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Foraging Patterns of Caspian Terns and Double-crested Cormorants in the Columbia River Estuary

Abstract

We examined spatial and temporal foraging patterns of Caspian terns and double-crested cormorants nesting in the Columbia River estuary, to potentially identify circumstances where juvenile salmonids listed under the U.S. Endangered Species Act might be more vulnerable to predation by these avian piscivores. Data were collected during the 1998 and 1999 breeding seasons, using point count surveys of foraging birds at 40 sites along the river's banks, and using aerial strip transect counts throughout the estuary for terns. In 1998, terns selected tidal flats and sites with roosting beaches nearby for foraging, making greater use of the marine/mixing zone of the estuary later in the season, particularly areas near the ocean jetties. In 1999, cormorants selected foraging sites in freshwater along the main channel with pile dikes present, particularly early in the season. Foraging trends in the other year for each species were generally similar to the above but usually not significant. During aerial surveys we observed 50% of foraging and commuting terns within 8 km of the Rice Island colony, and ≤ 5% of activity occurred ≥ 27 km from this colony in both years. Disproportionately greater cormorant foraging activity at pile dikes may indicate greater vulnerability of salmonids to predation at those features. Colony relocations to sites at sufficient distance from areas of relatively high salmonid abundance may be a straightforward means of reducing impacts of avian predation on salmonids than habitat alterations within the Columbia River estuary, at least for terns.

Introduction

Large coastal estuaries provide dynamic foraging environments for colonial nesting piscivorous waterbirds. At these interfaces between freshwater and marine systems, diverse habitats and high forage fish diversity and abundance can support large populations of nesting waterbirds, if suitable nesting habitat is also available (Weller 1999). In estuaries fed by large freshwater systems, anadromous fish species may also be highly abundant seasonally (Bottom et al. 2005), and an important food source for piscivorous waterbirds.

This study examined the foraging ecology of Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*) nesting in the Columbia River estuary during the 1998 and 1999 breeding seasons. The Columbia River estuary is large with high freshwater input where a number of habitat conditions exist such as tidal flats, deep water channels, tributaries, sloughs, and marine areas surrounding the ocean jetties. A strong salinity gradient exists across these habitats and periodic tidal fluctuations influence all areas as well (Fox et al. 1984). These diverse habitats support an abundant and wide variety of forage fishes, including anchovy (*Engraulis mordix*), herring (*Clupea pallasi*), smelt (Osmeridae), and surfperch (Embiotocidae), in addition to large seasonal runs of out-migrating juvenile anadromous salmonids (*Oncorhynchus* spp.; Bottom and Jones 1990). Populations of both Caspian terns and double-crested cormorants have grown dramatically in the Columbia River estuary over the past two decades as these birds have found suitable nesting habitat and have exploited apparently ample prey resources (Carter et al. 1995, Wires and Cuthbert 2000, Wires et al. 2001, Collis et al. 2002, Suryan et al. 2004).

Caspian terns are plunge-diving piscivores that briefly submerge themselves during a shallow plunge from flight to capture prey. They have been documented to nest and forage in freshwater lakes, rivers, and coastal environments but rarely in open ocean areas (Cuthbert and Wires 1999). Few prior studies of this species have examined habitat use within range of a breeding site and

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none have demonstrated disproportional habitat use (e.g., Sirdevan and Quinn 1997). Previous studies of diet have found little evidence of prey selection, with diet usually considered a reflection of local prey availability rather than habitat selection (Cuthbert and Wires 1999). Double-crested cormorants are pursuit-diving piscivores and forage underwater throughout the water column (dives possible to at least 12m deep; Hatch and Weseloh 1999). They typically forage in relatively shallow water environments (< 8m deep) and seldom in open seas, but little more is known about habitat use other than a high degree of diversity of prey types taken across their breeding range (Hatch and Weseloh 1999). Previous diet studies in rivers with juvenile salmonids have indicated that cormorants may sometimes make substantial use of salmonids as prey, and have frequently been documented to respond rapidly to concentrations of prey, such as at dams on coastal rivers (Blackwell et al. 1997, Hatch and Weseloh 1999).

Caspian terns and double-crested cormorants nesting in the Columbia River estuary were found to significantly rely on juvenile salmonids as prey (Collis et al. 2002). During the 1997 and 1998 breeding seasons, salmonids were 73-81% of the diet of terns and 46% of the diet of cormorants nesting at Rice Island (river kilometer 34; Collis et al. 2002). This reliance upon juvenile salmonids was cause for concern for resource managers because 12 of the 20 evolutionarily significant units of salmonids in the Columbia River basin are federally listed as threatened or endangered under the U.S. Endangered Species Act (ESA; NMFS 2000). In addition to conservation concerns for wild salmonids, vocal publics within the region advocated for increased commercial, sport, and tribal harvest opportunities, all of which have been limited in the past two decades. While double-crested cormorants had been previously documented to be significant predators upon juvenile salmonids in some locations (Blackwell 1995, Hatch and Weseloh 1999), Caspian terns had not (Cuthbert and Wires 1999) prior to the work of Collis et al. (2002), and little was known of the foraging ecology of either species in this location or other large estuaries with high freshwater input.

Enhanced understanding of foraging habitat use by terns and cormorants in the Columbia River estuary would both add to our understanding of the ecology of piscivorous waterbirds in coastal environments and be of use to resource managers seeking to reduce impacts of these birds on declining and valuable salmonid populations. Our specific objectives in this study were to:

1. Examine foraging habitat use of terns and cormorants at multiple spatial scales within the estuary.
2. Describe patterns of tern and cormorant use of estuary foraging habitat across the breeding season and tidal cycles.
3. Quantify the foraging range of Caspian terns around their breeding colony in the estuary.

We predicted that Caspian terns would use shallow water environments (e.g., tidal mud flats) more frequently than other habitats, given their ability to access only the top meter of the water column, and that double-crested cormorants would use deeper water channels within the estuary more frequently than other habitats, given their ability to exploit prey throughout the water column. Additionally, we expected central place foraging to be an important constraint on foraging in this system. Specifically, we predicted that terns would forage more frequently in freshwater areas close to the Rice Island colony site, and that cormorants would forage more frequently in marine areas of the estuary, closer to their primary nesting site at East Sand Island.

