FEEDING BEHAVIOR AND DIET OF THE LONG-BILLED CURLEW AND WILLET

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To study shorebird feeding ecology, most people collect birds and examine stomach contents although in a few instances regurgitated pellets (Hibbert-Ware and Ruttledge 1944, Swennen 1971) or observations of feeding birds (Baker and Baker 1973) have been used. In this study we used both observations and regurgitated pellets to examine the feeding behavior and the diet of the Long-billed Curlew (*Numenius americanus*) and the Willet (*Catoptrophorus semipalmatus*) on Bolinas Lagoon, in California. Our objective was to find a suitable method for studying shorebird diets without sacrificing the birds. In the literature we found little information on the diet of the Long-billed Curlew, and data on the Willet in California that we found are limited to the examination of 21 stomachs (Reeder 1951, Recher 1966, Anderson 1970). There is little information on the feeding behavior of either species. We felt, therefore, that any information we could add on the feeding behavior and diet of these shorebirds would be useful.

METHODS

Bolinas Lagoon is a shallow 570-ha estuary 24 km northwest of San Francisco, California. High hills, marshy pastures, and the Seadrift sand spit surround this wedge-shaped estuary except for a narrow opening to the ocean on the southwest side (Fig. 1). Pine Gulch Creek drains into the estuary year round and is the main source of the estuary's fresh water. Kent Island is a 40-ha island within the estuary. A large part of Kent Island and the Pine Gulch Creek delta are salt marsh where the chief plant species are *Salicornia virginica* and *Spartina foliosa*. At mean low water about 70% of the estuary comprises tidal flats which are divided by several channels (Ritter 1969).

This study was conducted from June 1973 to February 1974 and divided into a fall period (July through October) corresponding with a warm dry season, and a winter period (November through February) corresponding with most of the rainy season at Bolinas.

We made a census of all shorebirds on the estuary during every 5-day period from 31 May to 7 October and with one exception during every 10-day period from 8 October to 1 March. All but 2 censuses were taken on flood tides 1.1-1.7 m above mean low water. During the census the estuary was divided into 3 areas and an observer in each area counted or estimated all shorebirds in that area. The counts in the areas were made simultaneously.

Additional censuses of specific areas on or near the estuary were also made to find out which were most used by the birds. We censused shorebirds in the salt marsh on Kent Island at low and moderate tides several times a month, and on

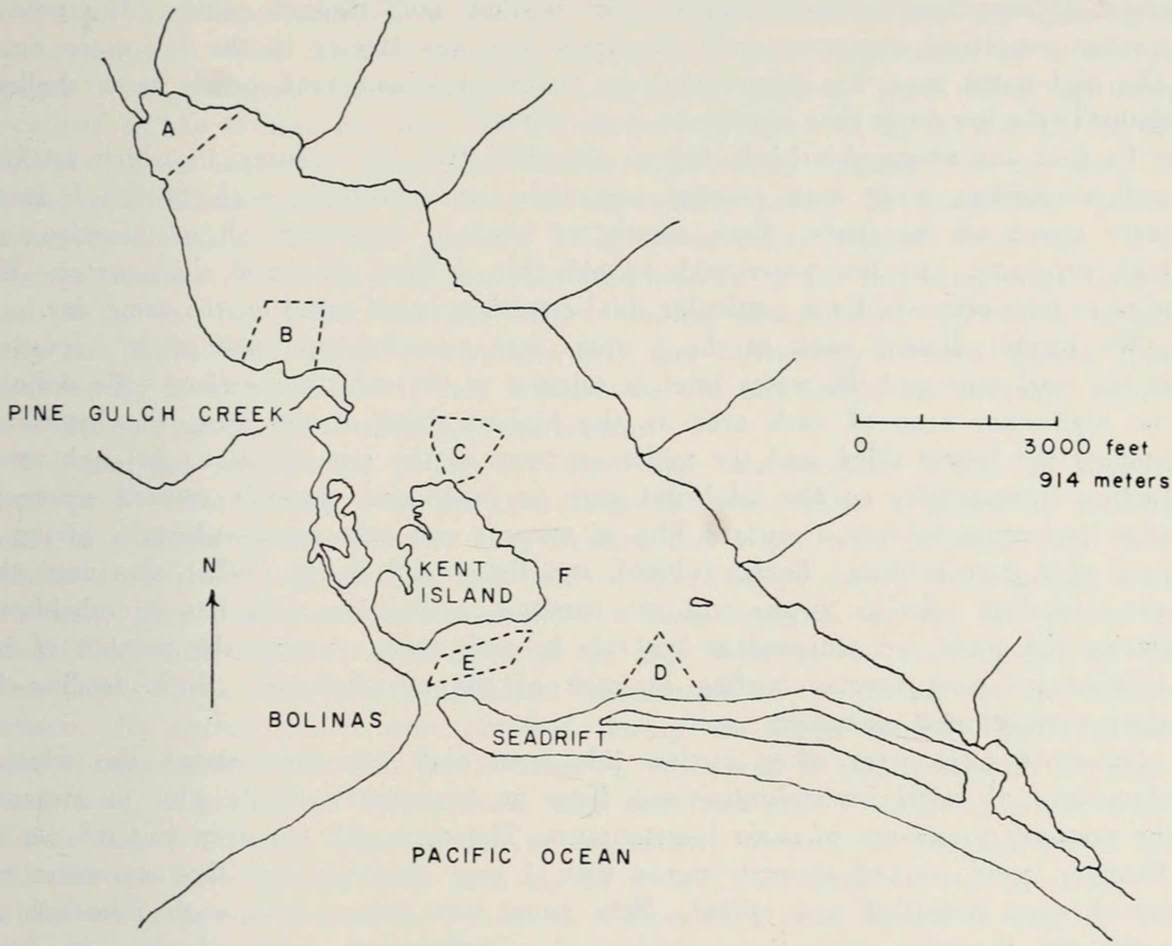

FIG. 1. Map of Bolinas Lagoon showing 5 areas of intensive study. Area A is approximately 12.6 ha; B, 9.8 ha; C, 8.0 ha; D, 7.0 ha; and E, 8.4 ha.

