Variation in Shorebird Use of Diurnal, High-tide Roosts: How Consistently are Roosts Used?

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Abstract.—In coastal environs during the non-breeding season, many shorebirds (suborder Charadrii) congregate at roosts, long considered to be traditional sites where flocks of individuals coalesce when high tides inundate feeding areas. Humboldt Bay, California was surveyed (9.5 months at roughly 10-d intervals) to assess temporal variation in incidence (proportion of 28 surveys birds used a roost), proportional abundance, concentrations, and repeatability (of seasonal average proportional abundances) of shorebird use of diurnal, high-tide roosts. Two hundred and forty roosting locations were identified and observations were made of 30 species. Fourteen species accounted for over 99% of observations. Shorebirds occurred at most roosts infrequently (<20% of surveys) and only 4% of roosts had roosting birds present on more than 80% of occasions. Abundant species occurred at more roosts (20-141 roosts per species) compared with less common species. Even at the most-used roosts, abundances at the species level varied greatly. Repeatability of roost use among seasons was high. At Humboldt Bay, roost use formed a continuum from ephemeral locations used by a few birds to sites used consistently by large numbers of individuals. *Received 10 March 2003, accepted 20 August 2003.*

Key words.—Charadrii, concentration, Humboldt Bay, repeatability of use, roosts, Shannon-Wiener index, shorebirds, tradition.

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During the non-breeding season, shorebirds (suborder Charadrii) commonly form dense flocks at roosts where they rest and preen but remain vigilant. Roosts are a conspicuous feature of shorebird activity patterns in coastal areas because tides predictably inundate and limit access to feeding areas for extended periods (Hale 1980). Shorebirds have been known to roost at some locations for decades (Hale 1980). These traditional roosts have yielded valuable information on shorebird ecology, which has enhanced conservation. For example, roosts have been used as foci to estimate individual home ranges (Warnock and Takekawa 1996) and to assess site fidelity (Rehfisch *et al.* 1996; Pearce-Higgins 2001). These multi-year studies show that individuals frequently move among a few roosts within an estuary. Based on this predictability, counts of roosting shorebirds have been used to assess local changes in numbers (Mitchell *et al.* 1988) and to evaluate success of constructed roosts in replacing those lost to human development (Burton *et al.* 1996). Hence, roosts have predictable use (species composition and abundances), although their use may vary with local changes in numbers (Mitchell *et al.* 1988), environmental variables (Burton *et al.* 1996), disturbance (Pfister *et al.* 1992) and habitat limitation (Gill *et al.* 2001).

In this study, the notion that individual roosts are used consistently was assessed by examining the frequency of use and variation in species' abundances at Humboldt Bay, California. Given the considerable variation in abundances at roosts (Hale 1980), it was reasoned that roosts could be arrayed on a continuum spanning traditional sites, where similar and large numbers occur time and again, to ephemeral locations, where small flocks coalesce on one or a few occasions. The objectives were to a) examine the extent to which the abundance of species at roosts around Humboldt Bay varied within and among seasons, b) estimate the consistency with which roosts were ranked from most to least used, and c) contrast patterns from seasons corresponding to the presence of resident and migrating individuals. The findings are discussed in relation to monitoring shorebirds by counts at roosts and the effectiveness of management to protect these habitats (Brown *et al.* 2001).

STUDY AREA

Shorebirds were surveyed from 2 January-16 October 2002 at Humboldt Bay, California (Fig. 1), the second largest estuary between San Francisco Bay and the mouth of the Columbia River along the Pacific flyway of North America. The area's importance to shorebirds (Page *et al.* 1999) resulted in its designation as an international site under the Western Hemisphere Shorebird Reserve Network. At any time from July through May, 10,000-100,000 birds of over 25 species occur (Colwell 1994). This rich species assemblage stems from the close juxtaposition of diverse foraging habitats including sandy ocean beaches, rocky intertidal zones, tidal flats, seasonal freshwater wetlands and pastures. Detailed descriptions of the study area are provided elsewhere (Barnhart *et al.* 1992; Danufsky and Colwell 2003).