Study Area

This study was conducted in the estuary of the Columbia River, which forms the border between the western portions of the U.S. states of Oregon and Washington (Figure 1). A variety of aquatic habitats exist in the estuary including deep channels (both the dredging-maintained shipping channel and unmaintained side channels), tidal flats, tributaries, sloughs, and marine areas near the ocean jetties. In addition, many islands are present with various levels of water inundation and a variety of vegetation types. Several islands have been either enhanced or entirely artificially created by the deposition of dredged materials (e.g., sand and silt) from shipping channel maintenance, and are in various stages of vegetational succession (USACE 1999). Salinity levels in the estuary follow a variable gradient from fresh to marine levels as one moves down the river; however, significant saltwater intrusion seldom occurs beyond river km 29 (Simenstad et al. 1990). Tidal amplitudes average 2.4 m at the river's mouth (Fox et al. 1984).

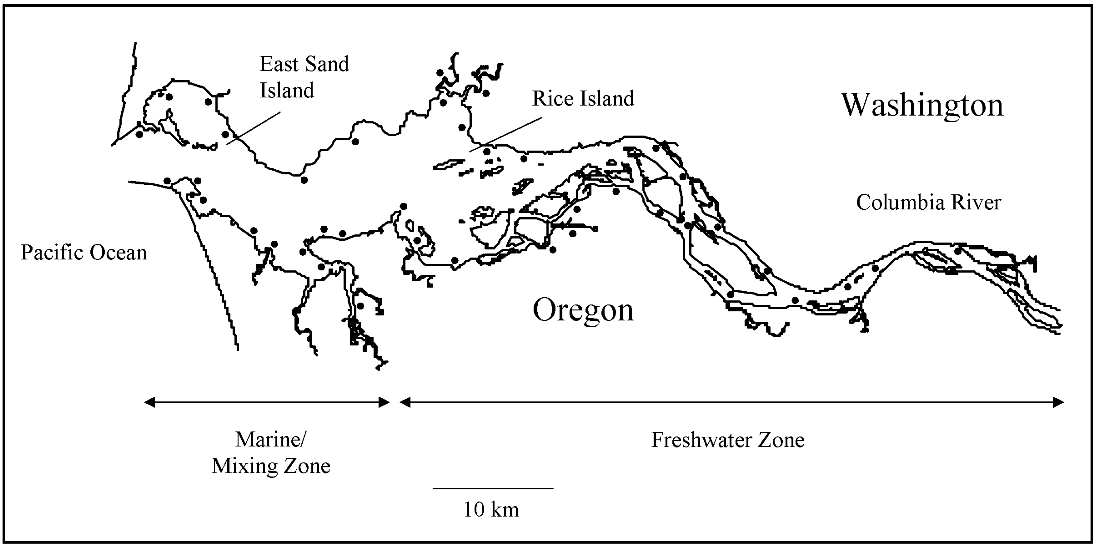

Figure 1. Columbia River estuary divided into the marine/mixing zone and the freshwater zone after Simenstad et al. (1990) and showing point count survey sites (•).

Rice and East Sand islands hosted large populations of nesting Caspian terns and double-crested cormorants during this study. Rice Island (river km 34) is an artificial island created by dredge material disposal that fully emerged in 1962 (USACE 1999). East Sand Island (river km 8) is a natural island that has seen occasional dredge disposal and other anthropogenic alterations (USACE 1999). Rice Island is located upstream of the typical maximum saltwater intrusion into the estuary, while East Sand Island is situated in the middle of the marine zone of the estuary (Figure 1; Fox et al. 1984, Simenstad et al. 1990).

Bird Populations

In 1998, all Caspian terns breeding in the estuary (8,650 pairs) nested on Rice Island, but in 1999 a small fraction of the estuary tern population was attracted to nest at a restored colony site on East Sand Island (Roby et al. 2002). In late May 1999, 550 pairs of terns were nesting at East Sand Island (6% of total), while 8,300 pairs nested at Rice Island (Roby et al. 2002). As the 1999 season progressed, some terns apparently moved their nesting activities from Rice Island to East Sand Island (Collis et al. 1999), with an estimated total of 1,400 nests (16% of all nests in the estuary) initiated there by early July (Roby et al. 2002).

Double-crested cormorants nested at Rice Island (1,082 adults counted in an aerial photo taken there in late May) and at East Sand Island (7,501 adults counted) in 1998 (Collis et al. 2002). In 1999, 10,226 adult cormorants were counted at the East Sand Island colony in late May (authors' unpublished data); however, no cormorants nested at Rice Island. In both years, smaller numbers (50-150 pairs) of double-crested cormorants nested on channel markers and pilings throughout the estuary.

Methods

Point Count Surveys

Riverbank point count surveys were conducted at 40 sites weekly from early April through July in both years (Figure 1). To select survey sites, both riverbanks (Oregon and Washington) were divided into 3-10 km segments, from the ocean jetty up to river kilometer 90, with segment length depending on shoreline accessibility. Within each segment, one survey site was selected, attempting to optimize the following criteria: (1) all sites together should sample all available aquatic habitats, (2) each site should provide visibility of presumed piscivorous waterbird foraging and/or roosting locations (e.g., pile dikes) when present, (3) adjacent sites should have non-overlapping views, and (4) each site should have access by automobile or short ($\leq$ 1 km) walk. A total of 21 sites were located on the Washington side of the river and 19 on the Oregon side. Rice Island was located at roughly the center of the survey area, with 22 and 18 sites located above and below the island, respectively.

It was possible for a single observer to sample all sites on one side or the other of the river in a single day (8-10 hours). For each day of surveying, the initial site visited was determined randomly; then the surveyor progressed up-river, visiting each site in sequence until the farthest up-river site on that side had been surveyed. The surveyor then drove directly to the most down-river site and proceeded up-river again until all sites on that side of the river had been visited that day. Surveys began between 06:30 and 08:00 at the first site and concluded at the last site between 17:00 and 19:30. This sampling pattern ensured that each site was visited at different times of day and at different stages of the tide cycle throughout the breeding season.

