most variation in skimmer area use. Feeding areas were characterized by shallow water (10–20 cm), maximal land-water interspersion, and an average of 43% mudflat and 23% open water. These conditions typically occurred only in certain areas at or just after low tide (the skimmers' primary foraging period) at Cedar Key (Black and Harris 1981). At low tide, unused areas typically had deeper water, less land-water interspersion, less mudflat, and more open water than highly used areas. In areas with deep water (>30 cm), 60% open water, and minimal land-water interspersion, edge zones created by land-water interfaces are reduced. Skimmers may not select these areas since they prefer to feed along edges. Because the skimmers' feeding range is restricted to the top 5–6 cm of water, it is seemingly advantageous for skimmers to forage in shallow water, i.e., edge zones, where prey are concentrated vertically and/or escape downward is not possible. Of 5461 forages recorded, 71% occurred within 2 m of a land-water interface. Thus, skimmers fed more in the shallow water along land-water interface zones and areas with more land-water interface zones were preferred.

SUMMARY

The winter feeding ecology of Black Skimmers (*Rynchops niger niger*) was observed for 1119 h in 16 areas at Cedar Key and four areas at St. Vincent National Wildlife Refuge on the Gulf coast of Florida. Skimmers used some tidal flat areas frequently, some intermittently, and some not at all; however, prey abundance and composition alone did not explain the Black Skimmers' selection of feeding areas. Of 5461 forages recorded, 71% occurred within 2 m of a land-water interface suggesting that the skimmer is best adapted to exploit prey in the shallow, smooth water along land-water interfaces. The structure of feeding areas

used by skimmers was typified by shallow water (10–20 cm), maximal land-water interspersion, 43% mudflat, and 23% open water. Feeding sites within marsh/tidal pool habitat were specifically selected by skimmers, and an assessment of specific habitat characteristics in two independent locations showed similar feeding habitat selection in two skimmer populations.

ACKNOWLEDGMENTS

We wish to thank R. Carter for statistical advice, C. R. Gilbert, J. Williams, and L. Bielsa for identifying fish and shrimp species and especially R. W. Gregory for assistance throughout the project. We are also grateful to M. Perry and the staff of St. Vincent National Wildlife Refuge for their cooperation and assistance, and to J. W. Hardy, R. M. Erwin, P. A. Buckley, and R. Zusi for reviewing and commenting on earlier drafts of the manuscript. This study was supported by the U.S. Fish and Wildlife Service, Contract No. 14-16-0009-79-063. The Florida Cooperative Fish and Wildlife Research Unit is supported jointly by the U.S. Fish and Wildlife Service, Florida Game and Fresh Water Fish Commission and the University of Florida.

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