8.5 km of open coast (comprising sand to pebble beaches and soft shale reefs) adjacent to and north of Bolinas Lagoon 3 times a month.

We selected 5 areas within the tidal flat of the estuary (Fig. 1) for the most intensive study. The substrate of area A was a very poorly sorted, very fine sand (Ritter 1969) containing considerable organic debris such as twigs and leaves. Much of the high-water zone of this area was covered by a layer of sediment, dried and cracked into leathery plates. The high-water zone abutted a small salt marsh through which a fresh-water stream ran year round; the low-water zone bordered a basin. Area B was similar to area A except that a fresh-water stream ran into it only during periods of heavy rain and that the substrate ranged from fine to medium sand (Ritter 1969). The substrate of area C was a well to moderately sorted, fine sand (Ritter 1969) and lacked the organic debris of areas A and B. Unlike areas A and B the high-water zone of area C was pock-marked with the burrow openings of the ghost shrimp (*Callianassa californiensis*) and was not covered by hard, dried plates of sediment. The high-water zone of area C abutted the Kent Island salt marsh on one side and a channel on the other; the low-water zone bordered a small basin. Area D had a substrate of moderately sorted, fine sand (Ritter 1969), and was bordered on 2 sides by channels and on a third side by a basin. The high-water zone in the center was less burrowed than area C. Area E differed markedly from the other areas. It comprised sediment ranging from medium sand through pebble. The pebble fraction contained numerous shell fragments and was largely in the low-water zone. The high-water zone was separated from the Kent Island sand beach by a shallow channel; the low-water zone bordered a main channel.

To find out where shorebirds fed on the tidal flat, 10 censuses, in which feeding and non-feeding birds were counted separately, were made in each of the 5 areas every month of the study. Each month we tried to census on all combinations of high, moderate, and low water with an ebb tide, a flood tide, and slack water. We tried to take censuses for a particular tidal condition in all areas on the same day.

We further divided each of the 5 areas into microhabitats, defined by elevation in the tidal zone and the water level in relation to the substrate surface. We defined the high-water zone of each area as the highest third of the area, the low-water zone as the lowest third, and the mid-water zone as the area between. In each zone, surface irregularities on the tidal flat such as pools and channels created emerged, edge (substrate holding a surface film of water), and submerged substrate, giving a total of 9 microhabitats. Recher (1966) and Baker and Baker (1973) also used the water level in relation to the substrate surface to describe tidal flat microhabitats. During the study, we censused at low tide in each area, counting the number of individuals of each species feeding in each of the microhabitats. Birds feeding in algae were counted separately.

Substrate cores were taken at low tide from each area to measure the relative abundance of small invertebrates, and from an invertebrate study plot to measure the seasonal abundance of some invertebrates. The cores, 9.8 cm deep and 6.6 cm in diameter, were washed through sieves with 1 mm openings and the organisms retained were identified and tallied. Nine cores were taken from each microhabitat (with the exception of a few very limited microhabitats) from all areas in June and from areas A, D, and E in December. The invertebrate study plot (280 $\times$ 20 m) lay along the southern border of area C and ran from the edge of the salt marsh to a basin in the low-water zone. Every month 2 cores were taken at random from each of 28 stations (10 $\times$ 20 m) along the length of the plot. Each month we estimated the algal coverage in each station.

As an estimate of the availability of the tidal flat to shorebirds, we calculated the number of daylight hours during which the tidal level was less than 1.4 m above mean low water. This calculation was made for one day of every 3-day period of the study; we used the tidal charts to estimate the rate at which the water ebbed or flooded and the time at which the water level reached 1.4 m above mean low water.

We watched individual Long-billed Curlews and Willets to determine their feeding rates, methods of searching for and capturing prey, use of microhabitats, and the type of prey they captured. We observed birds through 20-$\times$ spotting scopes and tape-recorded data. The type, success, and microhabitat location of each prey-capture attempt were recorded as well as interactions between the bird under observation and other birds. Prey-capture attempts were defined as follows. A *peck* was a single movement of the bill usually to the surface of the mud but occasionally at flying insects or organisms on snags or rocks. A *multiple peck* was a series of 2 or more consecutive movements of the bill to the surface of the substrate without lifting the bill back to the horizontal position. *Probes* were single movements of the bill into and out of the substrate, that appeared to penetrate the substrate at least 1 cm. *Multiple probes* consisted of 2 or more vertical motions of the bill during which it was not withdrawn from the substrate. All pecks and probes were considered prey-capture attempts although a few may have been search tactics. An observation was terminated when the bird stopped feeding and only observations of 4 min or longer were analyzed. Observations of Long-billed Curlews were taken at many locations on the estuary but those of Willets only in areas A, C, D, and E. In the fall period we made 46 Long-billed Curlew observations totaling 744 min and 28 Willet observations totaling 164 min; in the winter period, 22 Long-billed Curlew observations totaled 272 min and 67 Willet observations totaled 499.5 min. The average distance of the observer from the bird was 50 m for the Long-billed Curlew and 30 m for the Willet. In the Willet feeding observations, differences among areas are taken from winter observations only and differences between seasons from observations in areas A and C only because we did not collect an adequate sample of Willet observations in all areas for both seasons.

We analyzed regurgitated pellets of Long-billed Curlews and Willets to identify their prey. Most pellets were collected from locations where a group of roosting birds of a single species had just been flushed, but a few were collected from individuals after pellet regurgitation had been observed. Only moist, fresh pellets were collected; they were preserved in alcohol for later analysis. In the fall period 30 Long-billed Curlew pellets were collected on high tides in the salt marshes of the Pine Gulch Creek delta and Kent Island where most of the curlews on the estuary roosted. No curlew pellets were obtained during the winter period. Willet pellets were obtained from birds that fed in areas A, C, D, and E and roosted in the high-water zone of these areas during flood tides and from area F (Fig. 1) where many Willets that fed over a large portion of the estuary roosted. In the fall period we collected 19 Willet pellets from area A, 14 from C, 10 from D, and 15 from F; in the winter period, 2 from A, 7 from C, 4 from D, 2 from E, and 9 from F. We also obtained 6 stomachs from Willets that had been eaten by raptors and used 2 additional stomachs obtained in previous years from raptor kills. The contents of the pellets and stomach samples were examined under a 30-× dissecting microscope and the prey identified from characteristic fragments.

