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STATUS AND HABITAT USE BY AMERICAN AVOCETS WINTERING AT HUMBOLDT BAY, CALIFORNIA[1]

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Abstract. The wintering avocet (*Recurvirostra americana*) population at Humboldt Bay, California averaged 706 ± 35.6 (n = 30) and 567 ± 67.0 (n = 30) birds from October to May, 1982–1983 and 1983–1984 respectively. Avocets arrived from late-August to mid-November. Birds departed from February to late-April and early-May. Avocets are recorded only casually at other northern California coastal sites.

After construction of sewage oxidation ponds at the northeast corner of North Humboldt Bay in 1957, the number of avocets wintering at Humboldt Bay increased. The present wintering population of avocets at Humboldt Bay has increased from 30–35 in 1960 to 500–800 at present. Humboldt Bay probably has the capability to support a larger wintering population than presently exists.

Avocets used 868 ha in the northeast corner of North Humboldt Bay, California. Within this area, which covered approximately 25% of available habitat in North Bay, the four major habitats used were: (1) intertidal mud flats, used mainly for feeding and resting; (2) a sewage oxidation pond, used mainly for feeding and secondarily, as a source of fresh water; (3) a section of the North Bay's highest elevation mud flats, used as an early high tide roost; and (4) islands in a brackish 6.9 ha lake adjacent to the North Bay, used as the primary high tide roost.

Avocets typically roosted on shallow, submerged bars of islands in deep non-tidal ponds or in shallow water or exposed mud near the water's edge of tidal mud flats. Islands adjacent to deep, non-tidal ponds were used most frequently as roosting sites.

Avocets fed at the oxidation ponds mainly in October when high concentrations of invertebrate prey, especially *Daphne magna*, were present. All other foraging took place on intertidal mud flats within 3 km of roosts. Avocets primarily fed using tactile methods in the wettest substrates. They usually fed within 100 m of the tide edge, and most foraging took place when tide levels were between 0.5 and 1.2 m Mean Lower Low Water (MLLW).

Key words: Activity budgets; American Avocet; California; habitat use; historical status; Humboldt Bay; intertidal mud flats; Recurvirostra americana; *wintering biology.*

INTRODUCTION

The American Avocet (*Recurvirostra americana*) breeds in western United States and southern Canada and winters from southwestern United States to Guatemala (American Ornithologists' Union 1983). Humboldt Bay, California is the most northerly known wintering site for this species (American Ornithologists' Union 1983). Since the late 1950s, wintering American Avocets, formerly rare in northwestern California (Davis 1939, Grinnell and Miller 1944) have increased at Humboldt Bay, California (Yocom and Harris 1975, Evans 1988, Harris 1991). Although the behavior (Hamilton 1975) and breeding ecology (Gibson 1971) of avocets has been studied, relatively little is known about their wintering behavior and use of wintering habitats. Knowledge of how avocets use resources for maintenance, survival, and reproduction at northernmost portion of their wintering range could have implications for the management of this species.

STUDY AREA AND METHODS

Humboldt Bay consists of two large shallow tidal basins, North (Arcata) Bay and South Bay, connected by a narrow passage. Humboldt Bay has two high and two low tides of unequal height each day, exposing variable amounts of intertidal mud flats daily and seasonally (Gerstenberg 1979). The highest and lowest tidal levels encountered during this study were 2.9 m feet and −0.5 m Mean Lower Low Water (MLLW), respectively. Detailed behavioral studies were conducted on the intertidal mudflats near the Arcata

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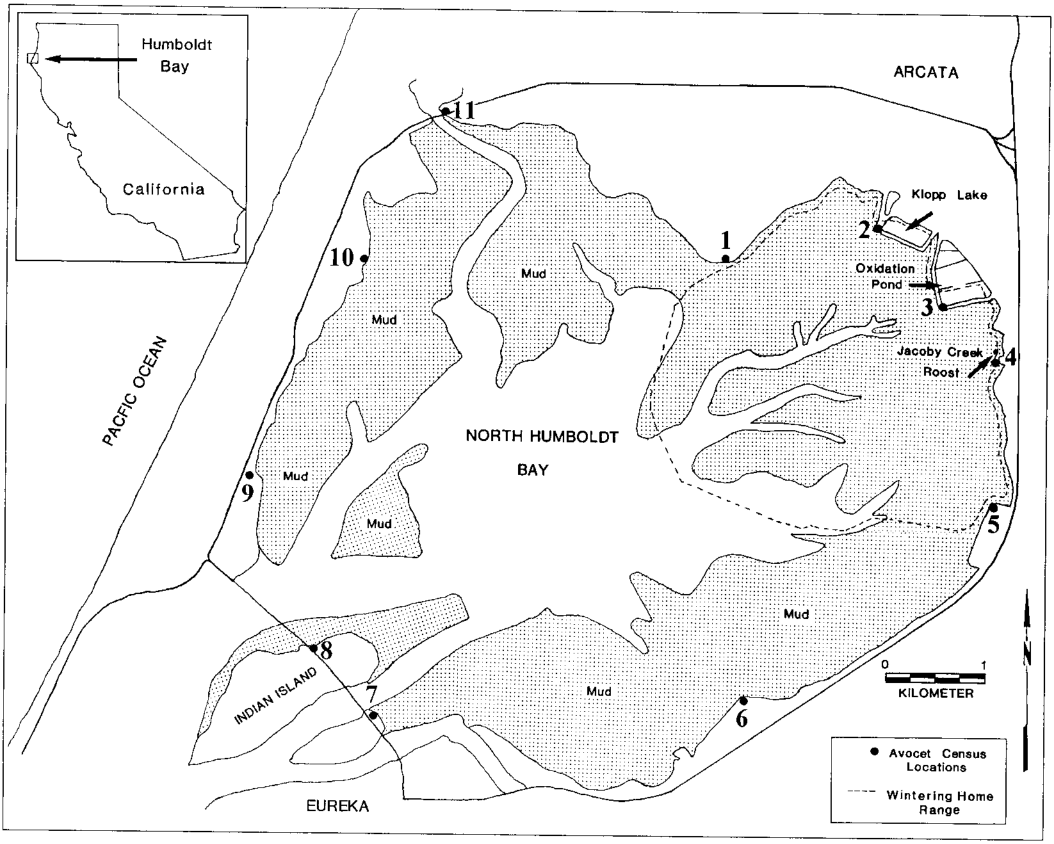

