Wilson Bull, 113(1), 2001, pp. 41-52

DYNAMICS OF HABITAT USE BY SHOREBIRDS IN ESTUARINE AND AGRICULTURAL HABITATS IN NORTHWESTERN CALIFORNIA

LINDA L. LONG[1,3,4] AND C. JOHN RALPH[2]

ABSTRACT.—We examined shorebird use of mudflats, marsh islands, and nearby agricultural fields near Humboldt Bay in northwestern California between September 1988 and April 1989. Most species used fields for both foraging and roosting, including some species usually considered to be mudflat specialists. After seasonal rains began in late fall, Dunlins (*Calidris alpina*), Least Sandpipers (*Calidris minutilla*), Long-billed Curlews (*Numenius americanus*), and Marbled Godwits (*Limosa fedoa*) became opportunists and used fields at intermediate and high tides when mudflats were inundated. Black-bellied Plovers (*Pluvialis squatarola*) and Greater Yellowlegs (*Tringa melanoleuca*) were seasonal generalists during the two wettest seasons, using fields at all tides and mudflats at low and intermediate tides. Western Sandpipers (*Calidris mauri*) were mudflat specialists, and Willets (*Catoptrophorus semipalmatus*) were salt marsh opportunists that mainly used mudflats, but shifted to salt marsh at high tide. Killdeer (*Charadrius vociferus*) and Common Snipe (*Gallinago gallinago*) were field specialists and did not use the other two habitats in significant densities during any season. The presence of short vegetation and the presence or absence of standing water were the two most important characteristics influencing increased use of fields by all species. *Received 5 June 2000, accepted 21 January 2001.*

Many shorebirds migrate and winter along continental coastlines and forage primarily on intertidal habitats (Recher 1966, Bengtson and Svensson 1968, Brennan et al. 1990). In these habitats, high tides periodically force birds off mudflats (Kelly and Cogswell 1979, Burger 1984, Brennan et al. 1985). Shorebirds compensate for this reduced foraging habitat by using other habitats, such as sandy beaches, salt marshes, or freshwater marshes (Burger et al. 1977, Gerstenberg 1979, Warnock and Takekawa 1995). Agricultural fields also have been reported as foraging habitats. In England, Eurasian Curlews (*Numenius arquata*; Townshend 1981) and Common Redshanks (*Tringa totanus;* Goss-Custard 1969) used fields, apparently to increase food intake during severe weather. Some curlews used fields at low as well as high tides. Several investigators in California also have reported shorebirds foraging or roosting in fields at high tides after the advent of winter rains (Page et al. 1979; Gerstenberg 1979; Shuford et al. 1989; Colwell and Dodd 1995, 1997).

[1] Dept. of Wildlife, Humboldt State Univ., Arcata, CA 95521.
[2] U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Dr., Arcata, CA 95521.
[3] Present address: U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Dr., Arcata, CA 95521.
[4] Corresponding author; E-mail: lllong@fs.fed.us

In our study, we (1) compared patterns of shorebird use in habitats at various tides and seasons, (2) analyzed the association of the tidal cycle and habitat type with habitat choice, (3) compared foraging in three habitats at various tides between seasons, and (4) examined the relationships between field characteristics and shorebird use.

METHODS

Study site.—We conducted this study at the north end of Humboldt Bay in Humboldt County, California (40° 53' N, 124° 07' W). Colwell (1994) estimated that the bay, including surrounding fields and nearby coastal beaches, supports 10,000-100,000 shorebirds of 25 species during migration and winter. Historically, Humboldt Bay was surrounded by marshes, but 95% of these were diked and drained for agriculture in the late 1800s and early 1900s (Haynes 1986).

Our study site was part of the Mad River Slough, a tidal estuary of Humboldt Bay. The slough is surrounded by dikes and encompasses several salt marsh islands dominated by cord grass (*Spartina foliosa*), pickleweed (*Salicornia pacifica*), and salt grass (*Distichlis spicata;* Gerstenberg 1979). Most islands normally were inundated by most high tides, but one remained above water during all but the highest tides. At an average low tide, about 15% of the slough was exposed salt marsh, 75% was unvegetated intertidal mudflats, and 10% remained as channels.

The study site also included nearby hay fields, cattle pastures, and croplands; some fields were plowed and planted with grasses or corn. The vegetation was a mixture of velvet grass (*Holcus lanatus*), bent grass (*Agrostis* sp.), Italian rye grass (*Lolium multiflorum*), orchard grass (*Dactylis glomerata*), and clover (*Trifo-*

TABLE 1. Number of shorebird surveys by season, habitat, and tide, Humboldt County, California, 1988-1989. Seasons used for analyses are from Higley (1989).

	Mid-fall 20 Sept-12 Oct	Late fall 13 Oct-3 Dec	Winter 4 Dec-24 Jan	Early spring 25 Jan-17 Mar	Late spring 18 Mar-24 Apr
Mudflat					
Low tide	5	15	13	22	14
Intermediate tide	5	17	18	31	23
High tide	5	15	20	21	11
Field					
Low tide	5	15	13	22	14
Intermediate tide	5	17	18	31	23
High tide	5	15	20	21	11
Salt marsh					
Low tide	0	11	13	22	14
Intermediate tide	0	10	18	31	23
High tide	0	10	20	21	11

lium pratense; Gerstenberg 1979). Rushes (*Juncus patens* and *J. effusus*) invaded wet, older fields. Soils saturated quickly, retained water, and flooded with the winter rains. Our field plots were separated from the slough by dikes, were drained by ditches to the slough, and were not influenced directly by tides.

Data collection.—Shorebirds were surveyed 20 September 1988 to 22 April 1989. Large numbers of shorebirds begin to arrive during early August and are established by late September (Gerstenberg 1979), when our study began. By late April, populations of most species have started to decline (Gerstenberg 1979).