At each site, prominent landmarks (shoreline features and/or in-river features such as islands, navigational markers, etc.) were used to define a "viewing area" inside of which the actual surveys were conducted. All terns and cormorants within the viewing area were counted three times during each site visit and the maximum count of each species was recorded. For subsequent foraging habitat analyses only counts of birds potentially foraging (for terns, individuals in flight looking downward towards water; for cormorants, individuals diving underwater or floating on the water surface) were used; roosting or commuting birds were removed from total counts. Global Positioning System coordinates were taken for all viewing area landmarks at each site and mapped onto a digital U.S. Geological Survey (USGS) topographical map for the area. Areas of water contained in the defined polygon of each viewing area were then determined using Geographic Information System software (ARC/INFO; ESRI, Redlands, CA) and varied from 0.03 – 2.7 km^2 (median area 0.9 km^2), totaling 45 km^2, or approximately 9% of the estuary. Counts of foraging terns and cormorants were converted to densities for subsequent analyses using the estimated water area surveyed at each site.

Because few data were available to delineate site characteristics using biological criteria (e.g., fish communities present), survey sites were categorized into habitats based on predominant physical characteristics at three different spatial scales: (1) "large" scale, reflecting coarse salinity zones across the lower 90 km of the estuary, (2) "intermediate" scale, reflecting proximate foraging site characteristics such as water depth (predominant conditions across the viewing area at each point count observation site), and (3) "fine" scale, reflecting the proximate availability of a fine scale habitat feature: roosting habitat (presence/absence anywhere within the viewing area at each point count observation site). At the large scale, we divided the estuary into the freshwater zone (above river km 29) and the marine/mixing zone (river km 29 and below) after Simenstad et al. (1990; Figure 1) and categorized sites accordingly. At the intermediate scale, most survey sites were categorized based on water depth into main shipping channel areas (n = 15 sites), side channels (n = 8), or tidal flats (n = 11). Main shipping channel areas referred to the channel defined and maintained by the U.S. Army Corps of Engineers for large cargo vessels (13 m minimum depth at mean lower low water). Other channels of greater than 3 m depth were classified as side channels. Shallower areas, frequently with exposed sand and mud flats at low tides, were classified as tidal flats. A few sites were sufficiently different physically that they were categorized separately: tributaries and sloughs (n = 4) and ocean jetty areas (n = 2). Tributaries and sloughs were significantly smaller waterways connected to the main river only at one end, with different current and tidal regimes. Ocean jetty sites (n = 2) were at the very mouth of the river, with the ocean jetties in view, and having unique depth profiles (beaches to 20+ m depths within the viewing area) and much more dynamic wave action. Bathymetry data used to categorize sites was obtained from digitized USGS maps. A number of sites contained a combination of habitats and were classified according to the habitat making up the largest proportion of the viewing area, as calculated using ARC/INFO. Finally, at the fine scale for terns, sites were categorized as either having or lacking beaches and/or sand bar roosting habitat (n = 8 with, n = 32 without). For cormorants at this scale, sites were categorized as having pile dikes (n = 7), pilings (n = 13), pile dikes and/or pilings (n = 25), or lacking both pile dikes and pilings (n =15).

Caspian Tern Aerial Strip Transect Surveys

Aerial strip transect surveys were conducted using a Cessna 206 fixed-wing aircraft. The plane was flown at an altitude of approximately 150 m above ground level and airspeed of 100 knots and followed the same flight path during each survey. Flights began in Kelso, WA, at river kilometer 110, and proceeded downriver, with survey counts beginning at river kilometer 95. At river kilometer 75, as the river widened, the flight path shifted to the northern half of the river for the rest of the way to the river mouth, so that the northern channels, bays, tidal flats, etc. could be observed. When the ocean was reached, the plane turned around and proceeded upriver following the southern half of the river back to river kilometer 75, allowing observation of southern channels, bays, etc., completing the survey. Terns were highly visible below the plane, usually flying at $\leq$ 50 m above the river. The plane had no discernable effect on the flight behavior of terns. Survey flights occurred only when visibility was not impaired due to fog, precipitation, etc.

Due to the high density of terns within portions of the study area (sometimes $\geq$ 50 terns encountered per minute), the distance from observer could not be recorded quickly enough to make distance sampling feasible, so counts of terns seen in strip transects were performed and later converted to tern densities. Two observers, each looking out one side of the plane, counted flying Caspian terns seen within ca. 300 m of the aircraft during 1-minute intervals. Observers were calibrated to the 300 m distance during each flight prior to entering the survey area by observing a stretch of river outside the survey area of that approximate width. A third person aboard the plane recorded location (GPS coordinates) at the midpoint of each 1-minute count interval and recorded counts of both observers following each interval. After one count interval was completed, a short pause (15-60 seconds) occurred for data recording and to relieve observer eye fatigue before the next count began. In 1998, a total of 346 1-minute counts were conducted across seven different survey flights between 19 May and 6 July. In 1999, a total of 220 counts were conducted across five survey flights between 28 April and 21 June. Each 1-minute aerial count was converted into a measurement of Caspian tern density, assuming a constant airspeed of 100 knots/hr, a transect width of 0.6 km, and an assumed blind spot below the plane of width 100 m. The resulting area surveyed during each count was 1.5 km^2; total area surveyed per flight averaged 74 km^2, or 14% of the estuary. Each density estimate was interpreted as an estimate of density at the midpoint of the respective strip transect, where GPS coordinates were recorded.

Data Analyses

For all statistical tests, significance was set at $P \leq 0.05$.

Habitat Use Across Season

Two measures were used to evaluate habitat use: (1) densities of foraging terns or cormorants, and (2) selection indices, where the index was defined as the proportion of all foraging terns or cormorants seen in a particular habitat divided by the proportion of available habitat within the surveyed area which was the particular habitat type (Manly et al. 1993). At each spatial scale, point count densities for individual site visits were averaged for each site, grouped by habitat, and compared using either Wilcoxon rank-sum tests (2 habitat categories) or Kruskal-Wallis one-way ANOVA on ranks (> 2 habitat categories). Also at each scale, Manly et al.'s (1993) G-test was used on the selection indices data to test the null hypothesis that terns or cormorants were selecting habitats at random. Confidence limits were estimated for individual selection indices using a Bonferroni correction for multiple comparisons (Krebs 1999).