Two statistical procedures were used to test the similarity of one result against another: the test for the equality of 2 percentages (Sokal and Rohlf 1969:607–608) and Student's *t*-test for the difference between means (Steel and Torrie 1960:73–75).

In this paper mud crab is used synonymously with *Hemigrapsus oregonensis*, ghost shrimp with *Callianassa californiensis*, and mud shrimp with *Upogebia pugettensis*.

RESULTS

Long-billed Curlew

Distribution.—During this study the number of Long-billed Curlews on Bolinas Lagoon consistently averaged 40. At nearby estuaries such as Limantour Estero, Tomales Bay, and Drake's Estero, 1 or 2 curlews were all that could be found on any date. On Bolinas Lagoon the curlews were scattered at low tide over the tidal flat, feeding primarily in emerged and submerged microhabitats; when the flats were covered at high tide the birds roosted in the salt marsh. Curlews were not seen feeding on the coast or in pastureland but occasionally one or two were seen feeding in the salt marsh.

TABLE 1

MEAN FEEDING RATES OF THE LONG-BILLED CURLEW FOR 2 FEEDING METHODS AND 2 SEASONS ON BOLINAS LAGOON

	Combined Seasons			Combined Methods		
	"Pause-probe"		"Burrow-probe"	Fall Period		Winter Period
PCA[a]/Min.	5.6	*[b]	9.4	8.5	*	11.1
Prey/PCA (%)	8.5	*	4.9	4.9		4.8
Prey/Min.	0.4		0.4	0.3	*	0.5

[a] PCA is prey-capture attempts.
[b] An asterisk indicates a significant difference ($P < 0.05$) between adjacent means.

Feeding behavior.—Long-billed Curlews used 3 methods to obtain prey. In the "burrow-probe" method, used primarily in the emerged areas, the curlews probed into burrows until prey was sensed, then probed rapidly in a burrow until the prey was seized. In the "pause-probe" method, used only in submerged areas, the curlews stood in 5–10 cm of water with their bills partly under water and slightly ajar. They remained motionless in this position for 5–10 sec, presumably until detecting some movement in a burrow below. The bill was then moved slowly down until, with a sudden lurch, the prey was captured. If this attempt was unsuccessful the movement was often repeated. The burrow-probe and the pause-probe methods were used by the curlews to obtain all of their major prey species. The third capture technique, the "peck," was used much less often than the other methods and only to obtain prey on the substrate surface. The curlews were not observed to obtain any small prey by this method and only a few small, surface-dwelling prey were detected in the pellets. However, the curlews did obtain the mud crab with this technique. When a crab was sighted the curlew ran swiftly toward it. If the crab escaped to a burrow, the curlew often ignored the burrow entrance and probed directly through the mud to capture the crab. The curlews often switched among the 3 feeding methods.

Birds using the burrow-probe method made significantly ($P < .05$) more attempts per minute but were successful less often than birds using the pause-probe method (Table 1). There was no significant difference ($P > 0.05$) between the methods in the number of prey obtained per minute and no apparent difference in the size of the prey taken. In the winter period more attempts were made and more prey obtained per minute ($P < 0.05$) than in the fall (Table 1). However, the number of prey captured per attempt was nearly the same for both seasons ($P > 0.05$).

Although many prey were eaten whole, prey that were particularly large or lively were not. The bird first removed some or all of the legs from such a prey by biting them off or by holding the prey by a leg and shaking it vigorously. The body was eaten first, then the legs. Claws of large male ghost shrimps were sometimes left uneaten. The curlews often washed muddy prey before eating them.

Willets and Ring-billed Gulls (*Larus delawarensis*) sometimes attempted to steal prey from Long-billed Curlews. In 9 attempts during feeding observations Willets were successful twice and in 10 attempts the Ring-billed Gulls successfully usurped a curlew's prey 3 times.

Diet of Long-billed Curlews.—Of the 30 pellets collected during the fall period 97% contained the remains of mud crabs, 77% of ghost shrimps, and 47% of mud shrimps. Of the 370 large invertebrates found in the pellets 59% were mud crabs, 34% ghost shrimps, 6% mud shrimps, and 1% unidentified decapods. In addition to the large prey, in the pellets were also remains from 9 insect pupae, 6 *Gemma gemma*, 3 seeds, 3 *Cryptomya californica*, 1 worm (Nereidae), and 1 *Littorina scutulata*. Fragments from several amphipods (Talitridae) were found in 2 pellets and traces of adult insects in 7 pellets.

From direct observations of 205 prey items observed being taken by curlews during the fall period, 55% were mud crabs, 24% ghost shrimps, 15% mud shrimps, and 7% were unidentified. During the winter period the direct observations on type of prey eaten were similar to those of the fall period: of 134 prey, 63% were mud crabs, 20% ghost shrimps, 7% mud shrimps, and 9% were unidentified. Occasionally during winter censuses on Bolinas Lagoon, but not during feeding observations, we saw Long-billed Curlews catch and eat small fish in submerged areas. No pellets were found during the winter period, perhaps because the curlews spent more time feeding and less time in the roosting areas than in the fall.