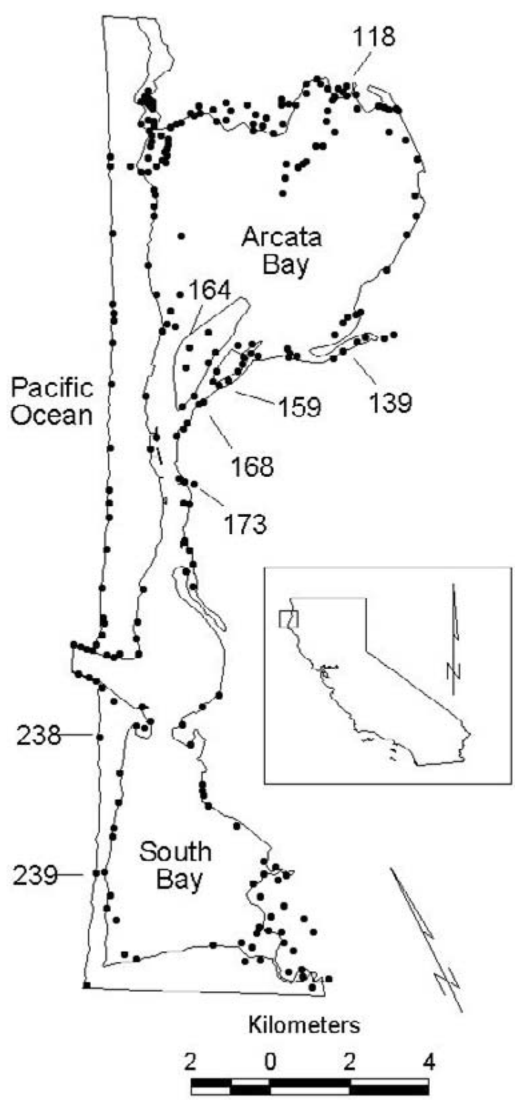

Figure 1. Humboldt Bay study area and locations (●) of 240 diurnal, high-tide shorebird roosts during autumn, winter and spring 2002. Numbers correspond to the top-ranked roosts of 14 species mentioned in Table 3.

METHODS

Surveys of Roosting Birds

The bay perimeter, pastures, islands and adjoining habitats, including ocean beaches immediately west of the bay, were surveyed during daylight hours coinciding with high tides ranging from approximately 1.2-2.6 m. Surveys of pastures were limited to areas immediately adjacent to the bay. Based on earlier studies (Colwell 1994; Colwell *et al.* 2001; Danufsky and Colwell 2003), 19 survey areas (hereafter referred to as routes) were established corresponding to linear stretches of ocean beach, bay shoreline and pastures, which could be surveyed during a 2-h period coinciding with predicted high tides. Depending on location and accessibility, surveys were conducted by walking (10), driving (7) or kayaking (2) routes with unobstructed views of surrounding habitat. Routes covered over 95% of intertidal and adjacent habitats of Humboldt Bay. Surveys were consistent in coverage, but do not fully document the spatial extent of Humboldt Bay roosts.

During surveys, observers scan sampled (Altmann 1974) habitats using binoculars and 20-60× spotting scopes. Upon encountering a roost (defined as two or more individuals in close proximity that were not feeding), observers recorded time, weather conditions (speed and direction of wind and precipitation), identified species, and either counted individual birds in small flocks or estimated their numbers in large flocks. Roost locations were mapped on laminated, high-resolution (0.3 m pixel) images. In the field, data for Long-billed and Short-billed Dowitchers (see Table 1 for scientific names) were tallied collectively because of difficulties identifying these species at a distance; similarly, small calidridine sandpipers (Dunlin, Western Sandpiper, Least Sandpiper) and large sandpipers (Willet, Whimbrel, Long-billed Curlew, and Marbled Godwit) were occasionally grouped. For the latter two groups, however, observations were apportioned into species totals based on known flock composition during other surveys (see Page *et al.* 1999). During any one season, these totals amounted to 1%-3% of species totals.

Twenty eight surveys (each survey covered the routes once) of the study area were completed during autumn (N = 10; 1 August-16 October), winter (N = 8; 2 January-28 February), and spring (N = 10; 1 March-15 May). Seasons correspond to periods of migration and winter residency for local shorebirds (Harris 1996). Each survey required 7-10 days to complete, depending on number of observers, weather conditions (surveys were not conducted during persistent rain), and timing of diurnal high tides (which occasionally did not occur during winter for several days). With the exception of kayaking routes covered by the first author, observers rotated among routes.

Data Summary and Analysis

Observers entered locations of roosts as polygon coverages into a geographic information system (GIS; ArcView, ESRI, Redlands, CA), including data on species' abundances. In the field, the ease with which roost locations could be accurately placed on images varied

Table 1. Seasonal variation in shorebird abundance at diurnal, high-tide roosts around Humboldt Bay, California.