We divided the study area into mudflat, field, and salt marsh plots. Within the slough, we studied four mudflat plots (4.8—11.2 ha), delineated by landmarks on the shore, that were chosen to represent the mudflats of the slough and totaled 29.9 ha. Three salt marsh plots (1.5-2.9 ha), added in late fall, totaled 7.1 ha, and consisted of all the islands of vegetation in the northern part of the slough. Field plots (1.5—6.2 ha) were chosen systematically along nearby roads about 0.5 km apart and delineated by fence lines. The 14 vegetated field plots totaled 47.5 ha. We later added four plowed field plots as they became available when farmers plowed them, for an additional 15.5 ha, making 63.0 ha in 18 field plots. The plowed fields were added within the first few weeks of the study. For purposes of analyses, we grouped plowed and unplowed field plots because they were independent of each other, and reflected the different intensities of grazing and cultivation regimes.

We chose to sample the shorebirds during daylight only, since logistical problems precluded sampling at night when at least some foraging takes place (Pienkowski et al. 1984, Townshend et al. 1984, Dodd and Colwell 1996). For each census day, we took data during the first tidal cycle of the day, which included one adjacent high and low tide. All low tides uncovered at least some portion of the tidal flats, though the area uncovered varied among days. The "low tide" was always the lowest point of the tidal cycle for each census day. Similarly, not all high tides covered the flats to equal proportions (depth or total area covered), but the "high tide" was always the highest point of the cycle for each census day. This sampling regime enabled us to examine the dynamics and choices the birds made between habitats through the first daylight tidal cycle.

We divided the tidal cycle into 2-h periods of low, intermediate, and high tides (Table 1). A "low tide" count either began or ended with the daylight period's tidal minimum, and a "high tide" count included the day's tidal maximum. The period between these two was the "intermediate tide." Two intermediate tides were included on days when the interval between tidal minimum and maximum was greater than seven h. During a 2-h tidal period, we used a 20x spotting scope to count all shorebirds in all 25 plots. Surveys were conducted three days/week.

We attempted to identify all species of shorebirds. Those identified to species were included in the analyses. About 2% of the *Calidris* sandpipers were unidentified, and almost all of those were on mudflat plots (Long 1993). At field plots, we surveyed to the back fence line, or within 300 m of the viewing station, whichever was closer. At salt marsh plots, we counted only those birds that were on the island of vegetation, and not those that were along the edges in the mud. A few birds may have been undercounted in fields and salt marsh habitats because of concealing vegetation, but Colwell and Dodd (1995) found <1% loss of detections from scanning, as opposed to walking through fields. If birds flushed before we finished counting, we estimated total flock size and composition.

After we surveyed each plot, we generated an index of foraging activity by systematically selecting up to 20 birds of each species and recording how many were foraging. Each bird was watched long enough to determine if the bird was foraging. The time was usually less than one min/bird. Focal birds were selected by choosing the first bird on the right side of the field that

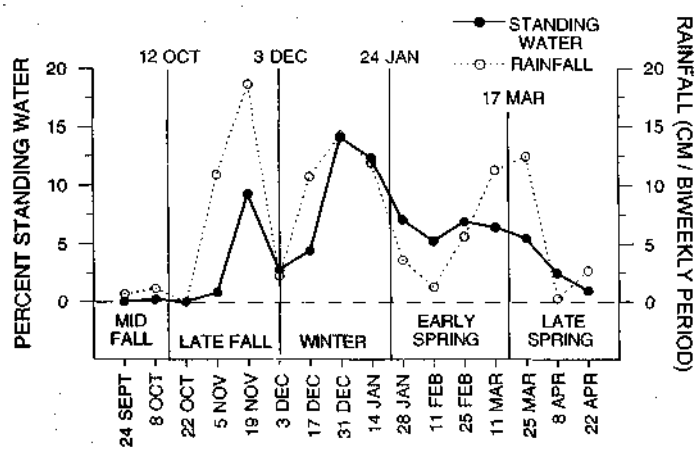

FIG. 1. Rainfall and average percent of field acreage covered by standing water for 2-wk periods during the study, Humboldt County, California, 1988-1989.

was facing right and every fourth bird to the left of that bird thereafter, until a sample of 20 birds had been recorded for each species. If there were ≤80 birds, we returned to the right side of the flock and continued selecting every fourth bird. If there were ≤20 birds, all individuals present were included. The index was expressed as a percentage of birds foraging. If birds flushed before activity was recorded, we estimated percent foraging from our observations during counting.

We estimated vegetation height, percent of plot covered by standing water, and number of cattle in field plots. The area of the fields covered by standing water mirrored rainfall over the study period (Fig. 1). During mid-fall, there was almost no standing water in fields and little rain. During late fall, water increased to an average 9% coverage, which coincided with the largest biweekly rainfall of 19 cm. Coverage of fields by standing water reached a high of 13% in winter, then steadily decreased through most of the rest of the study period, with a slight increase in early spring. Rainfall at a station 4 km to the east of the study area during 1988-1989 was 113.8 cm and the 20-yr average was 121.6 cm (Redwood Sciences Laboratory, unpubl. data).

Data analysis.—We used one of two criteria to choose the 10 species for analysis. We chose seven species that each comprised ≥3% of the 135,326 shorebirds counted in the study: Black-bellied Plover (*Pluvialis squatarola),* Killdeer (*Charadrius vociferus),* Willet (*Catoptrophorus semipalmatus*), Marbled Godwit (*Limosa fedoa*), Western Sandpiper (*Calidris mauri),* Least Sandpiper (*Calidris minutilla*), and Dunlin (*Calidris alpina*). We chose three additional species that were present in ≥20% of the 45 combinations delineated by season, tide, and habitat (5 seasons X 3 tides X 3 habitats): Greater Yellowlegs (*Tringa melanoleuca*), Long-billed Curlew (*Numenius americanus*), and Common Snipe (*Gallinago gallinago*). There were significant numbers of dowitchers (*Limnodromus* spp.) as a group but, because they were difficult to identify to species, neither Short-billed (*L. griseus*) nor Long-billed dowitchers (*L. scolopaceus*) were detected in densities sufficient for our analyses (Long 1993).

To examine the association between tide and habitat use, we tested if density of a species in a given habitat at a given tide for each season (each bar on Fig. 2) was significantly greater than zero. To do this, we divided the study period into five seasons, denned in earlier Humboldt Bay studies by Spitler (1985) and Higley (1989), based on extensive studies of shorebird migratory patterns (Table 1).