Within Season Trends

Seasonal changes in bird use of the estuary were examined at the large (salinity-zone) scale using Wilcoxon rank-sum comparisons of the average density of foraging terns and cormorants at point count sites in April and May versus June and July. These time periods approximated the nest initiation and incubating period (April and May) and chick-rearing and post-breeding residency period (June and July) for the birds. In addition, juvenile salmonid abundance was generally greater during the early period than the later period (Fish Passage Center 2002).

Tidal Influences

Effects of tides on densities of foraging terns and cormorants was investigated at the intermediate habitat scale. Periods of high and low tide stages were determined by centering 3-hour time periods on peak high and low tides; flood and ebb tide stages were defined to be the intervening (approximately 3-hour) time periods. Data from the U.S. Coast Guard tide gauge at Tongue Point (river kilometer 29) were used to identify peak high and low tides. For each survey day, density observations for each tide stage (high, ebb, low, flood) in each habitat were averaged together. Kruskal-Wallis one-way ANOVA tests on ranks were then used to compare these daily averages for each habitat.

Tern Foraging Range

Strip transect surveys were used to describe the relative distribution of foraging terns as a function of the distance from Rice Island. For each survey flight, the densities estimated for each 1 minute transect were sorted by distance from the Rice Island tern colony to the transect midpoint. The densities were then grouped into 5 km distance intervals and the average density for a given survey flight was generated for each distance interval (e.g., 1-5 km from colony, 6-10 km from colony, etc.; density was not estimated for the nearest 1 km to the colony due to the high level of tern activity this close to the colony that was not related to foraging). To determine estimates of the densities of terns for respective distances from the colony across the entire season, the density estimate for each distance interval was grouped for all flights in a given year and averaged. Once these density estimates were obtained, to estimate the actual number of terns using foraging habitat at each respective distance from the colony, the amount of river habitat (i.e. non-island, non-riverbank) was first estimated for each concentric ring of distance from the colony (i.e. the total river area within 1-5 km from the colony, 6-10 km from the colony, etc.) using ARC/INFO. Finally, for each distance interval, the density was multiplied by the area to estimate the number of terns.

Results

Median densities of foraging Caspian terns were higher in the marine/mixing zone of the estuary in both 1998 and 1999, but differences in density were not significant in either year (Figure 2A). Selection index analyses indicated proportionally greater use of the marine/mixing zone in 1998 ($\chi_1^2 = 22.4$, $P < 0.001$; Table 1), but not in 1999. Double-crested cormorant densities were similar in each zone in both years (Figure 2B) but disproportionately higher use of freshwater sites was indicated in 1999 ($\chi_1^2 = 7.8$, $P = 0.005$; Table 1).

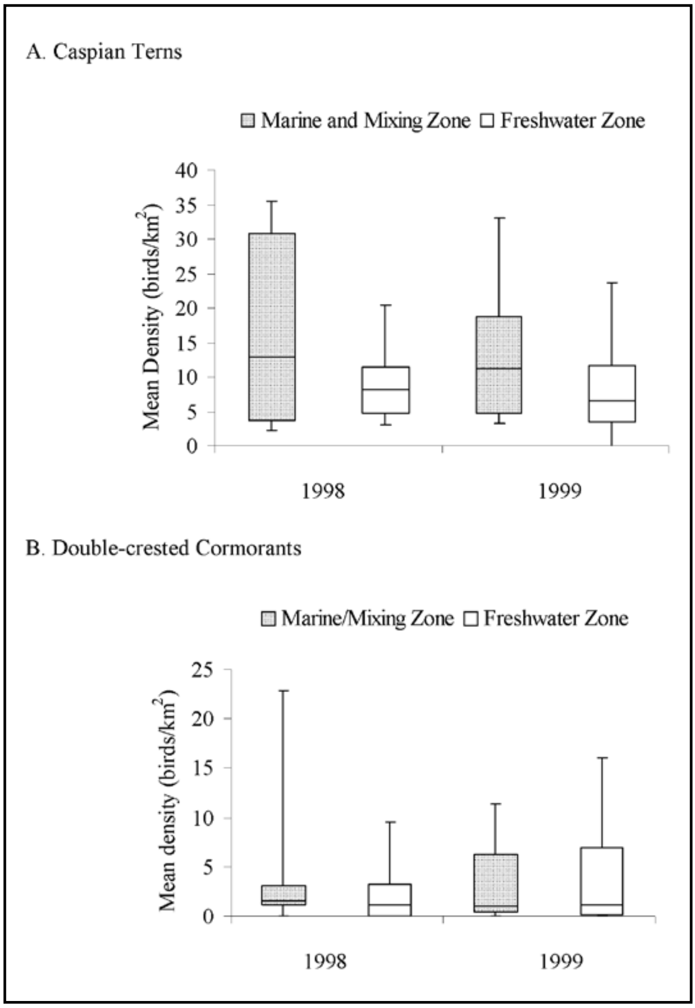

Figure 2. Densities of foraging (A) Caspian Terns and (B) Double-crested Cormorants in the marine/mixing zone and the freshwater zone of the Columbia River estuary in 1998 and 1999. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

TABLE 1. Selection indices (95% confidence intervals) for tern and cormorant use of the freshwater and marine/mixing zones of the Columbia River estuary. The selection index was defined as the proportion of all foraging terns or cormorants seen in a particular habitat divided by the proportion of available habitat within the surveyed area which was the particular habitat type (Manly et al. 1993). Values in bold are significantly different than zero at the 95% confidence level.