		Autumn		Winter		Spring	
Common name	Scientific name	Proportional abundance	N	Proportional abundance	N	Proportional abundance	N
Black-bellied Plover	*Pluvialis squatarola*	0.033	9632	0.037	5080	0.022	5819
Semipalmated Plover	*Charadrius semipalmatus*	0.012	3473	0.005	738	0.007	1752
American Avocet	*Recurvirostra americana*	0.005	1411	0.027	3705	0.005	1389
Greater Yellowlegs	*Tringa melanoleuca*	0.003	852	<0.001	93	<0.001	96
Willet	*Catoptrophorus semipalmatus*	0.042	12084	0.070	9489	0.025	6851
Whimbrel	*Numenius phaeopus*	<0.001	101	0.001	173	0.001	236
Long-billed Curlew	*Numenius americanus*	0.004	1106	0.013	1719	0.005	1352
Marbled Godwit	*Limosa fedoa*	0.198	56973	0.285	38663	0.185	49783
Black Turnstone	*Arenaria melanocephala*	0.003	788	0.005	653	0.002	457
Sanderling	*Calidris alba*	0.032	9115	<0.001	100	0.015	4085
Western Sandpiper	*Calidris mauri*	0.444	128109	0.240	32612	0.338	90962
Least Sandpiper	*Calidris minutilla*	0.182	52591	0.086	11687	0.083	22323
Dunlin	*Calidris alpina*	0.034	9753	0.221	30049	0.294	78951
Dowitchers	*Limnodromus griseus, L. scolopaceus*	0.007	2044	0.006	766	0.018	4772
Other species		<0.001	178	0.002	274	<0.001	112

among habitats. For example, mapping roosts on linear stretches of ocean beach with few distinctive habitat features was difficult compared to small islands, rafts or wharfs around the bay. In the vast majority of cases, however, observers were confident in their abilities to map and transcribe locations into the GIS.

For purposes of analysis, the following procedure was used to define the location of roosts using GIS. First, an image was produced overlaying all roosts (polygons) mapped during the 28 surveys and a 50 m buffer was applied to each polygon's perimeter as an arbitrary boundary to delimit roosts close together. Polygons with overlapping buffers were considered to be the same roost. In some cases, however, natural breaks in habitat (e.g., tidal channels separating jetties, wharfs, rafts and islands) between adjacent roosts separated roosts in close proximity. This approach produced nearly identical results to an independent, subjective assessment of winter roost locations based on direct interpretation of maps and knowledge of landscape features. Exceptions to the clear spatial delineation of roosts occurred on ocean beaches where multiple overlapping 50 m buffers yielded spatially continuous roosts over large areas. To provide spatial information on roost locations, roosts were numbered beginning on the ocean beach northwest of Arcata Bay (1), proceeding south to the jetty, then clockwise around the bay finishing at the south end of the ocean beach west of South Bay (240; see Fig. 1).

For each species, a matrix was assembled with rows and columns corresponding to 240 roosts and 28 surveys, respectively. Using roost totals, the average (±SD) proportional abundance at each roost was calculated based on 28 surveys. Survey totals were used to calculate the number of roosts and a concentration score. The number of roosts occupied during each survey was totaled and these values were averaged separately across autumn, winter and spring surveys. Incidence was defined as the proportion of 28 surveys in which at least one bird of a species occurred at a roost; hence, each roost had an incidence ranging between 0.04 (present on one of 28 surveys) to 1.0. To quantify each species' concentration among roosts within a survey, the Shannon-Wiener index ($H' = -\sum p_i \ln p_i$) was used, where p_i represents a species' proportional abundance at N roosts observed during a survey. This concentration index ranged from 0.0 (all individuals occurred at one roost) to approximately 2.5 (representing a more even distribution of observations among many sites). One objective was to compare variation in use of roosts among seasons, when migratory movements differ. Seasonal comparisons of the average number of roosts and concentration scores were made using Spearman's rank correlation for 14 focal species. Species' distributions at roosts were compared using average (±SD) number of roosts and concentration scores in each season with sample sizes of 10, 8 and 10 for autumn, winter and spring, respectively. Interspecific differences in average number of roosts and concentration scores were compared within each season using non-parametric analysis of variance (Kruskal-Wallis) tests. In each case, the number of species was 14 and sample sizes for each species were equal and equivalent to the number of surveys conducted in a given season (autumn N = 10; winter N = 8; spring N = 10). The Kruskal-Wallis tests yielded a chi-square statistic (and associated P-value) testing the significance of differences in species' number of roosts and concentration scores.