FIGURE 1. Study area, wintering home range and census locations of American Avocets in North Humboldt Bay, California.

Marsh Project and Jacoby Creek delta, the southernmost oxidation ponds of the Arcata Public Works sewage treatment facility, and the Klopp Lake Unit of Arcata Marsh Project (Fig. 1, Evans 1988).

The study was conducted 1 October 1982–15 May 1983, 3 October 1983–8 May 1984, and 19 December 1984–29 April 1985. A wintering population estimate was not calculated for 1984–1985 because population counts were not made prior to 19 December 1984. All data were gathered by direct observations using a 25× spotting scope and 9 × 36 binoculars. Counts of avocets were made during 76 weekly surveys at both high and low tide from 11 stations around North Bay (Fig. 1) and on 42 bimonthly surveys from eight stations around South Bay. The location of avocets was marked on maps of the study area. Low tide counts were begun after falling tides had exposed 30–50% of the tidal mud flat. High tide counts were begun one hour before the predicted time of highest water (NOAA 1982–1984).

A compensating polar planimeter and a dot grid with 64 dots to a square inch was used to determine the total hectares in the study areas on United States Geologic Survey 7.5 topographic map (Arcata-South, California). We used survey data plotted on maps from the weekly (North Bay) and bimonthly (South Bay) surveys and a modified version of the modified minimum area method (Harvey and Barbour 1965) to plot the "wintering home range" of the wintering avocet population in Humboldt Bay. Since avocets were never observed in upland sites, upland sites were excluded and the outermost avocet sightings adjacent to the upland areas were connected when drawing the "modified home range" boundary near the shoreline.

Daytime behavioral observations, activity budgets, and habitat use by avocets were deter-

FIGURE 2. Maximum number of American Avocets observed weekly in North Humboldt Bay, California, winters 1982–1985.

mined by scan sampling (Altmann 1974) on seven study sites on the intertidal mudflats and adjacent brackish and sewage ponds. The behavioral categories used were described by Hamilton (1975) and included resting, feeding, preening, comfort movements, alert, swimming, walking, and flying. A total of 197 hr of behavioral observations were made between 1 October 1982 and 12 January 1983 and 970 hr between 3 October 1983 and 3 May 1984. The duration of scans was determined by the time needed to record all birds present on the initial scan. The interval between scans was equal to the scan length. An average of 250–350 birds was scanned during scans of 5 min or less (>96% of all scans = 6,638), taken between 06:00 and 17:00 hr on 292 days of field work. When scanning large flocks, up to 750 birds, it was difficult to keep track of the movements of every bird and on occasions some individuals or small groups were counted more than once. Longer scans were therefore considered less reliable. Consequently, only scans 5 min or less were used in the analysis. Scans were taken during all daylight hours and at all tide stages. For analysis the time of day was divided into five 3-hr periods, or three 5-hr periods, starting at 05:00 hr. On any one day, behavioral observations were conducted on the study site with the largest number of birds. This usually yielded a study population of about 280 birds. The flock was repeatedly scanned until observer fatigue set in, or more than 50% of the birds initially present had left the area. Observation sessions averaged 4 hr long (range 10 min–5 hr). General observations were made on the intertidal mudflats on 32 dark nights (cloudy nights or nights with a new moon) and on 25 bright nights (clear nights with three-fourths to a full moon) during moderate to low tide heights to subjectively determine if avocets fed at night. Four to six nights each month were chosen to record the occurrence of nocturnal foraging.