	Caspian Terns		Double-crested Cormorants	
Zone	1998	1999	1998	1999
Freshwater	**0.81 (0.72-0.91)**	0.98 (0.87-1.10)	1.13 (0.90-1.36)	**1.20 (1.03-1.37)**
Marine	**1.23 (1.11-1.36)**	1.02 (0.88-1.16)	0.84 (0.55-1.12)	**0.75 (0.53-0.96)**

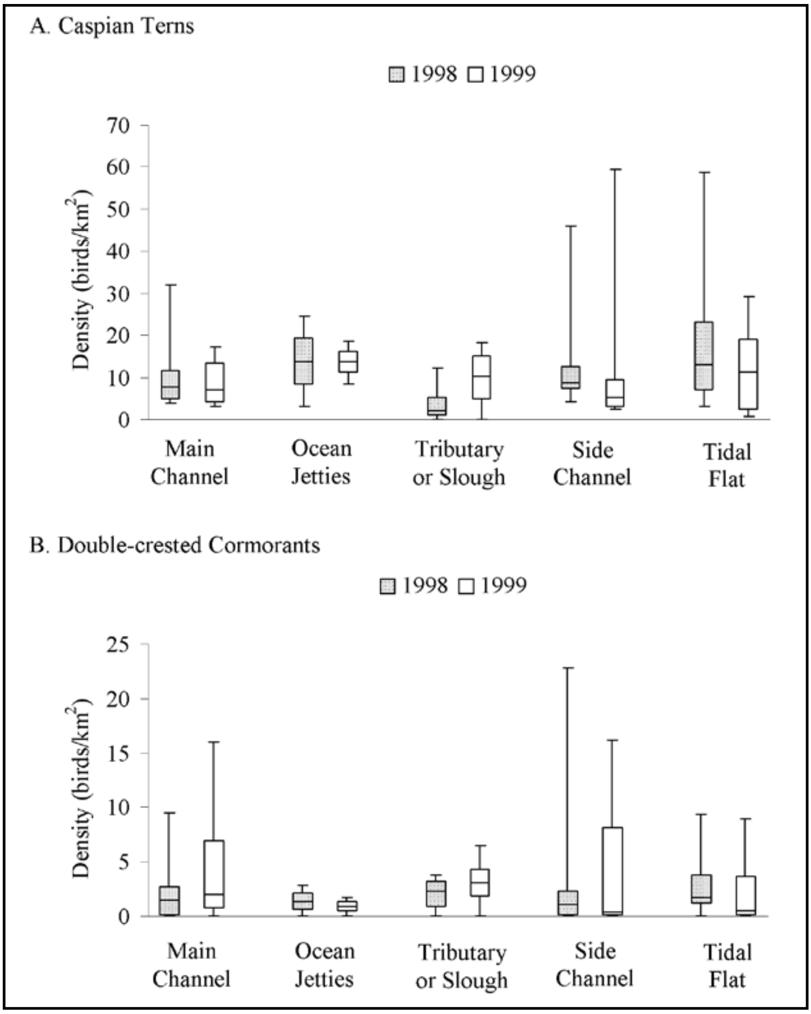

Figure 3. Densities of foraging (A) Caspian Terns and (B) Double-crested Cormorants in intermediate scale habitats of the Columbia River estuary in 1998 and 1999. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

At the intermediate scale, Kruskal-Wallis one-way ANOVA on ranks did not detect significant differences in densities of foraging terns between sites (Figure 3A). However, selection analysis did indicate disproportionate use of habitats, in both 1998 (χ_4^2 = 33.7, P < 0.001; Table 2) and 1999 (χ_4^2 = 15.6, P = 0.003; Table 2). In 1998, main channel and tributary/slough habitats were used

TABLE 2. Selection indices (95% confidence intervals) for tern and cormorant use of intermediate scale habitats of the Columbia River estuary. The selection index was defined as the proportion of all foraging terns or cormorants seen in a particular habitat divided by the proportion of available habitat within the surveyed area which was the particular habitat type (Manly et al. 1993). Values in bold are significantly different than zero at the 95% confidence level.

	Caspian Terns		Double-crested Cormorants	
Habitat	1998	1999	1998	1999
Main Channel	**0.82 (0.71-0.93)**	0.92 (0.78-1.05)	1.12 (0.84-1.39)	**1.48 (1.28-1.69)**
Ocean Jetties	**1.71 (1.11-2.31)**	**1.93 (1.19-2.67)**	**0.32 (0.00-0.96)**	**0.13 (0.00-0.45)**
Tributary or Slough	**0.28 (0.00-0.76)**	1.38 (0.14-2.63)	1.39 (0.00-3.96)	1.45 (0.00-3.49)
Side Channel	0.91 (0.64-1.17)	0.93 (0.62-1.24)	0.80 (0.20-1.40)	0.76 (0.30-1.21)
Tidal Flat	**1.22 (1.06-1.39)**	0.99 (0.80-1.17)	1.01 (0.63-1.39)	**0.52 (0.28-0.76)**

less by terns than expected and tidal flats more so. Ocean jetty areas were used disproportionately more by terns in both 1998 and 1999. Densities of cormorants were similar across intermediate habitat sites in both years (Figure 3B), however disproportionate use was observed in 1999 (χ_4^2 = 38.3, $P < 0.001$). Cormorants used main channel sites more than expected and tidal flats and the ocean jetty areas less so in that year (Table 2).