We calculated the density (birds/10 ha) for each habitat and 2-h tidal stage by combining the number of birds for all plots in a given habitat during a count. For all analyses based on these data, we reduced variance by using a logarithmic transformation in the form of $\log_{10}(x + 1)$ (Zar 1984).

We then calculated the mean density for each tide, habitat, and season combination. We used a one-tailed Mest (SAS Institute 1985) to determine if mean density in a given tide and habitat combination was significantly ($P < 0.05$) greater than zero.

We examined correlations between the presence of a species and the characteristics of the fields using stepwise logistic regression in BMDP (Dixon et al. 1988, Hosmer and Lemeshow 1989). Each field plot for each survey was classified by the following: grass height above or below the breast height of the species, presence or absence of standing water, and presence or absence of cattle. The coefficients for each characteristic of the regression equation were then used to compute the odds ratio, i.e., the probability ("odds") that a field with that characteristic was used by a species. For example, if the coefficient for W (standing water) was 0.77 for Killdeer, the odds ratio would be $e^{0.77}$ or 2.17, i.e., the probability was 2.17 to 1 that Killdeer would use a field with standing water rather than without. We used the χ^2 goodness-of-fit test to determine significance of the equation (Norman and Streiner 1986), and the Wald statistic (the coefficient divided

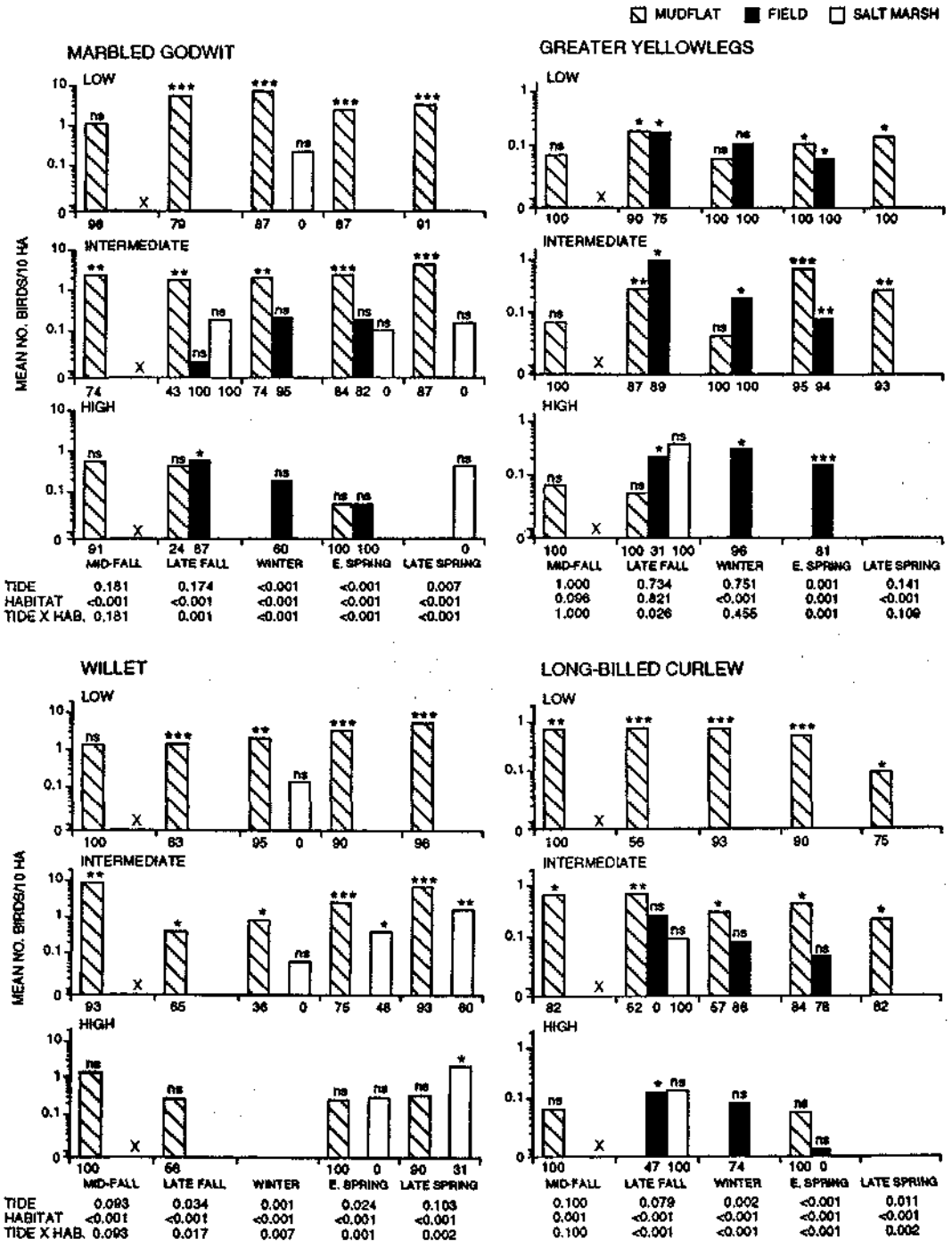

FIG. 2. Mean densities of shorebirds per count per 10 ha for three tides and five seasons, occurring on mudflats, fields, and salt marsh, Humboldt County, California, 1988-1989. A significant *t*-test indicates the species was present in a habitat at densities greater than 0: ns = not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, An "X" indicates no surveys were conducted in the habitat for the season. Numbers below each vertical bar indicate the overall percentage of birds foraging. The results of ANOVA for the associations between tide and habitat with habitat choice by season are shown at the bottom of each graph, including the *P*-value for each factor.