Avocets use both visual and tactile feeding methods while feeding in the water column or on exposed mudflats (Hamilton 1975). Visual feeding methods were classified as pecking, plunging, snatching, and bill pursuit and tactile feeding methods included filtering, scraping, and single and multiple scythe (Hamilton 1975).

Detailed descriptions of study sites, methodology, definitions of behavior, weather, and tides encountered during the study may be found in Evans (1988).

STATISTICAL ANALYSIS

We examined differences in avocet numbers exhibiting behaviors among habitats and tide heights using a Kruskal-Wallis one-way analysis of variance (ANOVA) ($P < 0.05$). When analysis demonstrated significant differences, we identified the differences using Dunn's distribution free, multiple comparison procedure (Zar 1984). Because of potential Type I errors (i.e., behaviors were correlated with each other) all multiple comparisons were made at a significance level of 0.003 to 0.0008 as suggested by Bonferroni (Bray and Maxwell 1986). Significance levels were adjusted by the Bonferroni method so that the probability of a Type 1 error was at most 5% for each group of comparisons. Alpha values for each comparison between a behavior (i.e., resting) and an environmental variable (i.e., tide height) using Dunn's distribution free, multiple comparison test are indicated in the text as follows (i.e., alpha = 0.0003).

The proportion of the flock engaged in an activity was analyzed using a normal approximation test for comparing more than two proportions followed by a Tukey-type multiple comparison test (Zar 1984). When the proportion of the flock engaged in a particular activity was tested against independent variables, significant ($P < 0.05$) differences occurred even when the differences between the proportions of the flock were only one percent. These differences were related to large sample sizes resulting in extremely high chi-square values. Therefore, in interpreting the results with respect to proportion of the flock, biological relevancy, as well as statistical significance, was given consideration. Non-parametric statistical programs from SPSS (Nie et al. 1975, Hull and Nie 1981) and BMDP (Dixon and Brown 1979) were used for data analysis.

Flight directions were analyzed using parametric measures (Zar 1984) and circular statistics (Batschelet 1981). For analysis of flight direction, heading of avocets leaving the roost were classified in eight directions: north (23°–338°), northeast (24°–68°), east (69°–113°), southeast (114°–158°), south (159°–203°), southwest (204°–248°), west (249°–293°), and northwest (294°–338°).

RESULTS

POPULATION SIZES

The earliest fall migrant American Avocets arrived at Humboldt Bay in August in 1982 and 1983 (Harris 1991). By 1 October the population had reached about 200 birds in 1982 and 511 birds in 1983. Between late October and early February overall population numbers remained fairly constant (Fig. 2). The November–March population averaged 706.4 (SD = 35.6) birds in 1982–1983 and 566.8 (SD = 67.0) birds in 1983–1984. Peak counts of 827, 667, 736 occurred on 27 November 1982, 22 January 1984, and 22 January 1985, respectively. Weekly fluctuations of up to 200 birds sometimes occurred especially in October 1983 and January 1985. Numbers declined steadily between February and late April. All birds were gone by 29 April 1985 and 8 May 1984, but 57 were still present on 15 May 1983, when the last population survey was made.

WINTERING HOME RANGE

Nearly all avocets present used a "wintering home range" of 868 ha, comprising only 23.6% of North Bay (Fig. 1) as determined by changing the modified minimum area method (Harvey and Barbour 1965). Although the concept of home range usually has been applied to individuals we use the term "wintering home range" to describe the area used by the avocet population wintering at Humboldt Bay, California.

Within the northeastern portion of North Bay avocets used four major habitats: (1) intertidal mudflats, used mainly for foraging; (2) the Arcata sewage oxidation pond, used as a feeding area in October each year; (3) a high elevation intertidal mudflat near the mouth of Jacoby Creek, used as an early high tide roost; and (4) islands in the Klopp Lake Unit of the Arcata Marsh and Wildlife Sanctuary, used as the primary high tide roost (Fig 1). During the weekly and bimonthly censuses in North Bay and South Bay, respectively, no avocets were ever seen on South Bay and none were recorded from census locations 6 through 11 (Fig. 1) located on the southeast, south, west, and north margins of North Bay (Table 1). There are only a few scattered records of avocets for the north coast away from North Humboldt Bay (Evans 1988, Harris 1991). Avocets were encountered outside the "wintering home range" only 30 times in 1,142 hours of behavioral ob-

TABLE 1. Average number of American Avocets recorded each month per census in North Humboldt Bay, California. Winters 1982–1985. *N*—number of surveys; HT—high tide; LT—low tide.