To assess consistency of roost use, the following was summarized for each species. Average proportional abundance was plotted against incidence for all roosts. If roosts are consistently used, then roosts should cluster together to the far right (high incidence) of the plot. By contrast, a pattern of ephemeral use would produce a plot of incidence values (infrequent use) skewed to the left. Variation in abundance was examined for the most used roost (highest incidence). To the extent that roosts are used consistently, these locations should exhibit limited variation in species' abundances, especially during winter when local populations are more stable than during migration. Data were collated by season to account for effects of transient birds during migration. Finally, seasonal consistency in use was evaluated by ranking roosts from most to least used (based on average proportional abundance) and correlating these ranks using Kendall's coefficient of concordance (W), which varies from 0 (no repeatability of ranks among seasons) to 1.0 (perfect concordance of ranks). A chi-square statistic was generated to test the significance of the concordance.

RESULTS

Shorebird Assemblages at Roosts

A total of 692,951 observations of 30 species were made at roosts during autumn (N = 288,210 birds; 26 species), winter (N = 135,801; 24 species) and spring (N = 268,940; 26 species). Analyses were restricted to 14 species (Table 1) that accounted for 99.9% of observations. These focal species varied in abundance, representing 0.07% to 36% of observations. Despite this variation, relative abundances of species correlated between seasons ($r = 0.73\text{-}0.92$, $P < 0.01$), indicating similar community composition among periods with migrants and winter residents.

Interspecific Differences

Each season, species differed significantly in average number of roosts and concentration scores at these sites (Table 2), and these differences correlated with species abundances. More abundant taxa occurred more evenly (autumn: $r_{s12} = 0.64$, $P < 0.02$; winter: $r_{s12} = 0.78$, $P < 0.001$; spring: $r_{s12} = 0.74$, $P < 0.005$) among more roosts (autumn: $r_{s12} = 0.82$, $P < 0.001$; winter $r_{s12} = 0.87$, $P < 0.0001$; spring $r_s = 0.80$, $P < 0.001$) compared with less common species.

Species varied greatly in total number of roosts (20-141), which correlated positively with overall abundance ($r_{s12} = 0.73$, $P < 0.005$). For each species, use of these roosts was graphed as the relationship between incidence and proportional abundance (Fig. 2), which produced similar patterns for all species. Regardless of species' abundances, most roosts were used infrequently by a small proportion of individuals. Conversely, roosts with higher incidences had higher proportional abundances. For all species, incidence correlated with mean proportional abundance ($r_{s238} = 0.94\text{-}1.0$, $P < 0.0001$). For nine of 14 species, the roost with the highest incidence also had the highest average proportional abundance. Within each season, interspecific variation in concentration scores correlated with number of roosts ($r_{12} = 0.88\text{-}0.97$, $P < 0.0001$).

Seasonal Variation

Most species showed seasonal differences in average number of roosts and concentration scores at these sites (Table 2). Nine of 14 species exhibited significant seasonal variation in the average number of roosts. In seven cases, the greatest number of roosts occurred during autumn, coincident with peak migration for these species. The two exceptions to this pattern (American Avocet and Dunlin) used more roosts during winter; these taxa migrate late to the Humboldt Bay area. Five species exhibited seasonal differences in concentration scores. When differences existed, species tended to be less concentrated during the season they used more roosts.

Consistency of Roost Use

Most (64%) of the 240 roosts identified harbored shorebirds on fewer than 20% of 28 surveys, whereas a few (4%) sites had birds on more than 80% of occasions (Fig. 3). Across the 14 species, the roost with the highest incidence value (Table 3) had birds 43%-93% of occasions, with half of the species using this roost on more than 75% of occasions. However, these roosts varied greatly in number of roosting birds, even during winter when there was limited regional movement of birds. Variation (SD) exceeded average values for eight, seven and eleven of 14 species in autumn, winter, and spring, respectively. In fact, in most (79% of species by season) cases, no individuals roosted at these sites on at least one occasion, and only six species showed significant concordance among seasons in the ranking of roosts (Table 4). Examining all species simultaneously, the most used roost occurred on the north-

Table 2. Seasonal differences in shorebird use and concentration at diurnal, high-tide roosts around Humboldt Bay, California, tested using Kruskal-Wallis one-way ANOVA.