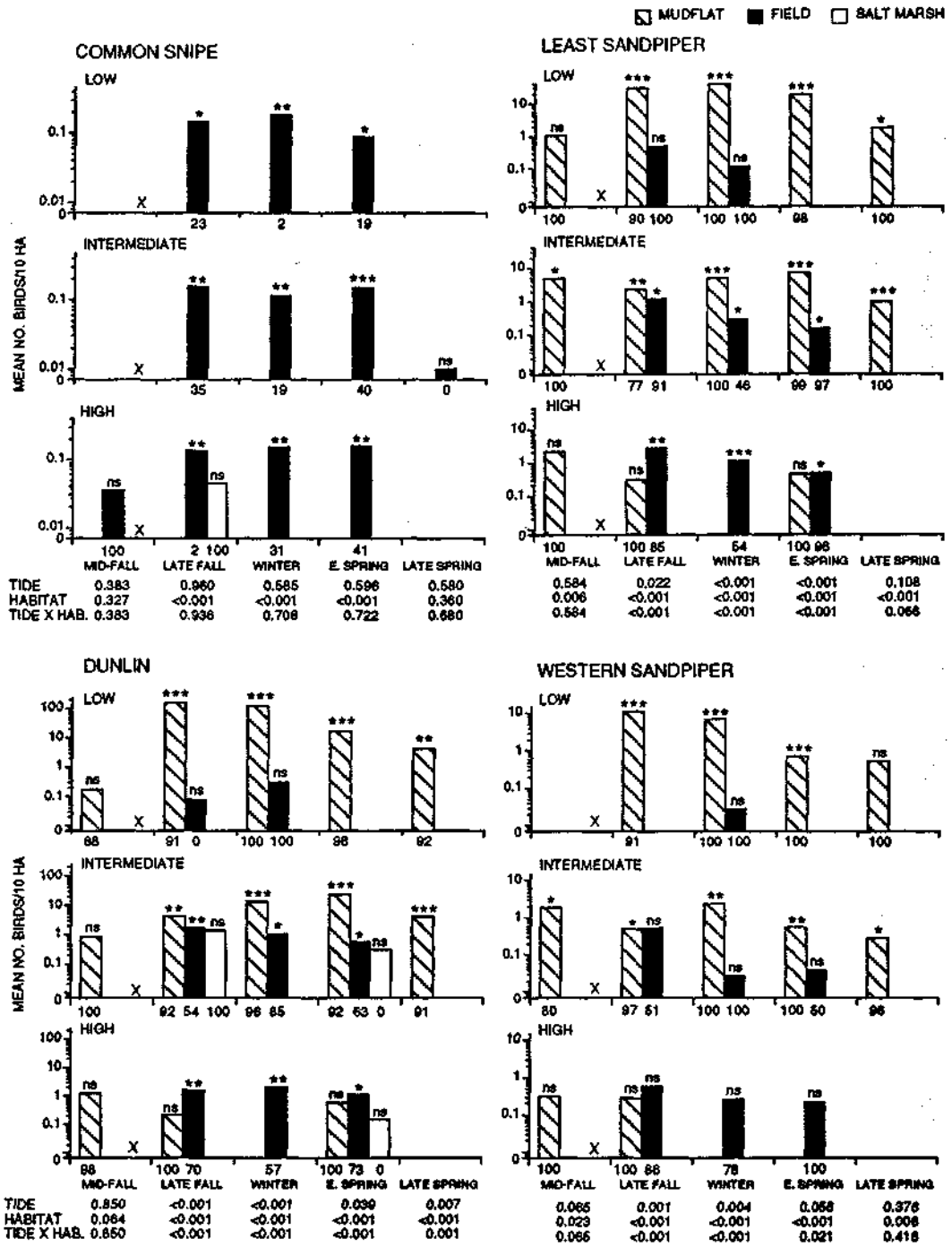

FIG. 2. Continued.

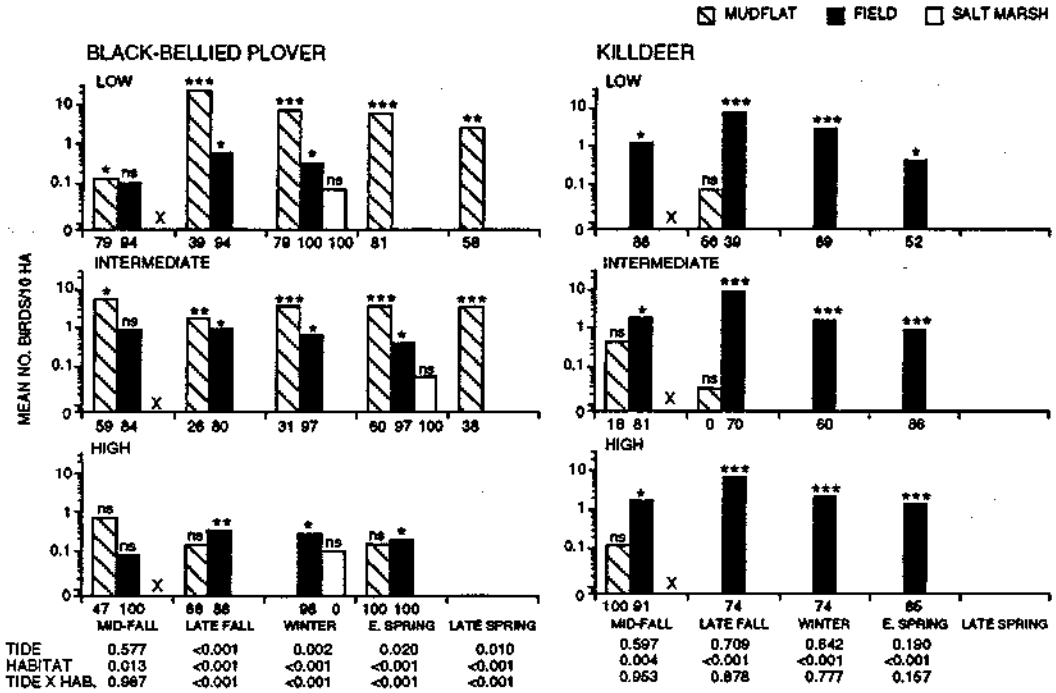

FIG. 2. Continued.

by the standard error of the coefficient) to determine significance of the coefficients (Hosmer and Lemeshow 1989).

To look further at the association between water in the fields and habitat use, we calculated the correlation coefficient between bird density and percent of fields covered with standing water for each species that occurred in significant densities in fields for each season and tide. For each count, we calculated the total percent of area covered by standing water on all field plots combined.