Willet

Distribution.—Willets were the most abundant large shorebirds both on Bolinas Lagoon (averaging 560 birds during the fall and 385 in the winter period) and also on the adjacent coast (averaging 58 birds during the fall and 76 in the winter period). On Bolinas Lagoon, at low tide, most Willets fed on the tidal flats; however, as the tide rose, the number of Willets in the salt marsh increased until, at high tide, many Willets were either feeding or roosting there. When high tides and rain coincided during the winter, flooding the intertidal areas, Willets fed in the water-soaked pastures adjacent to the estuary. During all periods Willets often flew

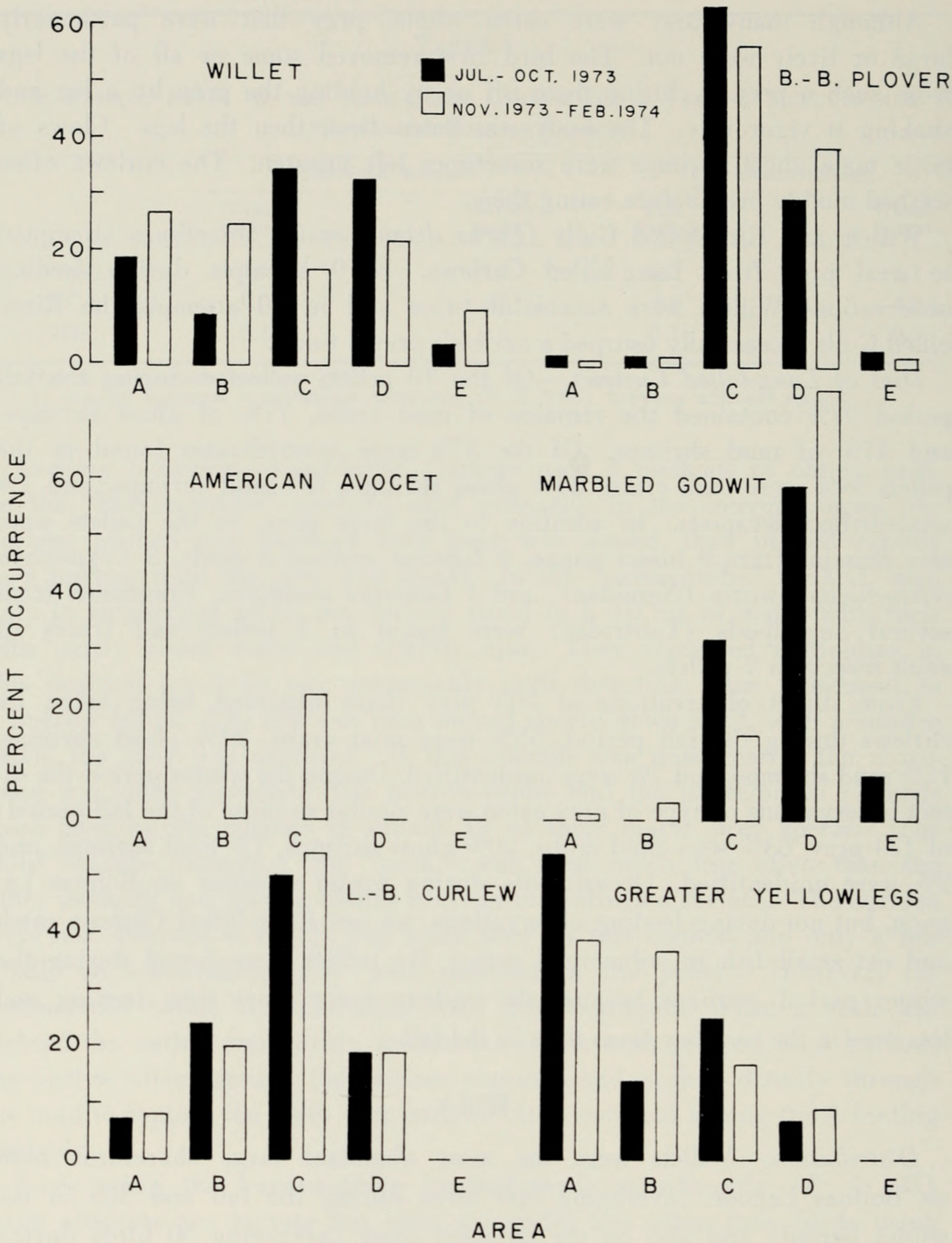

FIG. 2. Distribution of large shorebirds among 5 areas on Bolinas Lagoon. In the calculation of percent occurrence, equal weight was given to each month.

between the estuary and the adjacent coast indicating that both habitats were used by some of the birds.

Willets fed over all of the tidal flat on Bolinas Lagoon and were more equally distributed among the different areas (Fig. 2) and microhabitats

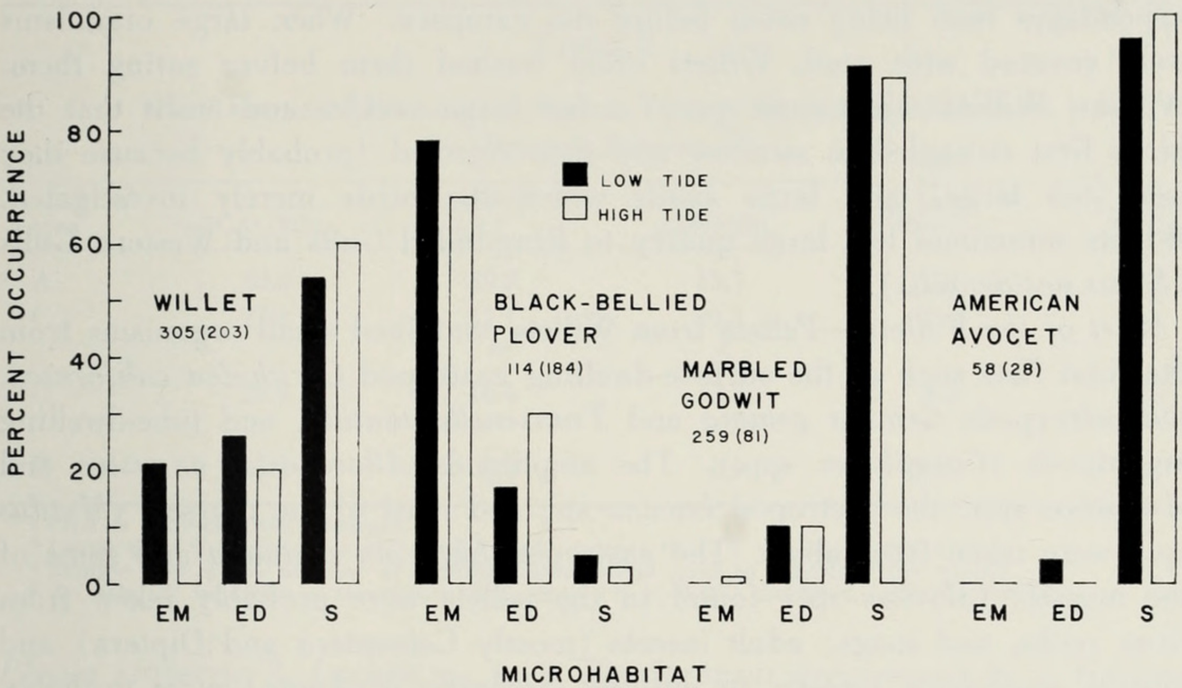

FIG. 3. Distribution of feeding shorebirds in 3 microhabitats on Bolinas Lagoon. EM is emerged; ED, edge; and S, submerged microhabitat. Sample sizes are under the species' names with the high-tide sample sizes in parentheses.