	Average (±SD) number of roosts					Average (±SD) concentration score (H')				
Species	Autumn	Winter	Spring	χ^2_2	P	Autumn	Winter	Spring	χ^2_2	P
Black-bellied Plover	15.9 ± 3.9	18.3 ± 3.3	14.4 ± 7.1	2.09	n.s.	2.1 ± 0.2	2.2 ± 0.3	1.9 ± 0.6	2.69	n.s.
Semipalmated Plover	7.6 ± 2.5	2.9 ± 1.5	5.3 ± 1.8	13.32	<0.005	1.3 ± 0.4	0.6 ± 0.5	1.3 ± 0.4	6.73	<0.05
American Avocet	3.1 ± 0.9	3.8 ± 2.2	1.8 ± 1.0	7.74	<0.05	0.8 ± 0.3	0.8 ± 0.3	0.5 ± 0.3	5.11	n.s.
Greater Yellowlegs	4.3 ± 2.0	2.0 ± 2.0	2.1 ± 1.2	8.22	<0.05	1.0 ± 0.4	0.5 ± 0.4	0.5 ± 0.5	5.40	n.s.
Willet	22.1 ± 3.3	23.3 ± 5.1	16.5 ± 10.4	2.29	n.s	2.5 ± 0.2	2.5 ± 0.2	1.9 ± 0.9	3.50	n.s.
Whimbrel	2.0 ± 1.8	2.3 ± 1.2	3.8 ± 2.7	2.84	n.s	0.5 ± 0.5	0.7 ± 0.4	0.8 ± 0.6	0.90	n.s.
Long-billed Curlew	9.6 ± 2.5	6.0 ± 2.1	5.7 ± 2.8	8.70	<0.05	1.8 ± 0.3	1.2 ± 0.3	1.0 ± 0.6	14.18	<0.001
Marbled Godwit	19.1 ± 4.6	20.4 ± 3.7	16.7 ± 7.2	2.03	n.s	2.1 ± 0.3	2.1 ± 0.3	1.8 ± 0.6	2.51	n.s.
Black Turnstone	7.4 ± 3.9	10.1 ± 5.0	5.3 ± 2.5	4.59	n.s	1.5 ± 0.5	1.8 ± 0.5	1.2 ± 0.6	4.06	n.s.
Sanderling	5.1 ± 2.0	1.5 ± 1.2	2.6 ± 1.8	11.80	<0.005	0.9 ± 0.3	0.4 ± 0.5	0.5 ± 0.6	4.46	n.s.
Western Sandpiper	22.8 ± 8.3	17.1 ± 3.7	14.0 ± 4.5	6.76	<0.05	1.8 ± 0.4	1.9 ± 0.4	1.6 ± 0.3	6.58	<0.05
Least Sandpiper	26.6 ± 7.3	13.0 ± 4.0	14.7 ± 5.3	15.91	<0.001	2.1 ± 0.4	1.6 ± 0.7	1.7 ± 0.5	3.98	n.s.
Dunlin	8.1 ± 7.6	19.0 ± 6.5	16.0 ± 3.7	8.71	<0.05	1.0 ± 0.7	2.0 ± 0.3	1.6 ± 0.4	9.88	<0.01
Dowitchers	9.0 ± 2.4	3.0 ± 1.3	8.9 ± 7.9	8.51	<0.05	1.6 ± 0.3	0.6 ± 0.4	1.2 ± 0.9	7.85	<0.05
Species differences χ^2_{13}	109.7	93.3	82.0			96.2	80.8	62.8		
P value	<0.0001	<0.0001	<0.0001			<0.0001	<0.0001	<0.0001		