Survey station	October (n = 10) HT	October (n = 10) LT	November (n = 8) HT	November (n = 8) LT	December (n = 9) HT	December (n = 9) LT	January (n = 12) HT	January (n = 12) LT	February (n = 9) HT	February (n = 9) LT	March (n = 11) HT	March (n = 11) LT	April (n = 12) HT	April (n = 12) LT	May (n = 5) HT	May (n = 5) LT
1) McDaniel Mudflat	0.0	107.9	0.0	106.4	0.0	243.1	0.0	30.9	0.0	240.5	0.0	143.5	0.0	77.3	0.0	41.8
2) Klopp Lake	477.0	0.0	630.0	0.0	629.1	0.0	666.8	0.0	540.6	0.0	297.9	0.0	119.6	9.1	52.8	0.0
3) Oxidation Pond	0.0	173.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4) Jacoby Creek	0.0	112.5	0.0	157.8	0.0	159.7	0.0	128.4	0.0	98.2	0.0	22.3	0.0	23.9	0.0	10.4
5) Bracut	0.0	58.6	0.0	286.8	0.0	178.6	0.0	312.9	0.0	194.9	0.0	142.8	0.0	0.0	0.0	0.0
6) Survey stations	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	477.0	559.9	630.0	551.0	629.1	581.4	666.8	472.2	540.6	534.0	279.9	308.6	119.6	110.3	52.8	52.2

servation, between October 1982 and April 1985, and always in groups of fewer than 52 birds. None of the 30 encounters occurred on weekly or bimonthly censuses and 26 of the 30 encounters involved birds on the intertidal mudflats along the eastern shoreline of North Bay immediately south of the "wintering home range."

GENERAL HABITAT USE AND BEHAVIOR

The general activity pattern was one of foraging on intertidal mudflats at low tide and resting at Klopp Lake at high tide. Temporary or seasonal variations to this general pattern involved early high tide roosting at Jacoby Creek, some October foraging at the Arcata sewage oxidation pond, and brief periods of resting on intertidal mudflats during moderate and low tides.

HIGH TIDE ACTIVITIES

Roosting. On incoming tides, avocets typically congregated along the water's edge on the high elevation mudflats north of Jacoby Creek (Fig. 1). Even though these were the highest elevation mudflats in the North Bay, they became flooded by most high tides and avocets remained at the Jacoby Creek roost throughout the tide cycle only twice in 292 days of observation. When flooded out at Jacoby Creek they flew to the three islands in Klopp Lake 1.35 km away.

About two thirds of all birds scanned at the high tide roost were resting (Table 2). Secondary activities at the roost sites were flying, alert behavior, and preening (Klopp Lake) and flying, preening, and feeding (Jacoby Creek) (Table 2). When the tide level was between 1.5 to 2.3+ m MLLW, 87.3% of the scanned birds were recorded as resting. At lower tides significantly fewer birds rested and significantly more birds engaged in other activities (alpha = 0.0003) (Evans 1988).

Avocets generally stood in shallow (2–13 cm) water at roosts. At Jacoby Creek, roosting birds were about evenly distributed between exposed mudflats with visible standing water, flooded mudflats with water just covering their feet, and mudflats with water depths up to their abdomens (Fig. 3). As tides approached high water, avocets consistently roosted on high elevation mudflats until the water levels forced them to move to islands in Klopp Lake. The islands in Klopp Lake ranged from 0.0012 to 0.0017 ha, were unvegetated, and bordered by a bar submerged under 2–13 cm of water. At Klopp Lake, avocets typ-

TABLE 2. Mean number of avocets per scan and percent of total birds engaged in various behaviors as measured by scan sampling in Humboldt Bay, California. Winters 1982–1983, 1983–1984. N = number of scans.

Habitat	Behaviors: Rest	Preen	Comfort movements	Alert	Swim	Wall	Feed	Fly	Total birds
Mainly roosting sites									
Klopp Lake (n = 1,860)									
$\bar{x}$ no. birds	265.4	27.8	2.5	38.2	27.8	0.71	1.5	47.3	411.2
(±SD)	(±22.5)	(±4.4)	(±0.31)	(±6.7)	(±4.6)	(±0.09)	(±0.04)	(±8.6)	
% Total	64.5	6.8	0.60	9.3	6.8	0.17	0.36	11.5	
Jacoby Creek (n = 96)									
$\bar{x}$ no. birds	209.8	16.8	2.4	12.2	5.3	3.8	13.5	39.2	303.0
(±SD)	(±36.2)	(±3.8)	(±0.52)	(±3.8)	(±0.14)	(±0.18)	(±3.0)	(±8.6)	
% Total	69.2	5.5	0.79	4.0	1.8	1.3	4.5	12.9	
Mainly feeding areas									
Oxidation ponds (n = 854)									
$\bar{x}$ no. birds	2.6	0.08	0.04	1.4	71.7	0.08	327.3	16.5	419.7
(±SD)	(±0.36)	(±0.01)	(±<0.01)	(±0.25)	(±12.9)	(±<0.01)	(±29.5)	(±2.7)	
% Total	0.6	0.02	0.01	0.33	17.1	0.02	78.0	4.0	
Intertidal mudflats (n = 3,828)									
$\bar{x}$ no. birds	57.4	12.9	1.0	12.0	1.2	2.6	171.5	23.0	281.6
(±SD)	(±14.9)	(±2.6)	(±0.21)	(±2.5)	(±0.23)	(±0.62)	(±18.2)	(±5.7)	
% Total	20.4	4.6	0.35	4.3	0.43	0.92	61.0	8.2	
Kruskal-Wallis H-value	468.15	17.27	2.75	5.01	62.60	16.76	52.69	17.92	
(test significance)	(<0.01)	(0.001)	(0.431)	(0.171)	(<0.01)	(0.001)	(<0.01)	(<0.01)	