(Fig. 3) than were the other common large shorebirds: Long-billed Curlew, Black-bellied Plover (*Pluvialis squatarola*), American Avocet (*Recurvirostra americana*), Marbled Godwit (*Limosa fedoa*), and Greater Yellowlegs (*Tringa melanoleuca*). When algae, *Enteromorpha* sp. and *Ulva* sp., covered areas of the tidal flat, Willets fed heavily on invertebrates in the algal beds. They were the only large shorebirds that fed extensively in the salt marsh.

Feeding behavior.—Willets most commonly searched visually for prey while walking. Another important search technique was lifting or flipping algae, rocks, debris, or dried, cracked mud with the bill. Less commonly, Willets in water up to their tibio-tarsi ran erratically and pecked in the water. By this method Willets obtained small unidentified prey and occasionally fish.

We distinguished 5 methods of capturing prey used by Willets: peck, multiple peck, probe, multiple probe, and theft from Long-billed Curlews. In all areas studied Willets captured 93% or more of their prey with pecks and multiple pecks.

Capture of small prey was detected indirectly by movements of the head and swallowing motions but capture of large prey was easily seen and large organisms were often identified. Large prey such as fish or pelecypods were swallowed whole; decapods were often shaken apart, the appendages then being eaten before the carapace. When large organisms were covered with mud, Willets often washed them before eating them. We saw Willets reject some prey: a few large cockles and crabs that the birds first struggled to swallow and then rejected (probably because they were too large) and large snails which the birds merely investigated. Willets sometimes lost large quarry to Ring-billed Gulls and Western Gulls (*Larus occidentalis*).

Diet of the Willets.—Pellets from Willets contained small organisms from the tidal flats such as the surface-dwelling gastropod *Cerithidea californica*, the pelecypods *Gemma gemma* and *Transenella tantilla*, and tube-dwelling amphipods (*Corophium* spp.). The amphipods *Allorchestes angustus* and *Ampithoe* spp., the gastropod *Lacuna* sp., and most of the mussels (*Mytilus* sp.) were taken from algae. The gastropod *Littorina scutulata* and some of the mussels (*Mytilus* sp.) found in the pellets were probably taken from tires, rocks, and snags; adult insects (mostly Coleoptera and Diptera) and talitrid amphipods (mostly or entirely *Orchestia traskiana*) were probably taken in the salt marsh. Remains of large prey in the pellets included the pelecypods *Protothaca staminea* and *Macoma* spp., the brachyurans *Hemigrapsus oregonensis* and *Cancer antennarius*, and the anomurans *Callianassa californiensis*, *Upogebia pugettensis*, and *Pagurus* sp. Other prey, occurring infrequently in the pellets, included the polychaetes *Capitella capitata*, *Lumbrineris zonata*, and an unidentified nereid, ostracods, the cheliferan *Leptochelia dubia*, the amphipod *Grandidierella japonica*, the brachyurans *Pachygrapsus crassipes*, *Hemigrapsus nudus*, and *Cancer magister*, larval and pupal dipterans, and the pelecypod *Clinocardium nuttallii*.

We detected additional tidal flat prey from feeding observations. While Willets took only one fish in 164 min of observation in the fall period, they captured 11 during 499.5 min of winter observation, mostly from areas D and E. During the winter period some Willets, feeding in the mid- and high-water zones of area A during rising tides, captured up to 19.7 worms per minute. Since several species of Spionidae constituted 85% of the worms in our samples from area A during the winter period, 1 or more of these were probably the worms that the Willets ate.

Cooper's Hawks (*Accipiter cooperii*), Red-shouldered Hawks (*Buteo lineatus*), and Marsh Hawks (*Circus cyaneus*) often hunted Willets in the salt marsh and sometimes left the entrails and flight feathers of Willets they had eaten there or under the pines on Kent Island. In the 8 stomachs left with such remains we found *Orchestia traskiana* in all, adult Coleoptera in 6, unidentified seeds in 6, *Littorina scutulata* in 4, the small gastropod

TABLE 2

MEAN FEEDING RATES OF THE WILLET DURING WINTER IN 4 AREAS ON BOLINAS LAGOON

Area	PCA[a]/Min.	Prey/PCA (%)	Prey/Min.	% Large Prey[b]	Sample Size[c]
A	30.0	39.2	13.1	2.0	12
C	27.3	31.7	9.1	2.5	14
		*[d]	*		
D	26.3	16.4	3.8	4.3	26
		*	*	*	
E	23.1	8.2	1.8	20.1	15

[a] PCA is prey-capture attempts.
[b] Large prey includes decapods, pelecypods greater than 3 cm long, and fish.
[c] Sample size is the number of feeding observations used to calculate the means.
[d] An asterisk indicates a significant difference ($P < 0.05$) between adjacent means.

Phytia setifer in 3, *Lacuna* sp. in 2, *Hemigrapsus oregonensis* in 2, *Gemma gemma* in 1, and *Mytilus* sp. in 1.

Inter-area variation.—The Willets' feeding success varied among different areas of the tidal flat. Although the number of prey-capture attempts per minute did not differ significantly between any of the areas (for all possible pairs of data, $P > 0.05$), the success rate (prey per prey-capture attempt) differed significantly ($P < 0.05$) between some areas and resulted in different rates of prey intake between areas (Table 2). A trend for the number of prey per minute to decrease from areas A to E may have been partially offset by a tendency for large prey to make up an increasing percentage of the diet from areas A to E (Table 2). Among areas there was also considerable variation among the microhabitats in which Willets fed (Table 3).