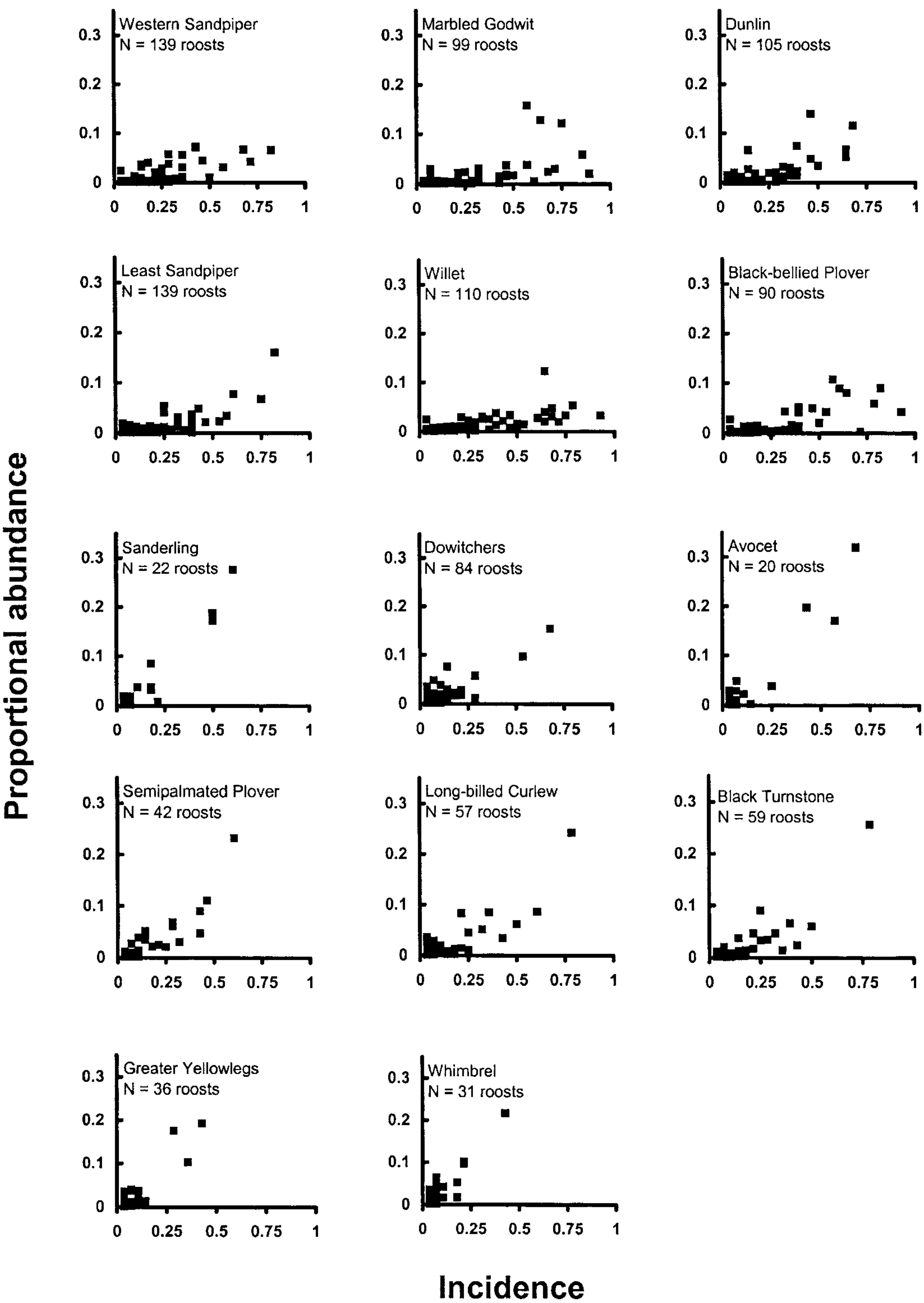

Figure 2. Interspecific variation in shorebird use of diurnal high-tide roosts (■) at Humboldt Bay, California. Incidence is the proportion of 28 surveys birds roosted at a site; proportional abundance is the average proportion of a species' bay-wide total that roosted at a site. Species are arrayed from most (upper left) to least (lower right) abundant.

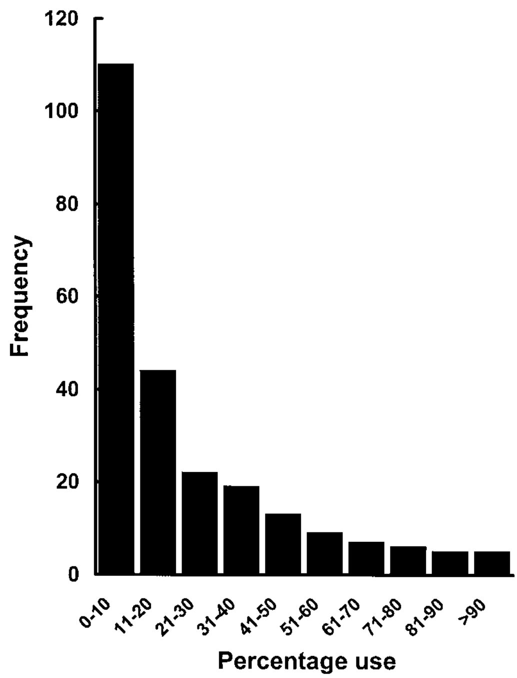

Figure 3. Frequency distribution of incidence scores for 240 roosts observed at Humboldt Bay, California showing that most roosts were used infrequently by shorebirds.

east shore of the bay (Fig. 1; 118), where incidences of four species (American Avocet, dowitchers, Dunlin and Greater Yellowlegs) were highest. Three other sites were the most used roosts for three species pairs (Semipalmated Plover and Sanderling; Willet and Marbled Godwit; Western and Least Sandpipers).