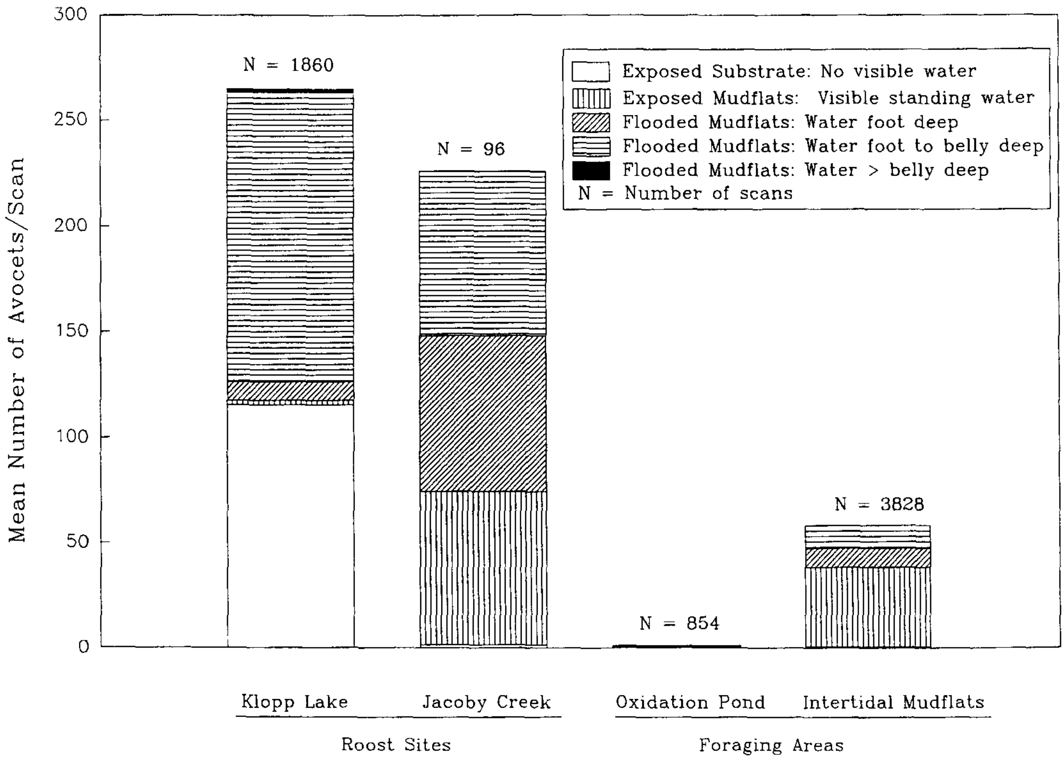

FIGURE 3. Mean number of avocets per scan resting relative to water depth. Humboldt Bay, California. Winters 1982–1983, 1983–1984. N = number of scans.

ically rested on exposed mud at the water's edge (43%) or on the submerged bars with water nearly up to their abdomens (51%). The area encompassed by the submerged bar was limited by the abrupt nature of the island contours and caused some avocets to rest on the higher areas. Often, wave action forced roosting avocets to move to higher ground. Large numbers of Marbled Godwits (*Limosa fedoa*), Black-bellied Plovers (*Pluvialis squatarola*), Least (*Caladris minutilla*) and Western (*Caladris mauri*) Sandpipers, Dunlins (*Erolia alpina*), and Willets (*Catoptrophorus semipalmatus*) also used the higher, dryer, center portions of the islands as roosts.

Foraging. The only intense foraging activity observed during high tides, above 1.5 m MLLW, occurred at the sewage oxidation ponds. Overall, 78% of all birds scanned at the oxidation ponds were foraging (Table 2). Avocets used the oxidation ponds only in October and early November 1982 and 1983. Dense flocks of up to 360 birds swam over concentrations of invertebrate prey, probably *Daphne magna*, where they fed intensively using single and multiple scythe techniques (Hamilton 1975) (784 observations) or pecking prey from the water (37 observations). Feeding bouts lasted 2–43 min ($\bar{x}$ = 8.2 min).

Even though water levels of the oxidation pond were independent of tide level, and theoretically avocets could have fed there at any time, the pattern of use there remained basically unchanged from the general tidal pattern. They roosted elsewhere during the highest tides and only moved to foraging areas, including the oxidation ponds, as the tide began to ebb. Although the intertidal mudflats first become available for foraging at tidal levels between 1.2 and 1.5 m MLLW, avocets often began to feed at the oxidation ponds when the tidal levels were still high, between 1.8 and 2.0 m MLLW. Most avocets left the oxidation ponds and moved to the intertidal mudflats when the tide dropped below 1.2 m MLLW. Although this was the general foraging pattern, avocets occasionally fed almost exclusively at the oxidation ponds even when tide levels were optimum for foraging on the intertidal mudflats.