RESULTS

Partitioning of habitats and tidal relationships.—Except for two species (Common Snipe and Killdeer), shorebirds were mudflat animals, occurring there in highest densities (Fig. 2). However, species differed in behavior related to habitats and tidal cycles. We found five patterns in the use of these three habitats between seasons. For purposes of discussion, we summarize these as field specialist, mudflat specialist, field opportunist, salt marsh opportunist, and seasonal generalist.

"Field specialists" occurred in significant densities in fields and were largely absent from mudflats and salt marshes; Common Snipe and Killdeer were field specialists (Fig. 2). For both, their density was related only to habitat, in this case fields, and not to tide during any season (ANOVA, $P \leq 0.05$).

"Mudflat specialists" occurred in significant densities primarily on mudflats, and were not present in significant densities in fields and salt marshes. Western Sandpipers were the only mudflat specialists, and their density was related to habitat (mudflats) during all seasons (Fig. 2). Unlike the field specialists, density was also related to tide and the interaction of tide and habitat, because mudflats are a tidally-influenced habitat, but fields are not.

"Field opportunists" were present in significant densities on mudflats at intermediate and low tides and in fields at intermediate or high tides during at least one season. They did not use salt marshes in significant densities. Four species were field opportunists: Least Sandpiper, Dunlin, Marbled Godwit, and Long-billed Curlew (Fig. 2). Because these species moved between habitats with the tidal cycle, density for all four was generally associated with tide as well as the interaction between tide and habitat during most seasons.

Least Sandpipers and Dunlins were opportunists during three of five seasons. Marbled Godwits and Long-billed Curlews were opportunists only during the late fall.

Willets, the only "salt marsh opportunists," were usually present on mudflats in significant densities during all seasons at low and intermediate tides (Fig. 2). They shifted to salt marshes to roost and forage as mudflats were flooded, rather than to fields, at intermediate tides during early and late spring, and at high tides during late spring. Density was related to habitat during all seasons. Beginning in late fall, density was also related to tide and/or the interaction between tide and habitat.

"Seasonal generalists" were generalists only during certain seasons. As with most other species, they were present in significant densities on mudflats at low and intermediate tides during most seasons. However, during at least one season they were generalists, present in significant densities in fields at all tides. They were also opportunists in fields during some seasons; they occurred in significant densities in fields mainly as mudflats were inundated at intermediate and high tides and they were absent from salt marshes. Two species were seasonal generalists: Greater Yellowlegs and Black-bellied Plover (Fig. 2). Yellowlegs were generalists during late fall and early spring. During winter, they were field specialists except at low tide, but during late spring they were mudflat specialists except at high tide. Density was most often related to habitat alone. During early spring, density was also related to tide and the interaction between tide and habitat, but during late fall it was only related to the interaction between tide and habitat. Black-bellied Plovers were generalists during late fall and winter except at high tide and opportunists during early spring. They were mudflat specialists during late spring except at high tide. During all seasons, density was associated with tide, and for most seasons, they were associated with habitat and the interaction between tide and habitat.

Use of habitats for foraging.—We found that more than half of the individuals of all species that occurred in significant densities in fields and mudflats were foraging rather than roosting, with the exception of Common Snipe. Killdeer and Common Snipe, as field specialists, foraged in fields (Fig. 2). Between 50 and 100% of Killdeer foraged at most tides. In contrast, 0-40% of snipe foraged.

Dunlins, Least Sandpipers, Long-billed Curlews, and Marbled Godwits, all field opportunists, foraged on both mudflats and fields (Fig. 2). While on mudflats, >75% of the birds foraged. When they switched to fields, about 50-100% of the birds foraged during most tides and seasons.

Both of the seasonal generalists, Greater Yellowlegs and Black-bellied Plovers, foraged on the fields during all tides (Fig. 2), with >75% of the individuals foraging. However, they differed from each other on the mudflats. There, 25-80% of plovers foraged, indicating that sometimes more than half were roosting, while >80% of yellowlegs foraged on the mudflats.

Willets, salt marsh opportunists (Fig. 2), did not use fields, but 30-60% of the birds using salt marsh were foraging. On mudflats, 30-100% of the birds foraged.

Western Sandpipers, mudflat specialists (Fig. 2), foraged mainly on mudflats, with nearly 100% of the individuals foraging during any given time period.

Even where a species was not significantly present, some individuals of a species would use a habitat for foraging. For example, Western Sandpipers were so variable and in low numbers that they did not occur in significant densities in fields (Fig. 2), but more than half of those few individuals were foraging.

Field characteristics and use of fields.—Vegetation height was associated with field use for most species (Table 2). Three of the species used fields with short vegetation: Killdeer, Common Snipe, and Least Sandpiper. No species used fields with tall vegetation. A second factor, the presence of cattle, would likely decrease the height of the vegetation, and Black-bellied Plovers and Killdeer used fields with cattle more often than fields without.

Presence or absence of standing water alone was also an important variable for three species. It was the only variable associated with field use of the Greater Yellowlegs, which used fields with water. Least Sandpipers also used fields with standing water. Common Snipe used fields without standing water.

Killdeer were most strongly associated with the interactions between cattle and vegetation

TABLE 2. Characteristics influencing the presence of shorebird species in fields, Humboldt County, California, 1988-1989. Listed are the overall significance (Model *P)* of the multiple regression logistic model, the coefficients with their significance (coeff. *P),* and the odds ratio". Field characteristics are listed in the order they entered the equation. There were no significant models for Dunlin, Long-billed Curlew, and Marbled Godwit.

Characteristic	Model *P*	Coefficient	Coeff. *P*	Odds ratio	Interpretation: Birds used fields with
Killdeer	0.86				
Vegetation height		-0.37	<0.001	0.69	Short vegetation
Standing water		-0.02	>0.500	1.02	No standing water
Cattle		0.45	<0.001	1.57	Cattle
Cattle * vegetation height		0.58	<0.001	1.79	Cattle and short vegetation
Cattle * standing water		0.35	<0.001	1.42	Cattle and standing water
Common Snipe	0.96				
Vegetation height		-0.66	<0.05	0.52	Short vegetation
Standing water		-0.23	<0.001	0.79	No standing water
Least Sandpiper	0.90				
Standing water		0.84	<0.001	2.30	Standing water
Vegetation height		-0.52	<0.001	0.60	Short vegetation
Black-bellied Plover	1.00				
Cattle	1.29	<0.001		2.44	Cattle
Vegetation height		-0.27	<0.100	0.76	Short vegetation
Cattle * vegetation height		0.65	<0.001	1.91	Cattle and short vegetation
Greater Yellow-legs	0.99				
Standing water		1.29	<0.001	3.63	Standing water

[a] The odds ratio was calculated by taking the natural anti-logarithm of the coefficent. The odds ratio describes the odds (compared to even odds of 1: 1) that a field with that characteristic was used by that species. See text for further details.

or standing water. A field with cattle and short vegetation had a higher chance of being used than a field with either variable alone. Killdeer also used fields with standing water when cattle were present, while the presence of water alone had no significant effect. Black-bellied Plovers used fields with cattle and short vegetation.