DISCUSSION

Consistency of Use of Roost Sites

Results of this study offer new insights and contrasting views on the notion that high-tide roosts are consistently used locations where shorebirds congregate (Furness 1973; Hale 1980). On the one hand, many roosts occurred at precisely the same location during the 28 surveys. As noted by Hale (1980), the predictability of encountering birds at roosts is evidence that they may be traditional sites, with some roosts in England (e.g., Crossens roost on the Ribble marshes) being used for more than 100 years. Indeed, movements of radio-marked birds within winter home ranges suggest that individuals return to the same roost time and time again (Warnock and Takekawa 1996), although this question has not been fully explored from the perspective of the roost. Additional support for the concept of consistent use derived from analyses of roosts ranked according to average proportional abundance during autumn, winter and spring. This anal-

Table 3. Seasonal variation in average (±SD) abundance of 14 shorebird species at the most used diurnal, high tide roosts at Humboldt Bay, California.

	Autumn		Winter		Spring	
Species	$\bar{x}$ ± SD	Range	$\bar{x}$ ± SD	Range	$\bar{x}$ ± SD	Range
Black-bellied Plover (139)[a]	58 ± 25	25-110	7 ± 8	0-24	27 ± 34	0-100
Semipalmated Plover (238)	53 ± 63	0-161	61 ± 93	0-270	55 ± 62	0-162
American Avocet (118)	40 ± 53	0-130	248 ± 184	38-475	87 ± 141	0-381
Greater Yellowlegs (118)	31 ± 21	0-61	0 ± 0	0-1	3 ± 7	0-17
Willet (173)	50 ± 20	20-81	12 ± 9	1-22	19 ± 18	0-58
Whimbrel (159)	4 ± 6	0-14	1 ± 2	0-4	6 ± 9	0-29
Long-billed Curlew (164)	23 ± 20	1-59	82 ± 40	0-115	33 ± 53	0-149
Marbled Godwit (173)	33 ± 56	1-189	49 ± 63	0-187	178 ± 160	0-430
Black Turnstone (168)	19 ± 14	0-47	13 ± 11	0-25	12 ± 10	0-30
Sanderling (238)	87 ± 142	0-400	6 ± 12	0-35	24 ± 41	0-134
Western Sandpiper (239)	881 ± 1640	19-5366	166 ± 188	0-475	565 ± 1063	0-3500
Least Sandpiper (239)	892 ± 852	4-2772	222 ± 289	0-834	332 ± 528	0-1616
Dunlin (118)	57 ± 173	0-550	758 ± 758	10-1994	1055 ± 1284	0-3700
Dowitchers (118)	31 ± 44	0-132	6 ± 6	0-15	32 ± 45	0-130

[a]Numbers correspond to roost locations in Fig. 1.

Table 4. Between-season repeatability of diurnal, high-tide roosts used by 14 shorebird species at Humboldt Bay, California. Repeatability is gauged using Kendall's coefficient of concordance (W), which varies from 0.0 (no correlation among seasons in the average ranked importance of roosts) to 1.0 (perfect concordance). Degrees of freedom for each species = total roosts - 1.

Species	Total roosts	Autumn roosts	Winter roosts	Spring roosts	W	χ^2	P
Black-bellied Plover	90	51	51	56	0.52	138.2	<0.001
Semipalmated Plover	42	30	15	22	0.45	55.8	n.s.
American Avocet	20	11	12	6	0.43	24.3	n.s.
Greater Yellowlegs	37	18	14	18	0.30	32.3	n.s.
Willet	111	61	62	69	0.50	166.2	<0.001
Whimbrel	31	14	9	21	0.37	32.9	n.s.
Long-billed Curlew	58	33	24	33	0.40	67.6	n.s.
Marbled Godwit	99	61	53	63	0.49	144.0	<0.01
Black Turnstone	59	28	37	28	0.43	75.1	n.s.
Sanderling	22	18	6	11	0.57	35.9	<0.05
Western Sandpiper	139	90	66	65	0.43	177.0	<0.02
Least Sandpiper	141	97	56	67	0.39	164.0	n.s.
Dunlin	105	40	65	67	0.45	140.5	<0.01
Dowitchers	84	41	13	61	0.30	74.9	n.s.

ysis showed that for some species similar proportions of birds used sites across seasons. It can be assumed that this relative consistency of use derives from individuals repeatedly using the same roost, which is supported by studies of local movements of marked individuals over intervals spanning days (Warnock and Takekawa 1996; Sanzenbacher and Haig 2002) to years (Rehfisch *et al.* 1996; Pearce-Higgins 2001). The positive correlation between incidence and abundance, and the observation that multiple species shared top ranked roosts supports the notion that roosts are traditional. Conversely, that a small percentage (4%) of the 240 roosts had high incidences indicates that few roosts around Humboldt Bay are consistently used locations to which birds return as flooding tides inundate intertidal feeding habitats.