As expected, variations among different areas in the abundance of the

TABLE 3

USE OF DIFFERENT MICROHABITATS BY WILLETS DURING WINTER IN 4 AREAS ON BOLINAS LAGOON

Area	Percent of PCA[a]			Sample Size	Percent of Prey Taken			Sample Size
	Em[b]	Ed	S		Em	Ed	S	
A	0.2	55.9	43.9	2273	0.1	68.0	31.9	1025
C	1.0	5.8	93.1	2477	1.6	4.2	94.2	738
D	8.8	15.2	76.0	4731	12.1	19.4	68.5	660
E	38.0	2.9	59.1	2141	49.7	2.5	47.8	157

[a] PCA is prey-capture attempts.
[b] Em is emerged, Ed is edge, and S is submerged.

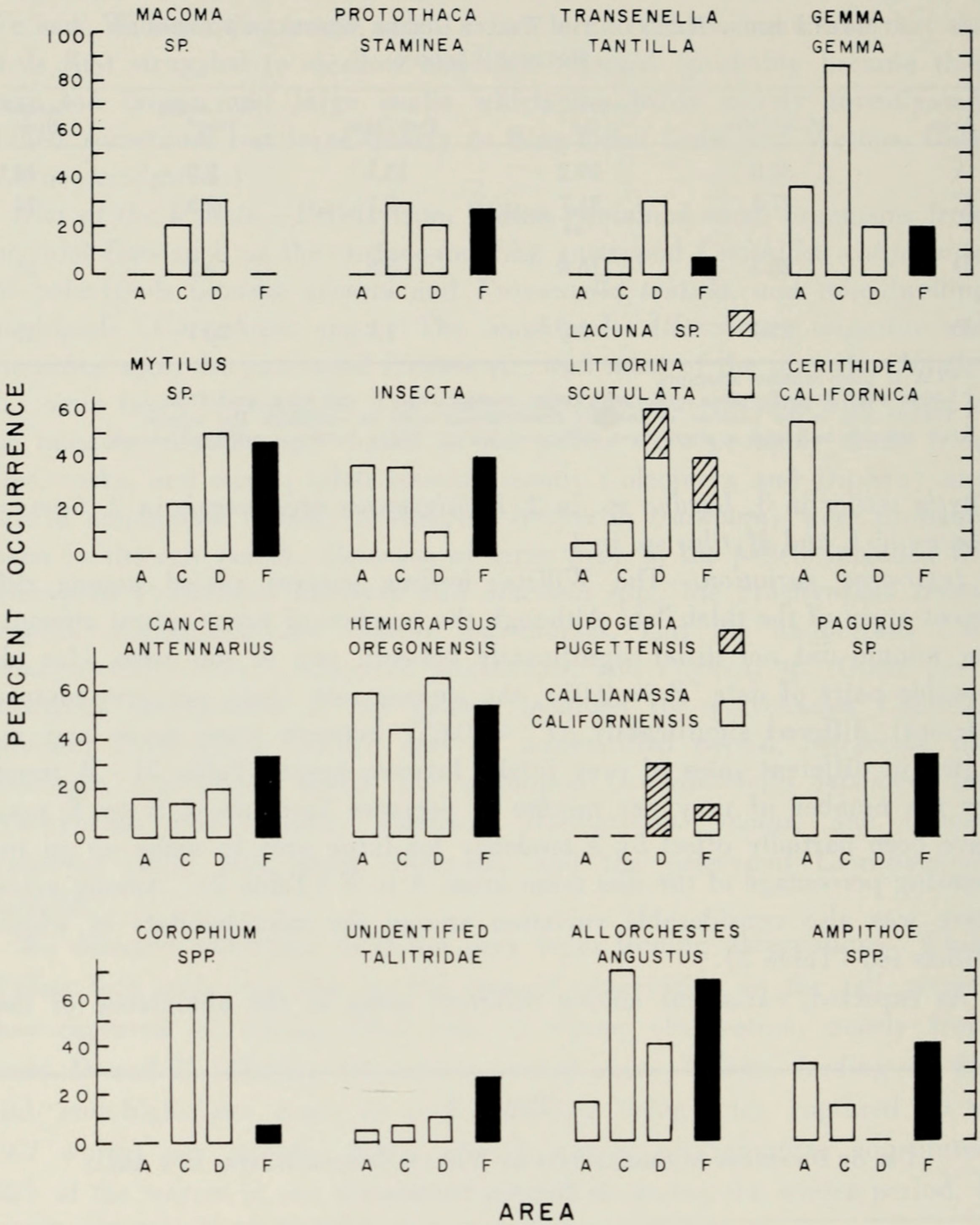

FIG. 4. Percent occurrence of prey in Willet pellets collected from 4 areas of Bolinas Lagoon from July to October 1973. Pellets collected in areas A, C, and D were from birds feeding in or in the vicinity of those areas; pellets from area F were from birds feeding over a large area of the estuary. Sample size for A is 19; C, 14; D, 10; F, 15. Two additional pellets from area E contained a total of 4 *Pagurus* sp., 5 *Pachygrapsus crassipes*, and 3 *Hemigrapsus oregonensis*.

TABLE 4

RELATIVE ABUNDANCE OF SELECTED INVERTEBRATES IN 4 AREAS ON BOLINAS LAGOON IN JUNE 1973

Species	Mean Number per Core in Area[a]			
	A	C	D	E
Cerithidea californica	0.1	0.1	0.0	0.0
Gemma gemma	152.6	28.0	4.6	0.0
Transenella tantilla	0.0	0.1	12.1	0.0
Corophium spp.	21.7	41.0	56.9	45.4
Number of cores	9	9	9	9

[a] Means are from microhabitats with the highest abundance of the organism in each area.

tidal flat invertebrates were sometimes reflected in the pellets. There was an increase in the abundance of *Transenella tantilla* in the substrate (Table 4) and pellets (Fig. 4) from area A to C to D. *Gemma gemma* and *Cerithidea californica* were less abundant in the substrate (Table 4) and pellets (Fig. 4) of area D than areas A and C, and *Corophium* spp. were found only in pellets (Fig. 4) from the areas in which these amphipods occurred most abundantly (Table 4). The relative abundance of prey in pellets from different areas did not always occur in direct proportion to the relative abundance of invertebrates in the substrate. For example, *Gemma gemma*, which occurred most frequently in pellets from area C, occurred most abundantly in the substrate of area A. The abundance of prey in each area, such as *Littorina scutulata* on rocks and snags or *Ampithoe* spp., *Allorchestes angustus*, *Lacuna* sp., and *Mytilus* sp. which occurred primarily on algae, depended on properties that we did not measure. We did not sample for the abundance of the large invertebrates.