LOW TIDE ACTIVITIES

Avocets typical left the Klopp Lake roost when the tide was between 1.2 and 1.5 m MLLW. Avocets departing Klopp Lake flew south (mean angle of departure = 178° ± 6.0°) to foraging areas more often than in any other direction ($\chi^2 = 837.33$, df = 7, $P < 0.001$). On the few occasions when avocets departed in other directions, they avoided flying over upland areas.

The pattern of avocet distribution in the study area was described only in qualitative terms. Flocks were described as either compact or loosely-knit (Goss-Custard 1969). More than 95% of all avocets foraged in loosely knit groups on the intertidal mudflats. Occasionally large compact groups fed along the tidal edge or in water deeper than an avocet's abdomen. Although most birds followed the ebb tide edge out into North Bay, a few birds always remained on higher exposed mudflats containing visible surface water.

Sixty-one percent of birds on mudflats were foraging (Table 2) with peak periods occurring when the tide levels were 0.5 and 1.2 m MLLW (mean of peak periods = 69.6%). At tide heights greater than 1.4 m few birds fed and at heights lower than 0.5 m, they remained on mudflats and alternated periods of feeding with periods of resting, preening, and comfort movements. Birds feeding at tides below 0.5 m MLLW usually concentrated along the edges of tidal channels.

Birds resting on mudflats at low tide levels used exposed sites adjacent to tidal channels. Significantly more avocets ($\bar{x}$ = 84.1%) rested on mudflats within 100 m of water, in channels or at the tidal edge, than on mudflats at distances greater than 100 m from water ($\chi^2 = 5.02$, df = 1, $P < 0.05$). An average of 84.1% of all birds resting on the mudflats were within 100 m of water in the channels or at the tidal edge ($\chi^2 = 5.02$, df = 1, $P < 0.05$). These avocets typically rested in loose flocks of two to 75 birds; however, the overall number of avocets resting on intertidal mudflats was relatively low compared to the numbers feeding (Table 2).

Avocets foraging on the intertidal mudflats mostly waded in water covering their feet (43%), in water up to belly deep (34%), or walked on mudflats with visible surface water (22%). When avocets occurred in areas with water covering their feet, water up to belly deep, and on mudflats with visible surface water, 71%, 64% and 49% of the flock were observed feeding, respectively (Fig. 4). Overall, tactile feeding methods were used much more frequently than visual feeding methods ($\chi^2 = 18.26$, df = 1, $P < 0.001$). Single scythe was the primary feeding method used when using tactile methods ($\bar{x}$ = 89.6% of birds scanned). When avocets fed visually, pecking was the primary visual feeding method used ($\bar{x}$ = 93.1% of birds scanned).

After dark, no avocets were found feeding in October (two dark nights, two bright nights) or April (four dark nights, two bright nights) but an average of 172 American Avocets was seen feeding per night on dark nights (28 counts) and 217 on bright nights (19 counts) between November and March.

The proportion of avocets foraging showed no significant diurnal differences, when comparing different times of day during flood or ebb tides.

DISCUSSION

POPULATION TRENDS

The first record of an American Avocet in Humboldt Bay was on 17 August 1935 (Davis 1939). Anderson (1943–1947) recorded one bird in North Humboldt Bay on 27 November 1943. C. I. Clay, an active collector at Humboldt Bay between 1909 and 1982, first recorded an avocet on 26 January 1944. Between 1943 and March 1961 there were only 15 sightings of avocets (ranging from one to 75 birds) at Humboldt Bay (Clay 1901–1953, Anderson 1943–1947, Harris 1991). After the city of Arcata created a 22-ha sewage oxidation pond at the northeast corner of Humboldt Bay in 1957, wintering avocet numbers increased from 30 to 40 in the early 1960's to 250 in 1970 (Gerstenberg 1972), and from 400 to 500 in 1979 (Harris 1991) to 827 on 27 November 1982 (Fig. 2).

The population at Humboldt Bay begins to arrive in August (Harris 1991). Most of the wintering population was present by November (Fig. 2). This appears to be somewhat earlier than farther south in coastal California. At Bolinas Lagoon between 1971 and 1976, avocets increased in numbers from November (150 birds) to January (578 birds, Page et al. 1979). At south San Francisco Bay, avocets began to arrive in Oc-