Although Dunlins, Marbled Godwits, and Long-billed Curlews used fields, we found that vegetation height, presence of standing water, and presence of cattle were not significantly associated with their use of fields.

Amount of standing water and field use.—We examined the association of a single variable, the proportion of field covered by standing water, with the density of birds in fields (Table 3). The proportion of the field covered was used to standardize variability in field size. During mid-fall, Killdeer were the main species present in fields, and showed a trend (though not significant) of increased densities with increasing standing water. During late fall, the density of most species in fields increased with an increase in standing water. Only Killdeer decreased as standing water increased during this season. During winter, all species decreased with increasing standing water, with the exception of Greater Yellowlegs. During early spring, no species significantly responded to standing water.

DISCUSSION

Partitioning of habitats by shorebirds and use for foraging.—Shorebirds moved with the tidal cycle in discernable patterns that changed between seasons and resulted in the partitioning of resources among species in this complex of mudflats, salt marshes, and fields. This partitioning may be the result of differences in available food resources between habitats, since most birds foraged.

The question of when a species becomes a habitat generalist, opportunist, or specialist may depend on the overlap of food habits with other species and the abundances of preferred food resources (Recher 1990, Col well and Landrum 1993). A generalist would be able to avoid some competitors on the crowded mudflats by taking advantage of less-used food resources in the fields at low tides during some seasons, though prey in fields may be less preferred. Habitat opportunists, which also moved between habitats with the tidal cycle,

TABLE 3. Relationship between the density (log_{10}) of shorebirds and the percent coverage of standing

Species	Mid-fall	Late fall	Winter	Early spring
Field specialists				
Killdeer	49.71	-4.43**	-8.06***	0.03
Common Snipe	—	0.05	-2.96***	-1.54
Field opportunists				
Dunlin	—	15.43***	-6.96**	-0.56
Least Sandpiper	—	8.61*	-2.27	7.01
Long-billed Curlew	—	2.12	—	—
Marbled Godwit	—	7.09*	—	—
Seasonal generalists				
Black-bellied Plover	—	5.91**	-4.75***	-2.03
Greater Yellowlegs	—	2.37	3.45***	1.78

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, species did not use the fields.

would also be able to exploit food resources in more than one habitat. However, unlike seasonal generalists, opportunists remained on the mudflats, their preferred habitat, until they were unavailable, and were thus able to forage on possibly preferred prey items. Habitat specialists may be able to forage more efficiently in their preferred habitats, and so would use this as exclusively as possible.

Partitioning might also reflect different foraging strategies, which could influence how well birds can exploit different habitats (Baker and Baker 1973, Colwell and Landram 1993). Some species, such as Dunlins and Least Sandpipers, used different foraging strategies for different habitats (Long 1993).

Nocturnal foraging, which we did not investigate, could also play an important role by allowing birds to forage longer in preferred habitats. Dugan (1981) found intake by Black-bellied Plovers during nocturnal foraging on estuarine mudflats in England may equal daylight foraging because of the increased activity of larger prey during the night. Both Dunlins and Black-bellied Plovers have been shown to forage at night on mudlfats during the winter (Pienkowski et al. 1984, Townshend et al. 1984). Robert et al. (1989) found that Least and Western sandpipers foraged more often at night on a tidal lagoon in Venezuela, while yellowlegs and Willets foraged as often during the night as during the day. In contrast to the above studies, Robert et al. (1989) found Black-bellied Plovers did not forage at night as often as during the day.

Patterns of field use.—Field specialists (Killdeer and Common Snipe) and seasonal generalists (Black-bellied Plovers and Greater Yellowlegs) regularly used fields for foraging at high tides but also at low tides when mudflats were available during some seasons. Most other shorebird studies have surveyed fields at mainly high tides (Colwell and Dodd 1995, 1997; Kelly and Cogswell 1979; Page et al. 1979; Butler 1999). Gerstenberg (1979) did preliminary surveys at low tides, but felt that the highest use of fields was at high tide, and subsequently conducted the majority of his surveys then. Rottenborn (1996) found that although Killdeer and Common Snipe used fields in Virginia consistently at all tides, Black-bellied Plovers used them mainly at high tides.

Field opportunists (Dunlins, Least Sandpipers, Long-billed Curlews, and Marbled Godwits) foraged in fields, but mainly when mudflats were not available. Rottenborn (1996) also found that Dunlins and Least Sandpipers used plowed fields opportunistically. Other researchers also found these species in fields at high tides (Stenzel et al. 1976, Kelly and Cogswell 1979, Gerstenberg 1979, Colwell and Dodd 1995, Butler 1999).

Although important, agricultural fields were not used as much as mudflats by most species. Mudflat specialists (Western Sandpipers) and salt marsh opportunists (Willets) did not use them at all. Salt marshes were also used less frequently by most species; only Willets used marshes in significant densities. Fields and

mudflats have nearly equal areas around the north end of Humboldt Bay, 1820 and 1860 ha respectively (Monroe 1973). Thus, the denities we found may reflect the relative proportions of the birds using these two habitats. However, we did not rind similar densities of individuals at low tide and high tide surveys, so we cannot infer that our study area was a closed system. For example, Western Sandpipers were consistently absent in our study area at high tide, and other species, such as Dunlins, were absent during only some seasons. Some birds probably moved at high tides to other areas or habitats that we did not survey, such as the mudflats and salt marsh islands of Humboldt Bay, or to the nearby sand beaches (Gerstenberg 1979, Colwell and Sundeen 2000).