Seasonal variation.—There were several environmental changes that affected the availability of prey to the Willets on the tidal flats from the fall to the winter period. The number of daylight hours that were available for feeding on all but the highest portion of the tidal flat decreased from a mean of 10.1 h in the fall to 7.8 h in the winter period. Prolonged rain during the winter period sometimes flooded the estuary for several days and further reduced the number of daylight hours that the tidal flats were available.

There was a decrease in the abundance of some of the Willets' prey from the fall to the winter period. Numbers of substrate-dwelling invertebrates *Gemma gemma* and *Corophium* spp. and alga-dwelling invertebrates *Allorchestes angustus* and *Ampithoe* spp. all declined from the fall to the winter period (Table 5). The decline in alga-dwelling amphipods was probably

TABLE 5

SEASONAL ABUNDANCE OF SOME OF THE WILLETS' PREY ON BOLINAS LAGOON

Species	Location[a]	Mean Number per Core in: Fall Period		Winter Period
Gemma gemma	Area A	152.6	*[b]	14.7
	I.S.P.	4.9	*	2.3
Corophium spp.	I.S.P.	20.1	*	4.0
	Area D	56.9	*	10.6
Transenella tantilla	Area D	12.1		4.9
Allorchestes angustus	I.S.P.	6.1	*	0.1
Ampithoe spp.	I.S.P.	0.2	*	0.0

[a] Data from areas A and D taken from 9 cores from the microhabitat in each area in which each organism occurred most abundantly. Data from the invertebrate study plot (I.S.P.) taken from 56 cores per month during each period.
[b] An asterisk indicates a significant difference ($P < 0.05$) between fall and winter period means.

related to a decline in the extent of the algal beds on the estuary. In July algae (primarily *Enteromorpha* sp.) covered 57% of the invertebrate study plot, in August 41%, in September 20%, in October 3%; from November to February only an insignificant area was covered. *Ulva* sp., another green alga, covered 2.1% of the invertebrate study plot in the fall period and only 0.4% in the winter.

The success of Willets' feeding attempts (prey per prey-capture attempt) decreased ($P < 0.05$) from 70.7% in 22 fall observations to 35.2% in 26 winter observations. In censuses of birds in the different areas the proportion of Willets feeding at any time increased ($P < 0.05$) from a mean of 84.0% of the total birds censused in fall to 92.1% in winter. This was probably due to increased pressure on the birds to use more of the available feeding time in the winter than in the fall period. There were also seasonal changes in the Willets' use of different feeding areas within and near the estuary. During fall 26.1% of 890 Willets censused in areas A, B, C, and D were feeding in algae but during the winter period only 6.7% of 878 birds were feeding in the much depleted algal beds. The number of Willets feeding in the Kent Island salt marsh at low and moderate tides increased ($P < 0.05$) from 5.0% of the estuary's Willets in fall to 17.5% in winter. The number of Willets found on the open coast also increased ($P < 0.05$) from 9.2% of the combined estuary and open coast Willet population in the fall to 17.3% in the winter period. It appears that the decreased availability of the tidal flat and the decline in abundance of some tidal flat invertebrates resulted in increased daytime use of feeding areas other than the tidal flat from the fall to winter period for the Willets. We found Willets feeding

TABLE 6

SEASONAL DIFFERENCES IN WILLETS' PREY FROM PELLETS[a] COLLECTED FROM AREAS C AND F ON BOLINAS LAGOON

Prey of Willet	% of Pellets in which Prey Occurred		
	Fall Period		Winter Period
Pagurus sp.	17	*	0
Gemma gemma	52	*	12
Corophium spp.	31	*	0
Ampithoe spp.	28	*	0
Allorchestes angustus	69	*	6
Mytilus sp.	34	*	6
Cancer antennarius	24		6
Lacuna sp.	10		12
Cerithidea californica	10		12
Littorina scutulata	17		19
Macoma spp.	10		12
Protothaca staminea	28		38
Transenella tantilla	7		12
Callianassa californiensis	3		12
Upogebia pugettensis	3		19
Hemigrapsus oregonensis	48	*	94
adult Insecta	38	*	69
Talitridae[b]	17	*	50
sample size	29		16

[a] Significant seasonal differences ($P < 0.05$, test for equality of 2 percentages) are indicated by an asterisk.
[b] Talitridae are mostly or entirely *Orchestia traskiana*.

on the tidal flats at night during the winter, but during the fall our observations suggest that most Willets leave the estuary at or shortly after dusk. There may be a greater tendency for Willets to feed at night during the winter than during the fall period.

A change in the diet from the fall to the winter period was detected in the pellets (Table 6). *Allorchestes angustus*, *Ampithoe* spp., and *Corophium* spp. were major prey in the fall but nearly absent from the winter pellets. The presence of *Gemma gemma* in the pellets decreased from the fall to the winter period. As already described, our substrate samples also showed a decline in these species during winter (Table 5). *Mytilus* sp. and *Pagurus* sp. decreased from the fall to the winter period in the pellets but we have no information on their seasonal abundance. The increase during the winter period of some amphipods (Talitridae) and insects (mostly Coleoptera) in the pellets is probably a reflection of the increased use of the salt marsh by the Willets during this period.