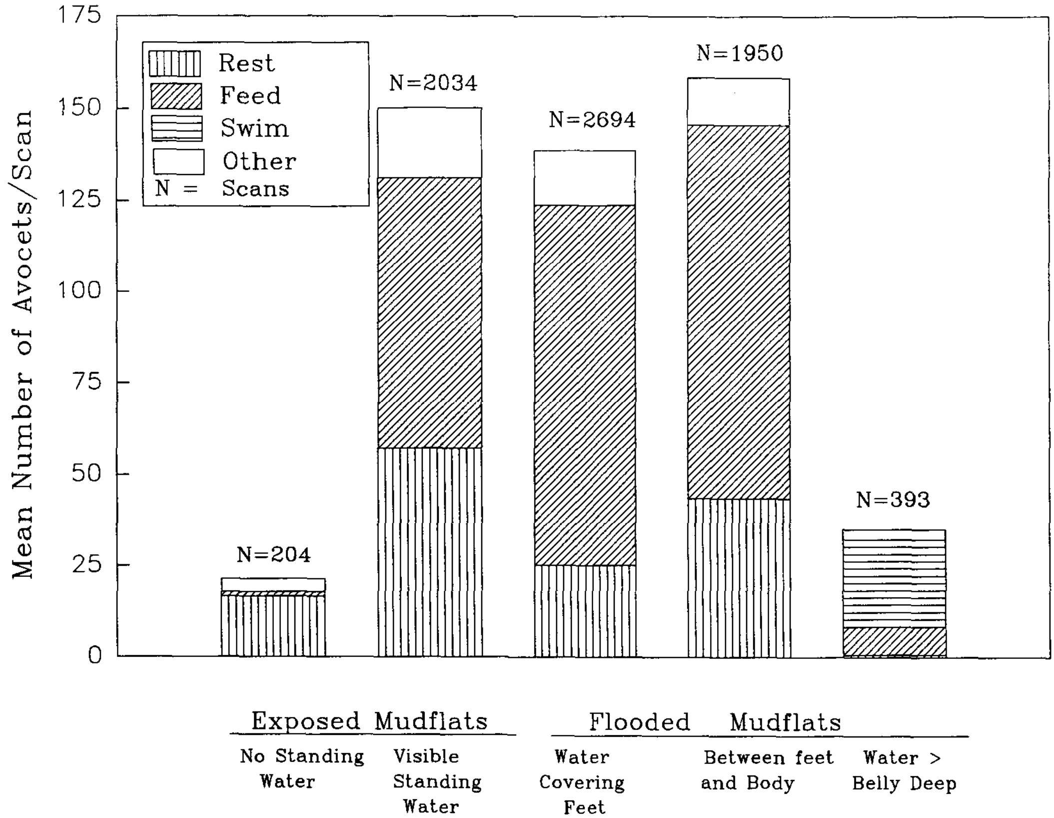

FIGURE 4. Mean number of avocets per scan present on intertidal mud flats engaged in various behaviors related to water depth, Humboldt Bay, California. Winters 1982–1983, 1983–1984. N = Number of scans.

tober and November (100 birds) and increased until February (1,100 birds, Recher 1966). While fluctuating numbers in October suggested that some fall birds recorded at Humboldt Bay may be passage birds on their way to more southern wintering areas, we found no evidence of a similar spring flight. Rather, beginning in February, the Humboldt Bay population steadily declined and was essentially gone by early May. Because we recorded only one migratory flight in 1,168 hours of diurnal observation, we presume most avocet migration occurs at night.

ROOST SITES

Migrating shorebirds prefer staging areas (Pienkowski and Evans 1984) and wintering areas with safe roost sites (Myers 1984). Typically shorebirds in tidal areas roost at high tide and at night (Goss-Custard 1969, Wolff 1969, Thomas and Dartnell 1971, Kelly and Cogswell 1979, Puttick 1979, Pienkowski 1982). The tendency of avocets to roost near or in shallow water, to avoid flying over land, and to land in water when disturbed or threatened shows that islands are superior to shorelines as roosts and that deep, nontidal ponds containing islands for roosts are important components of their wintering habitat.

SEWAGE OXIDATION PONDS

Avocets used oxidation ponds for foraging, drinking, and sanctuary (Evans 1988). Except for occasional phalaropes (*Phalaropus* spp.), avocets were the only shorebirds recorded feeding on concentrations of invertebrates in the oxidation ponds. The timing and size of the populations of *Daphne magna* in the sewage oxidation ponds were highly variable (Frodge 1985). Therefore, it would be reasonable to expect that use of this food source by avocets also would vary. Lee (unpubl. manuscript) found that concentrations of *Daphne* under "swarms" of foraging ducks were greater than in adjacent areas where no waterfowl were present. When avocets fed at the oxidation pond, they occurred in dense flocks (less than one body length apart) similar to the "swarms" reported by Lee (unpubl. manuscript) for ducks and coots. Lee (unpubl. manuscript) recorded waterfowl swarms throughout the fall, but avocets fed only in swarms during October and early November. This swarming behavior suggests that the avocets at the oxidation ponds were probably feeding on dense concentrations of *Daphne magna.*

Although avocets occasionally visited the oxidation ponds, Jacoby Creek, and Klopp Lake to drink or bathe in fresh water it is unlikely that fresh water is critical to avocet survival because they can exist in hypersaline or alkaline environments without using fresh water for long periods (Mahoney and Jehl 1985).