Substantial variation in species' abundances was recorded at even the top-ranked roosts and shorebirds occupied most roosts infrequently, which contradicts the idea that roosts are consistently used. Most species were absent from the most used roosts on at least one occasion, especially during migration. These observations indicate that sites vary in consistency of use by shorebirds. These findings are not necessarily unusual, as other studies have documented appreciable within season variation in numbers of shorebirds at roosts (Hale 1980). For example, in Patagonia, Red Knots (*Calidris canutus*) were numbered in the thousands, but were absent at other times from specific roosts (Sitters *et al.* 2001). This variation indicates that individuals vary in their use of roosts and that birds move among multiple locations (Rehfisch *et al.* 1996; Pearce-Higgins 2001). Given these contrasting views, reconsideration of the concept that roosts are consistently used sites is warranted. Rather, roosts can be arrayed on a continuum of ephemeral to traditional roosts. Ephemeral roosts are those used infrequently by few individuals whereas traditional roosts are those occupied regularly by large numbers of birds over successive years. Finally, there are many roosts that fall mid-range on the ephemeral to traditional continuum.

Causes of Variation in Use of Roosts

The sources of the substantial variation in species' abundances at roosts are probably many, including a) height of high tide coinciding with observations at roosts differing in elevation, b) availability of alternative foraging habitats, c) disturbance, either by predators or humans, and d) migratory movements. For roosts located in the upper reaches of the intertidal zone, high spring tides may inundate some roosts and force birds to alternative sites (Burton *et al.* 1996). By contrast, these same locations may be used to a greater extent during neap tides. Although many birds roost during high tide, some feed in the upper reaches of intertidal habitats (Hale 1980) and in non-tidal areas (Colwell and Dodd 1995). The availability of alternative, non-tidal foraging habitats may attract birds away from roosts. For instance, pastures near Humboldt Bay offer productive high-tide feeding opportunities, especially when winter rains increase availability of earthworms (Colwell and Dodd 1997). Disturbance, whether natural or anthropogenic, also may cause birds to abandon roosts. In Patagonia, Red Knots do not use some roosts at night, leading Sitters *et al.* (2001) to suggest that vulnerability to predation was a cause. Human disturbance caused several shorebird species to leave roosts on beaches of the Dee estuary (Kirby *et al.* 1993). And, chronic disturbance associated with recreational activity has been implicated in long-term abandonment of roosting habitats (Pfister *et al.* 1992).

Roost use varied between seasons and this correlated with migratory movements of species. This study was designed to distinguish between seasons when migrant and resident birds are present. For example, Western Sandpipers wintering at San Francisco Bay have well defined home ranges centered on roosts (Warnock and Takekawa 1996). At Humboldt Bay, some species (e.g., avocets and curlews) are predictably found in consistent numbers in certain areas of the bay (Colwell *et al.* 2001; Colwell and Mathis 2001), suggesting that individuals confine local movements to a small area and return to the same roosts time and again (Warnock and Takekawa 1996). By contrast, spring migrants such as Western Sandpipers spend 3-4 days staging at Humboldt Bay (Warnock and Bishop 1998). Compared to winter residents, these passage birds probably move more widely among foraging habitats of the bay and are less predictable in their use of roosts. Even if they are predictable in their use of roosts, however, the 7-10 day survey interval on the bay exceeds the average duration of stay for Western Sandpipers. Hence, many different individuals are present and may use different roosts, increasing variation in roost use.

Conservation Implications

The notion of consistency of use of roosts by shorebirds should be qualified to include estimates of the frequency with which individuals occur at a roost on multiple occasions as well as variation in species' abundance. Although locations may be "traditional" (sensu Hale 1980), variation in species' abundances at these roosts indicates that most individuals move amongst multiple sites over short or long intervals (Rehfisch *et al.* 1996; Pearce-Higgins 2001). Multiple surveys of high-tide roosts may provide valuable information on areas of concentration and, hence, vulnerability to habitat degradation and loss. Moreover, given the variability in species' abundances observed in this study, usefulness of monitoring shorebird populations at roosts may be questioned. Certainly, surveys at roosts can easily provide such information but variation in use of roosts suggests that multiple surveys synchronized across large areas may be warranted to account for substantial short-term variation in shorebird abundances at roosts (Mitchell *et al.* 1988). The causes of this variation undoubtedly reflect seasonal differences in patterns of habitat use by individuals of different age and sex, responding to environmental factors such as variation in tide height (Burton *et al.* 1996), suitability of alternative, non-tidal foraging areas during high tide (Colwell and Dodd 1997), and disturbance by predators (Sitters *et al.* 2000) and humans (Pfister *et al.* 1992).

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