DISCUSSION

On Bolinas Lagoon the Long-billed Curlew is a hunter of large burrow-dwelling prey and its exotic morphological features are in harmony with this pursuit. Its major prey species live in different habitats but all have curved burrows. Mud shrimps live at low tide levels in U-shaped burrows that extend about 45 cm into the substrate (MacGinitie and MacGinitie 1968). Ghost shrimps live in a higher tidal zone than mud shrimps, in many-branched burrows that extend vertically into the substrate (MacGinitie 1934). Both organisms feed near the entrance of their burrows. Mud crabs live throughout most of the estuary in horizontal burrows or under algae and debris. The curlew is well adapted to obtain these prey as the length of its bill (average 16.5 cm, Dawson 1923) allows it to probe deeply into the substrate and the bill's curve fits nicely into the burrows. Curlews often twist their heads as much as 180°, apparently to follow the curve of a burrow with their bills.

The diet of the Long-billed Curlew on Bolinas Lagoon is not representative of the species in California since in California Long-billed Curlews are more abundant inland than along the coast (Jurek 1973). Curlews that live inland must rely on terrestrial and fresh-water organisms for their food. Such a diet is indicated from the limited information in the literature which gives insects of several families, spiders, berries, crayfish, snails, fiddler crabs, amphipods, and occasionally nestling birds as food of the Long-billed Curlew (Wickersham 1902, McLean 1928, Sugden 1933, Palmer 1967, Timken 1969). Comprehensive studies of curlews feeding in various inland habitats are necessary for a more representative picture of this bird's diet in California.

In contrast to the curlew, the Willet occurs primarily along the coast when not on the breeding grounds (Jurek 1973). At Bolinas Lagoon the Willet was much more opportunistic in obtaining prey than was the Long-billed Curlew. Willet pellets contained at least 30 different prey from a wide variety of habitats but curlew pellets contained primarily 3 burrow-dwelling decapods and only small numbers of other invertebrates. Seasonal changes in the diet were prominent for the Willet but not the Long-billed Curlew. Other people studying shorebirds along the California coast found the Willet eating different organisms than at Bolinas Lagoon. Reeder (1951) found *Hemigrapsus oregonensis* present in 2 and cirratulid worms present in 1 of 2 Willet stomachs collected in May from Orange Co. Recher (1966) collected 16 Willets at one location on San Francisco Bay from September through May and found in decreasing order of abundance in the stomachs *Gemma gemma*, *Ilyanassa obsoleta*, *Nereis succinea*, *Mya arenaria*, *Macoma inconspicua*, *Hemigrapsus oregonensis*, and

TABLE 7

PREY OF WILLETS COLLECTED IN THE SAN FRANCISCO BAY AREA

	Number of Stomachs in which Each Prey Occurred		
		San Francisco Bay	
	San Pablo Bay[a]	Bay Tidal Flats[a]	Leslie Salt Ponds[b]
Annelida	1	6	
Decapoda	1	1	
Isopoda		1	
Ephydra cinerea larva			3
Ephydra cinerea pupa			1
Ephydridae larva		2	
Ephydridae pupa		2	
Ephydridae adult		1	
Corixidae		1	
Insecta		1	
Arachnida	1		
Macoma inconspicua	5	3	
Protothaca semidecussata		1	
Gemma gemma		4	
Mytilus sp.		6	
Pelecypoda		2	1
Ilyanassa obsoleta	3	4	
Gastropoda		4	2
Cottus sp.		4	
Pisces	1		
empty stomachs	3	1	
total number of stomachs	9	11	3

[a] Unpublished data from California Department of Fish and Game.
[b] Data from Anderson 1970.

Volsella demissa. Additional information on the diet of the Willet, collected by the California Department of Fish and Game, is summarized in Table 7. Because the Willet's diet is so varied it is apparent that studies from many coastal habitats are necessary before a representative diet for the Willet on the California coast will be adequately documented.

If we had obtained stomachs instead of pellets in this study it would have been equivalent to removing 75% of the Long-billed Curlews and 21% of the Willets on Bolinas Lagoon during the winter period. Consequently, we needed an alternative to collecting the birds in order to study their diet and an important consideration of the study was to determine the usefulness of feeding observations and pellets to meet this end. The Long-billed Curlews' 3 major prey were easily identified in feeding observations because of their large size and in pellets because of their digestion-resistant claws. The relative frequency with which the 3 prey species were taken by Long-billed Curlews on Bolinas Lagoon could not be measured from feeding observations because the observations were not taken with regard to the distribution of the curlews on the estuary, or from pellets because pellets were collected at high tide and consequently emphasized the prey taken on a rising tide. Most of the Willets' prey were too small to be identified in feeding observations and too broken down in the pellets for us to tally the number of individuals making up the remains. Swanson and Bartonek (1970) for waterfowl and Tuck (1972) for shorebirds reported that wide variation occurs in the digestibility rates of different prey. Considerable variation in the digestibility rates of the Willets' many prey certainly must have occurred and further hindered interpretation of the results. Hartley (1948) has discussed in detail the problems in analyzing stomach contents posed by variation in digestibility rates of different prey. Many of the problems are similar for the analysis of stomach contents and pellets, but our lack of knowledge of the factors causing pellet regurgitation in shorebirds and our inability to collect pellets under all tidal conditions are specific problems related to pellets. Because the shortcomings of analyzing stomach contents and pellets are similar in many ways, we feel that shorebird pellets and stomach contents in many instances can provide comparable information on the birds' diet. Observations of feeding birds can be very useful in extending the information on diet drawn from the examination of pellets or stomach contents.

SUMMARY

Visual observations and regurgitated pellets were used to study the feeding behavior and the diet of the Long-billed Curlew and Willet on Bolinas Lagoon from July 1973 through February 1974. Samples of the invertebrates in the tidal flats were collected at different locations and at different times to obtain information on their spatial and temporal distribution for comparison with the shorebirds' diets. The Long-billed Curlews' major prey were 3 large, burrow-dwelling decapods that the curlews obtained primarily by probing into burrows. No seasonal change was detected in the curlews' diet. Most of the Willets' prey were too small to identify in visual observations and too finely divided in the pellets to permit determination of the number of individual prey in each pellet. Therefore, the percentage of the pellets in which each prey occurred was used to compare the abundance of each prey species in the Willets' diet. The Willets' feeding behavior and diet were much more variable than the curlews'. The Willets' diet and feeding success varied among different areas in the estuary and between a fall and winter period.

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