At the fine scale, median densities of foraging terns were higher at sites having roosting beaches in both years (1998: 22.3 terns/km^2 at sites with roosts and 8.0 terns/km^2 without; 1999: 10.6 and 7.5 terns/km^2 respectively), but differences were not statistically significant. Selection analysis again indicated disproportionate use in both years, however (1998: χ_1^2 = 51.5, $P < 0.001$; 1999: χ_1^2 = 9.8, P = 0.002), with use for foraging of sites with roosting habitat at higher levels than expected (Table 3). Higher densities of foraging cormorants were observed at sites with pile dikes and/or pilings in 1999 (median density = 2.1 cormorants/km^2) compared to sites without pile dikes or pilings (median density = 0.5 cormorants/km^2; Wilcoxon approximate z = 1.96, P = 0.05), but this trend was not significant in 1998 (1.7 and 1.0 cormorants/km^2, respectively). Foraging cormorants were also seen at higher densities at sites with only pile dikes (i.e., no pilings) in 1999 (6.9 vs. 0.5 cormorants/km^2; z = 2.05, P = 0.04) but not in 1998 (1.7 vs. 1.0 cormorants/km^2). Trends in densities between sites having only pilings and those lacking both pilings and pile dikes followed the same pattern but were not statistically different in either year (1998: 1.8 vs. 1.0 cormorants/km^2; 1999: 1.0 vs. 0.5 cormorants/km^2). Selection analysis followed a similar pattern—disproportionate use of sites with pile dikes and/or pilings was observed in 1998 and 1999 (1998: χ_1^2 = 4.7, P = 0.03; 1999: χ_1^2 = 26.7, $P < 0.001$), and for sites with only pile dikes in 1999 (χ_1^2 = 34.6, $P < 0.001$), but not for sites having only pilings in either year (Table 3).

Densities of foraging terns and cormorants generally increased at sites in the marine/mixing

TABLE 3. Selection indices (95% confidence intervals) for tern and cormorant use of sites for foraging based on the presence or absence of particular roosting habitat features in the Columbia River estuary. The selection index was defined as the proportion of all foraging terns or cormorants seen in a particular habitat divided by the proportion of available habitat within the surveyed area which was the particular habitat type (Manly et al. 1993). Values in bold are significantly different than zero at the 95% confidence level.

	Caspian Terns		Double-crested Cormorants	
Roosting habitat availability	1998	1999	1998	1999
With roosting beaches	**1.73 (1.44-2.02)**	**1.36 (1.05-1.67)**		
Without roosting beaches	**0.84 (0.78-0.90)**	**0.92 (0.85-0.99)**		
With pile dikes and/or pilings			1.16 (0.99-1.32)	**1.28 (1.17-1.39)**
Lacking both pile dikes and pilings			0.69 (0.36-1.02)	**0.44 (0.23-0.66)**
With only pile dikes			1.42 (0.81-2.03)	**2.07 (1.64-2.51)**
Lacking both pile dikes and pilings			0.79 (0.50-1.09)	**0.48 (0.27-0.69)**
With only pilings			1.07 (0.73-1.42)	1.15 (0.84-1.47)
Lacking both pile dikes and pilings			0.92 (0.54-1.30)	0.83 (0.49-1.17)

zone during the latter half of the breeding season, while densities at sites in the freshwater zone either decreased or did not increase as substantially (Figures 4 and 5). The increase in densities at sites in the marine/mixing zone was significant for terns in 1998 (Wilcoxon approximate $z = 2.58$, $P = 0.01$), but not in 1999 ($z = 1.42$, $P = 0.16$). For cormorants there was also a significant increase in densities in the marine/mixing zone in 1998 ($z = 2.45$, $P = 0.01$), but not in 1999 ($z = 0.93$, $P = 0.35$). At sites in the freshwater zone, tern densities increased in 1998 ($z = 2.99$, $P = 0.003$), although not as markedly as sites in the marine and mixing zone, but in 1999 no difference in tern densities with stage of the breeding season was seen ($z = 1.22$, $P = 0.22$). Densities of foraging cormorants at sites in the freshwater zone were significantly lower ($z = 1.97$, $P = 0.05$) in the latter portion of the 1999 breeding season, but did not significantly change in 1998 ($z = 0.10$, $P = 0.92$).

Tide stage significantly affected densities of foraging terns and cormorants in some habitats during 1998. In tidal flats, tern densities were higher at low and intermediate (ebb and flood) tides (median densities were 20.4 and 9.0 terns/km^2 respectively), than those observed at high tides (5.3 terns/km^2; Kruskal-Wallis $\chi_2^2 = 19.7$, $P < 0.001$). In side channel areas, median cormorant densities were 1.13 cormorants/km^2 during high tides, compared to 0.12 cormorants/km^2 at other tide stages ($\chi_3^2 = 10.0$, $P = 0.02$). Near ocean jetties, median cormorant densities were 1.77 and 1.46 cormorants/km^2 during high and ebb tide stages, respectively, and 0.04 and 0.02 cormorants/km^2 during low and flood tide stages, respectively ($\chi_3^2 = 8.08$, $P = 0.05$). No significant differences

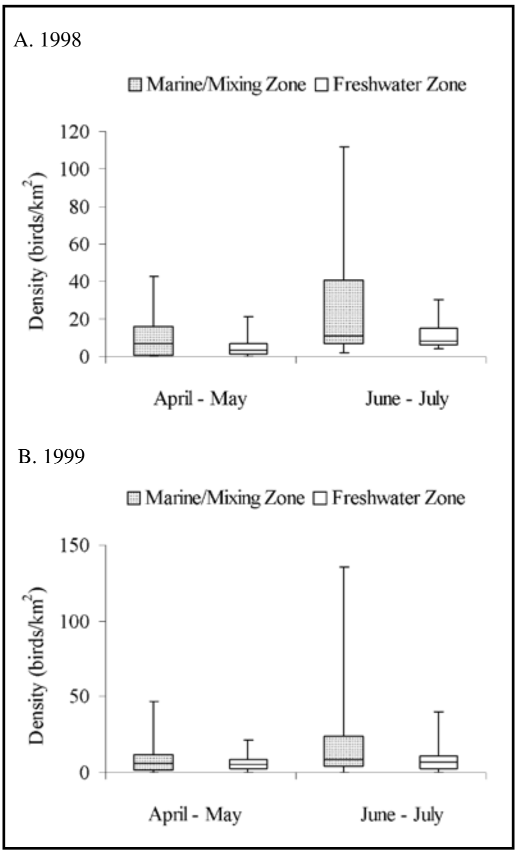

Figure 4. Seasonal use of the Columbia River estuary by foraging Caspian Terns. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