Field characteristics and use of fields.—Rain appeared to be one of the main factors associated with shorebird field use. No species, which otherwise depended on mudflats, used fields until the advent of the fall rains, and then all but two species used fields as opportunists or generalists. Rain and temperature may influence the food availability by driving mudflat invertebrates deeper into the substrate or, conversely, increasing the activity of animals such as earthworms on the surface of fields (Townshend 1981). Colwell and Dodd (1997) found Dunlin and Black-bellied Plovers more likely to use fields when it was raining. Warnock et al. (1995) found that the number of Dunlins at coastal sites was negatively correlated with local rainfall, and that radio-tagged and marked Dunlins moved inland after heavy rains.

Standing water increased as the study progressed and its relationship to species use was mixed. When included with other field variables (cattle and vegetation height), two species showed a positive relationship to standing water, one showed a negative relationship, while the others showed none. However, when we examined this relationship by season, we found Dunlins and Black-bellied Plovers used fields with standing water during the late fall, but switched to fields without standing water during the winter. Least Sandpipers and Marbled Godwits also used fields with standing water during late fall, but showed no significant relationship during the winter. This may explain the overall lack of relationship with standing water for three of these species. In central California, Elphick and Oring (1998) found that Black-bellied Plovers, Killdeer, Dunlins, Least Sandpipers, and Greater Yellowlegs, but not Long-billed Curlews, used flooded rice fields in preference to unflooded rice fields.

Many species used fields with short vegetation, generally maintained by grazing cattle. In two studies, Colwell and Dodd (1995, 1997) found Dunlins, Marbled Godwits, Black-bellied Plovers, Killdeer, dowitchers, and Common Snipe used fields with short vegetation. Marbled Godwits, Black-bellied Plovers, and Killdeer, however, did not show preference for vegetation height in both analyses. Dunlin did not show a relationship with vegetation height in our study, in contrast to Colwell and Dodd's studies. Rottenborn (1996) also found most shorebirds foraged in fields with short (<10 cm) or no vegetation. Short vegetation may allow birds to better see predators, especially raptors (Colwell and Dodd 1995).

Importance of the habitat mosaic.—Myers et al. (1979) felt that shorebirds exploiting several habitats are dependant upon the mosaic as a whole, rather than on any individual part. The increased complexity of the landscape allows shorebirds to exploit higher quality food patches and at the same time minimize the energetic costs of searching for food (Farmer and Parent 1998). In the Humboldt Bay area, the current mosaic, which includes pastures, salt marsh, and mudflats, is a recent development (Haynes 1986). The fields may have replaced freshwater marshes that bordered the salt marsh, but with the addition of cattle which keep the vegetation short, fields may even attract additional numbers of shorebirds that the bay could not support in the past. However, the fields could not replace the value of the salt marshes entirely, since some species (such as the Willet) forage in salt marshes, and others use marshes for roosts (White and Harris 1966, Gerstenberg 1979, Kelly and Cogswell 1979).

Future studies should examine more closely the portion of the shorebird population that uses alternative habitats, not only at high tides when mudflats are inundated, but through the entire tidal cycle and at night. Our study showed that shorebirds will sort themselves

into discernable patterns by habitats, tidal regimes, and seasons. Other researchers have found that shorebird distribution between habitats can change between years (Smith and Connors 1993), so more years of similar studies in this area might find that the patterns we found change between years. Studies should also address the food resources and shorebird diets in these varied habitats, as well as predation pressures. The extent of each habitat in a complex would likely influence choice of habitat, and should be examined in multiple estuarine complexes. Studies should also examine the extent of nocturnal foraging in all habitats and tides. All these factors must be taken into account when attempting to quantify the ecology of shorebird species in such a varied ecosystem.

ACKNOWLEDGMENTS

We thank S. L. Miller for helping with data collection. J. Bart, M. A. Colwell, S. W. Harris, R. Hurley, W. D. Koenig, J. S. Marks, T. A. Matsumoto, L. W. Oring, C. P. Ralph, L. E. Stenzel, S. Vigallon, N. Warnock, and five anonymous reviewers made helpful comments and gave advice on the manuscript. G. Alien and R. Cooper helped with the statistical analyses; L. E. Stenzel and H. F. Recher helped in various stages; and A. Rutherford provided the rainfall data from Redwood Sciences Laboratory. We also thank S. L. and W. D. Long for their financial support.

LITERATURE CITED

BAKER, M. C. AND A. E. M. BAKER. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecol. Monog. 43:193-212.

BENGTSON, S. AND B. SVENSSON. 1968. Feeding habits of *Calidris alpina* E. and *C. minuta* Eeisl. (Aves) in relation to the distribution of marine shore invertebrates. Oikos 19:152-157.

BRENNAN, L. A., J. B. BUCHANAN, S. G. HERMAN, AND T. M. JOHNSON. 1985. Interhabitat movements of wintering Dunlins in western Washington. Murrelet 66:11-16.

BRENNAN, L. A., M. A. FINGER, J. B. BUCHANAN, C. T. SCHICK, AND S. G. HERMAN. 1990. Stomach contents of Dunlins collected in western Washington. Northwestern Natur. 71:99-102.

BURGER, J. 1984. Abiotic factors affecting migrant shorebirds. Pp. 1—72 *in* Behavior of marine animals, current perspectives in research. Vol. 6 (J. Burger and B. E. Olla, Eds.). Plenum Press, New York.

BURGER, J., M. A. HOWE, D. C. HAHN, AND J. CHASE. 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. Auk 94:743-758.

BUTLER, R. W. 1999. Winter abundance and distribution of shorebirds and songbirds on farmlands on the Fraser River Delta, British Columbia, 1989-1991. Can. Field-Nat. 113:390-395.

COLWELL, M. A. 1994. Shorebirds of Humboldt Bay, California: abundance estimates and conservation implications. West. Birds 25:137-145.

COLWELL, M. A. AND S. L. DODD. 1995. Waterbird communities and habitat relationships in coastal pastures of northern California. Conserv. Biol. 9: 827-834.

COLWELL, M. A. AND S. L. DODD. 1997. Environmental and habitat correlates of pasture use by nonbreeding shorebirds. Condor 94:337-344.