INTERTIDAL MUDFLATS

Tides exert great influence on the distribution, abundance, and behavior of estuarine organisms (Burger et al. 1977, Evans 1979, Connors et al. 1981, Burger 1984). For shorebirds, tides affect the amount of foraging space, length of time mudflats are available, and availability of prey (Recker 1966, Puttick 1981, Evans and Dugan 1984). At Humboldt Bay, large expanses of high and mid-level mudflats become exposed nearly simultaneously with a slight drop in the tide. Yet the birds did not spread out over the entire exposed mudflats, but rather remained in the northeast corner of the Bay. Prey availability near the water's edge in this relatively small section of North Humboldt Bay may have influenced which flats were used.

Like other shorebirds (Recher 1966, Smith 1975, Burger et al. 1977, Evans 1979, Pienkowski 1981, Goss-Custard 1984) foraging avocets generally avoided feeding in dry areas. Substrate wetness influences prey behavior and availability to shorebirds (Burger et al. 1977, Evans 1979, Pienkowski 1981, Goss-Custard 1984). Carrin (1973) found that 93.5% of the individuals and 60% of the biomass of benthic invertebrates occurred in the wettest substrates in Humboldt Bay. This may explain why the proportion of avocets foraging decreased at low tidal levels (−0.5–0.2 m MLLW). Prey also may be more abundant or active near the tide edge (Smith 1975), which may explain why avocets generally foraged near the tide edge.

During heavy rains avocets rested on the mudflats and were never observed feeding (Evans 1988). During light rains or overcast skies avocets fed primarily on mudflats with visible surface water and flooded mudflats with less than 3 cm of water. Prey availability may increase during light rains because marine invertebrates become more active to avoid fresh water (Page et al. 1979) or because the mudflats remain wet, enhancing feeding. Under overcast skies prey availability may increase because negatively phototactic benthic invertebrates may move closer to the surface and/or may be more active under low illumination (Hynes 1970).

Avocets were never seen feeding in upland sites during or after rains although other shorebird species have been reported to feed on earthworms forced to the surface by rain (Gerstenberg 1972, Kelly and Cogswell 1979, Townshend 1981). Goss-Custard (1969) and Smith (1975) found that prey capture rates by shorebirds decreased during rainfall. Moderate to heavy rains may decrease surface activity of prey (Goss-Custard 1969, Smith 1975) and reduce prey availability due to increased turbidity and water and mud flat distortion (Dugan et al. 1981).

Several shorebird species have been reported to forage at night only because they could not find enough food during daylight (Smith 1975, Evans 1976, Goss-Custard et al. 1977). Dugan (1981) and Pienkowski and Evans (1984) found that shorebirds may obtain more than 50% of their mid-winter food at night. Many invertebrates are active at the surface at night (Vader 1964, Dugan 1981, Pienkowski 1982). Waterfowl (Swanson and Sargent 1972) and shorebirds (Goss-Custard 1970, Dugan 1981) have been reported to feed at night in response to increased prey activity. Visual feeders may have reduced success at night due to difficulties in detecting prey or locating foraging sites (Smith 1975, Evans 1976, Pienkowski 1983). Redshanks foraging at night switched from visual to tactile foraging methods and changed foraging sites (Goss-Custard 1969). Since avocets primarily used tactile methods and were observed feeding, from November to March, in the same locations at night as during the day, we presume they can forage effectively at night assuming sufficient quantities of prey are available. The ability to feed at night may be important during extended periods of severe weather during mid-winter, especially when high winds, heavy rainfall, and cool temperatures occur simultaneously.

The earliest wintering populations of American Avocets at Humboldt Bay were recorded in the northeast corner of the Bay (Harris 1991). Despite increasing wintering populations since the early 1960s the pattern of habitat use has not changed. The establishment and increase of this wintering population follows closely the construction of the oxidation pond in 1957. In 1969 the high-level mudflats adjacent to the oxidation pond were used by avocets at three times the rate as moderate-elevation mudflats and 10 times the rate as the low-elevation mudflats farther away (Gerstenberg 1972). This suggests the oxidation ponds with their seasonal *Dapne* blooms and nutrient-rich discharge into the northeastern portion of Humboldt Bay may have contributed to both the establishment and spatial pattern of foraging for this population. The later creation of the islands in Klopp Lake has reinforced this pattern of habitat use by providing secure, suitable islands for roosts near the feeding areas.

It is advantageous for roost sites to be adjacent to foraging areas (Zwarts and Wanink 1984). In North Humboldt Bay these avocets foraged within 3 km of the roosts. If food resources near winter roosts are depleted, shorebirds have to shift roost locations or travel farther to forage (Zwarts and Wanink 1984). Since the Humboldt Bay avocets did not shift foraging patterns or roost locations and did not forage at high tide, we assume the food resources on the mudflats were adequate to support the 500–800 birds present in 1982–1984. Because they only used one quarter of North Bay and did not use South Bay at all, the potential for further increases in the wintering population seems high.

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