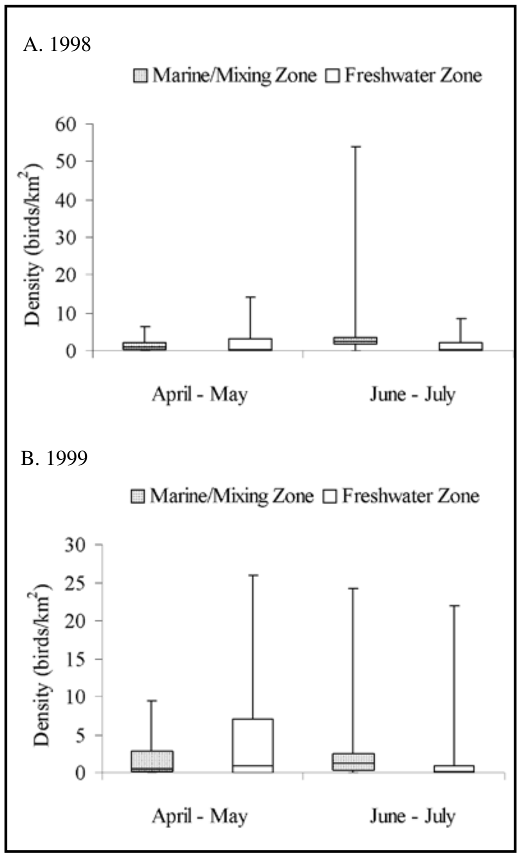

Figure 5. Seasonal use of the Columbia River estuary by foraging Double-crested Cormorants. Boxplots show 25th, 50th, and 75th percentiles; whiskers indicate minimum and maximum values.

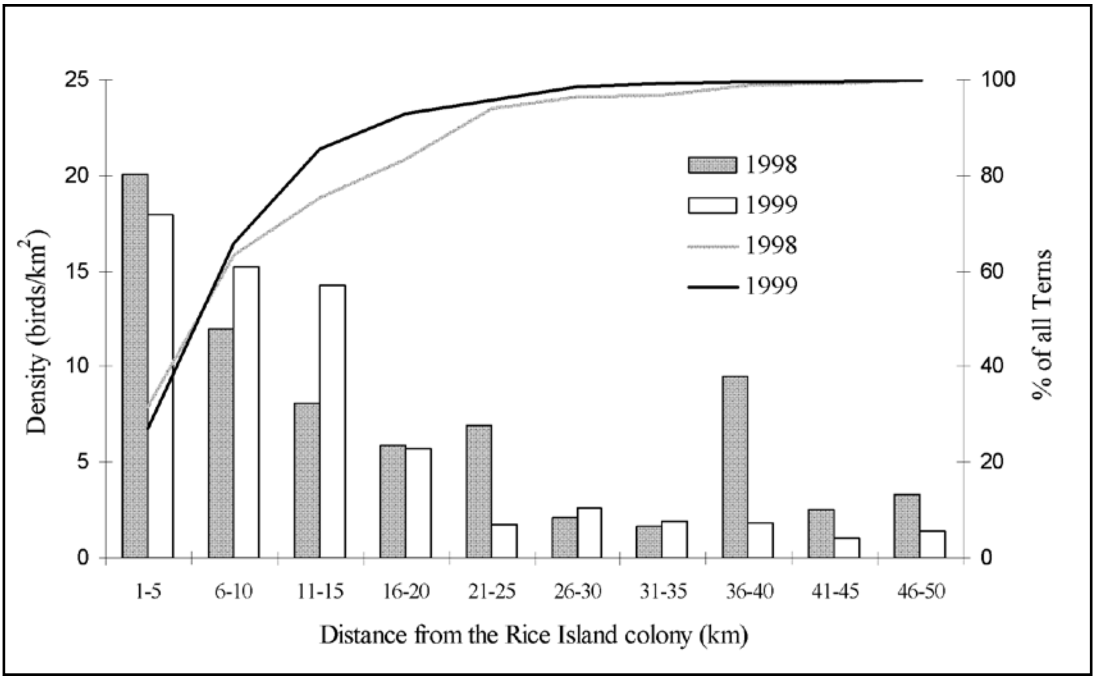

Figure 6. Densities (bars, left axis) and cumulative percentages (lines, right axis) of foraging Caspian Terns in the Columbia River estuary by distance from the Rice Island colony site.

in foraging densities at different tide stages were seen for either terns or cormorants in any habitat in 1999.

Densities of foraging terns were highest within 5 km of Rice Island in both 1998 and 1999 and generally decreased with increasing distance from Rice Island (Figure 6). In 1998, spikes in densities were observed 21-25 km from Rice Island and 36-40 km from Rice Island, corresponding to areas near the river mouth and at Eureka Bar (river kilometer 80-85). In 1999, densities of foraging terns trended higher for areas within 15 km of Rice Island compared to 1998.

Estimates of numbers of foraging and commuting terns sorted by distance from the Rice Island colony indicated that in 1998, 50% of terns were within 8 km of Rice Island, 90% within 23 km, and 95% within 27 km (Figure 6). In 1999, 50% were within 8 km, 90% within 18 km, and 95% within 24 km.

Discussion

In the Columbia River estuary during 1998 and 1999, Caspian terns and double-crested cormorants sometimes appeared to be generalist predators that utilized survey site habitats in proportion to their availability. Foraging densities of each species did not differ significantly among habitats, in many cases. Selection indices analysis was apparently a more sensitive measure of habitat selection, however, and often indicated birds were not using sampled habitats randomly.

Of the exceptions to a generalist foraging pattern that were observed, a few suggest the underlying prey availability that often drives particular habitat selection. First, densities of foraging cormorants were sometimes higher at sites with pile dikes (or with pile dikes and/or pilings) – cormorants often selected for these sites early in the season. We frequently observed cormorant foraging aggregations (often associated with terns and gulls [*Larus* spp.]) in the downstream wake of pile dikes, apparently taking advantage of disoriented or resting fish in the slower current of the wake. Second, as we predicted, terns sometimes made disproportionately greater use of tidal flats particularly at low tide and, to a lesser extent, intermediate tide stages. Shallow water during lower tides may make more benthic fishes available to plunge-diving terns, which likely do not capture fish deeper than a meter below the water surface

(Cuthbert and Wires 1999), and low tides may also concentrate fish in narrow channels surrounded by exposed mud flats and presumably make the fish more vulnerable to tern predation. Third, both terns and cormorants made greater use of the marine/mixing zone of the estuary, relative to the freshwater zone, in the latter half of the breeding season. This corresponds to the decline in abundance of out-migrating juvenile salmonids after early June (Fish Passage Center 2002) and also is reflected in the seasonal decline in salmonids in the diet of terns and cormorants at both Rice and East Sand islands (Roby et al. 2002).