COLWELL, M. A. AND S. L. LANDRUM. 1993. Nonrandom shorebird distribution and fine-scale variation in prey abundance. Condor 95:94-103.

COLWELL, M. A. AND K. D. SUNDEEN. 2000. Shorebird distributions on ocean beaches of northern California. J. Field Ornith. 71:1-15.

DIXON, W. J., M. B. BROWN, C. ENGELMAN, M. A. HILL, AND R. I. JENNRICH. 1988. BMDP statistical software manual. Univ. California Press, Berkeley.

DODD, S. E. AND M. A. COLWELL. 1996. Seasonal variation in diurnal and nocturnal distributions of non-breeding shorebirds at North Humboldt Bay, California. Condor 98:196-207.

DUGAN, P. J. 1981. The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. Pp. 251—260 *in* Feeding and survival strategies of estuarine organisms (N. V. Jones and W. J. Wolff, Eds.). Plenum Press, New York.

ELPHICK, C. S. AND L. W. ORING. 1998. Water management of Californian rice fields for waterbirds. J. Appl. Ecology 35:95-108.

FARMER, A. H. AND A. H. PARENT. 1998. Effects of the landscape on shorebird movements at spring migration stopovers. Condor 99:698-707.

GERSTENBERG, R. H. 1979. Habitat utilization by wintering and migrating shorebirds on Humboldt Bay, California. Stud. Avian Biol. 2:33-40.

GOSS-CUSTARD, J. D. 1969. The winter feeding ecology of the Redshank (*Tringa totanus*). Ibis 111:338-356.

HAYNES, C. S. 1986. The Arcata Bottoms: flooding on a changing landscape. M.A. thesis, Humboldt State Univ., Arcata, California.

HIGLEY, J. M. 1989. Waterbird and raptor use of the Arcata Marsh and Wildlife Sanctuary, Humboldt County, California, 1984-1986. M.Sc. thesis, Humboldt State Univ., Arcata, California.

HOSMER, D. W, JR. AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley & Sons, New York.

KELLY, P. R. AND H. L. COGSWELL. 1979. Movements and habitat use by wintering populations of Willets and Marbled Godwits. Stud. Avian Biol. 2: 69-82.

LONG, E. E. 1993. The daytime use of agricultural fields by migrating and wintering shorebirds in

Humboldt County, California. M.S. thesis, Humboldt State Univ., Arcata, California.

MONROE, G. 1973. The natural resources of Humboldt Bay, California. California Fish and Game Coastal Wetland Series No. 6., Sacramento, California.

MYERS, J. P., P. G. CONNORS, AND F. A. PITELKA. 1979. Territoriality in non-breeding shorebirds. Stud. Avian Biol. 2:231-246.

NORMAN, G. R. AND D. L. STREINER. 1986. PDQ statistics. B. C. Decker, Philadelphia.

PAGE, G. W, L. E. STENZEL, AND C. M. WOLFE. 1979. Aspects of the occurrence of shorebirds on a central California estuary. Stud. Avian Biol. 2:15-32.

PIENKOWSKI, M. W., P. N. FERNS, N. C. DAVIDSON, AND D. H. WORRALL. 1984. Pp. 29-56 *in* Coastal waders and wildfowl in winter (P. R. Evans, J. D. Goss-Custard, and W. G. Hale, Eds.). Cambridge Univ. Press, Cambridge, United Kingdom.

RECHER, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393-407.

RECHER, H. F. 1990. Specialist or generalist: avian response to spatial and temporal changes in resources. Stud. Avian Biol. 13:333-336.

ROBERT, M., R. MCNEIL, AND A. LEDUC. 1989. Conditions and significance of night feeding in shorebirds and other water birds in a tropical lagoon. Auk 106:94-101.

ROTTENBORN, S. C. 1996. The use of coastal agricultural fields in Virginia as foraging habitat by shorebirds. Wilson Bull. 108:783-796.

SAS INSTITUTE. 1985. SAS user's guide, statistics, version 5. SAS Institute, Inc., Gary, North Carolina.

SHUFORD, W. D., G. W. PAGE, J. G. EVANS, AND L. E. STENZEL. 1989. Seasonal abundance of waterbirds at Point Reyes: a coastal California perspective. West. Birds 20:137-265.

SMITH, K. G. AND P. G. CONNORS. 1993. Post breeding habitat selection by shorebirds, water birds, and land birds at Barrow, Alaska: a multivariate analysis. Can. J. Zool. 71:1629-1638.

SPITLER, J. R. 1985. Avian use of newly created wetlands: Arcata, California—April 1980 to April 1981. M.Sc. thesis, Humboldt State Univ., Arcata, California.

STENZEL, L. E., H. R. HUBER, AND G. W. PAGE. 1976. Feeding behavior and diet of the Long-billed Curlew and Willet. Wilson Bull. 88:314-332.

TOWNSHEND, D. J. 1981. The importance of field feeding to the survival of wintering male and female Curlews *Numenius arquata* on the Tees Estuary. Pp. 261—273 *in* Feeding and survival strategies of estuarine organisms (N. V. Jones and W. J. Wolff, Eds.). Plenum Press, New York.

TOWNSHEND, D. J., P. J. DUGAN, AND M. W. PIENKOWSKI. 1984. The unsociable plover—use of intertidal areas by Grey Plovers. Pp. 140-159 *in* Coastal waders and wildfowl in winter (P. R. Evans, J. D. Goss-Custard, and W. G. Hale, Eds.). Cambridge Univ. Press, Cambridge, United Kingdom.

WARNOCK, N., G. W. PAGE, AND L. E. STENZEL. 1995. Non-migratory movements of Dunlins on their California wintering grounds. Wilson Bull. 107: 131-139.

WARNOCK, S. E. AND J. Y. TAKEKAWA. 1995. Habitat preferences of wintering shorebirds in a temporally changing environment: Western Sandpipers in the San Francisco Bay estuary. Auk 112:920-931.

WHITE, M. AND S. W. HARRIS. 1966. Winter occurrence, foods, and habitat use of snipe in northwestern California. J. Wildl. Manage. 30:23-34.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.