As we predicted, cormorants sometimes selected main channel habitat for foraging, reflecting their ability to pursuit dive to depths after prey. A strong deviation from random selection of foraging sites that we did not anticipate was the disproportionately greater use of sites with roosting beaches by terns for foraging. It is not clear if the availability of roosting habitat drives this greater foraging use or if favorable prey conditions drive both greater foraging and roosting at these sites. The area surrounding the south river jetty was a location particularly favored for foraging and roosting, especially later in the season, and drove the result of disproportionately greater use of sites both with roosting habitat and ocean habitat.

Proximity to the colony site was apparently a more important factor than salinity in determining foraging locations for Caspian terns as we predicted, although not for cormorants. Across the entire season, terns displayed disproportionately greater foraging in the freshwater portion of the estuary in 1998 close the Rice Island colony site; however, apparently no selection occurred between fresh and marine waters in 1999. This lack of greater foraging activity in the freshwater zone in 1999 at least in part reflects the relocation of a portion of the tern population to nest at East Sand Island, located in the marine zone of the estuary. Contrary to our expectations, we did not see significantly greater numbers of double-crested cormorants in the marine/mixing zone of the estuary in either year, close to where the majority of cormorants nested at East Sand Island, however, and did see disproportionate use of the freshwater zone in 1999. This suggests that even though it was more distant, the freshwater zone of the estuary was an important foraging area for cormorants, particularly early in the breeding season. This is consistent with observations of radio-tagged cormorants nesting at East Sand Island frequently traveling to the freshwater zone of the estuary to forage (Anderson et al. 2004).

Despite documentation of foraging trips of breeding Caspian terns in excess of 60 km (Soikkeli 1973, Gill 1976), our observations indicate that in the Columbia River estuary most foraging occurs much closer to the breeding colony. In both 1998 and 1999, 50% of activity was within 8 km of Rice Island and less than 5% occurred further than 27 km away. Our foraging range results are potentially biased by the geographic extent of our survey sampling area. Opportunistic surveys we occasionally conducted at sites outside the Columbia River estuary, including the Oregon coast to the south, the Washington coast to the north, and Willapa Bay (a large coastal bay ≥ 8 km to the north of the Columbia River), indicated that terns and cormorants sometimes foraged in these areas. Occasional observations of commuting flights (birds flying toward the Columbia River estuary carrying fish) indicated that at least a portion of these birds traveled between these sites and the Columbia River estuary, and presumably some portion were birds breeding in the Columbia River estuary. In general, densities of foraging terns and cormorants were lower in these areas than within the Columbia River estuary, and we did not find evidence of any preferred foraging sites outside the estuary. The general conclusion that both species are responding opportunistically to nearby prey resources within the estuary is supported.

Additional studies to identify prey taken by terns and cormorants and/or to sample fish communities present in the respective habitats with disproportionately greater use by birds could further focus habitat management priorities for resource managers seeking to reduce avian predation upon ESA-listed juvenile salmonids. Our anecdotal observations did suggest, for example, that salmonids are the primary prey taken by cormorants at sites with pile dikes, so reduction of foraging and roosting by cormorants at these sites might reduce consumption of salmonids. Even if foraging by cormorants was reduced at these sites, however, further studies would be necessary to demonstrate actual reductions in total salmonid consumption by the cormorant population, given the numerous other foraging areas in the Columbia River estuary where cormorants may prey upon salmonids. Significant loss of habitat has occurred in the estuary in the last 150 years, particularly marsh and swamp habitat, due to mostly anthropogenic causes, such as diking and filling wetlands for conversion to pasture (Thomas 1983). It is not possible based on our study to assess how large scale restoration of these now largely absent habitats would influence foraging patterns of terns and cormorants.

Relocation of tern and cormorant colony sites to locations where nearby foraging environments would have lower relative abundance of salmonids may be a more straightforward method to reduce predation on smolts. One such relocation has occurred within the Columbia River estuary, where by 2001, all Caspian terns nesting in the estuary were attracted to nest at East Sand Island, and Rice Island had been abandoned as a nesting site (Roby et al. 2002). Juvenile salmonids made up a much smaller proportion of the diet of terns nesting at East Sand Island (32 – 46 % during 1999– 2002) than at Rice Island (76 – 90% during 1997 – 2000; Roby et al. 2002). Our foraging range data help explain why this dietary shift occurred. Only a small fraction of foraging activity occurred farther than 20 km from the Rice Island colony when all or most of the terns nested there during the two years of this study. If foraging behavior was similar for terns nesting at East Sand Island, then the majority of foraging by those terns was confined to the surrounding marine/mixing zone of the estuary, where marine forage fish species, such as anchovy, herring, and surfperch were more available. These species were rarely present in the freshwater zone of the estuary where terns nesting at Rice Island typically foraged (Hinton et al. 1995).

Attraction of a portion of the Caspian terns currently nesting at the East Sand Island colony to new and/or restored colony sites elsewhere along the Pacific Coast has been suggested as a technique to further reduce impacts of terns upon Columbia River salmonid populations (Roby et al. 2002, USFWS 2005). This technique may also reduce risks to this large fraction (ca. 2/3) of the Pacific Coast Caspian tern population from potential local catastrophes, such as disease, storms, predators, human disturbance, and oil spills (USFWS 2005). Many factors would influence site selection for any future relocation efforts, but proximity to local fisheries of conservation concern would be one important factor. The foraging range data presented here allow preliminary judgments on possible interactions between terns nesting at proposed colony sites and nearby forage fish resources, although investigation of local conditions may still be warranted. Further research would be required to develop similar foraging range estimates for cormorants.

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