Foraging Ecology of Caspian Terns in the Columbia River Estuary, USA

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Abstract.—Comparisons were made of the foraging ecology of Caspian Terns (*Sterna caspia*) nesting on two islands in the Columbia River estuary using radio telemetry and observations of prey fed to chicks and mates at each colony. Early in the chick-rearing period, radio-tagged terns nesting at Rice Island (river km 34) foraged mostly in the freshwater zone of the estuary close to the colony, while terns nesting on East Sand Island (river km 8) foraged in the marine or estuarine mixing zones close to that colony. Late in the chick-rearing period, Rice Island terns moved more of their foraging to the two zones lower in the estuary, while East Sand Island terns continued to forage in these areas. Tern diets at each colony corresponded to the primary foraging zone (freshwater vs. marine/mixing) of radio-tagged individuals: Early in chick-rearing, Rice Island terns relied heavily on juvenile salmonids (*Oncorhynchus* spp., 71% of identified prey), but this declined late in chick-rearing (46%). East Sand Island terns relied less on salmonids (42% and 16%, early and late in chick-rearing), and instead utilized marine fishes such as Anchovy (*Engraulis mordax*) and Herring (*Clupea pallasi*). Throughout chick-rearing, Rice Island terns foraged farther from their colony (median distance: 12.3 km during early chick-rearing and 16.9 km during late chick-rearing) than did East Sand Island terns (9.6 and 7.7 km, respectively). The study leads to the conclusion that Caspian Terns are generalist foragers and make use of the most proximate available forage fish resources when raising young. *Received 18 August 2004, accepted 25 March 2005.*

Key words.—Caspian Tern, *Sterna caspia*, salmonids, *Oncorhynchus*, Columbia River, radio telemetry.

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The foraging ecology of nest-based central place foragers, such as birds, is constrained by the location of the nest site. Foraging close to the nest allows individuals to minimize travel time and energetic expense, and thereby allocate a greater proportion of available time to foraging, rather than commuting to foraging areas, and a greater proportion of acquired energy to demands at the nest. Other factors may influence this fundamental constraint. More distant foraging sites may be utilized if they are particularly profitable because of greater prey availability, greater nutritional or energetic value of prey, or when site-specific knowledge confers an advantage on the forager.

This study examined the foraging ecology of the Caspian Tern (*Sterna caspia*), a piscivorous forager, during the chick-rearing period at two breeding colonies in the Columbia River estuary, on the Pacific coast of North America. One of the colony sites, Rice Island, is a dredged material disposal island at river km 34 (i.e., 34 km from the mouth of the river) in the freshwater zone of the estuary (*sensu* Simenstad *et al.* 1990), and had been used by nesting terns since 1986. Diet studies indicated that terns nesting on Rice Island relied primarily on out-migrating juvenile salmonids (*Oncorhynchus* spp.) as prey (73-81% of diet; Collis *et al.* 2002). Of particular management concern were potential impacts of tern predation upon the 12 of 20 "evolutionarily significant units" of Columbia River salmonids that are listed under the U.S. Endangered Species Act (National Marine Fisheries Service 2000; Roby *et al.* 2003). In 1999, in addition to nesting on Rice Island, Caspian Terns nested at a new colony site on East Sand Island at river km 8 (Roby *et al.* 2002), in the marine zone of the estuary (*sensu* Simenstad *et al.* 1990). Resource managers suggested that terns nesting at East Sand Island would rely less on juvenile salmonids as prey and implemented a pilot study to attract terns there to test this hypothesis (United States Army Corps of Engineers 1999).

Several factors suggested that terns attracted to nest on East Sand Island might continue to forage primarily in the freshwater zone of the estuary and to rely heavily on juvenile salmonids. Rice Island is 21 km (straight line distance) from East Sand Island, well within the 60 km documented maximum foraging range of nesting Caspian Terns (Soikkeli 1973; Gill 1976). Salmonid abundance, buoyed by hatchery production, was high and predictable; annual hatchery production of juvenile salmonid smolts totaled 150-200 million fish per year throughout the Columbia River basin during 1987-1998 (Collis *et al.* 2001). Combined with wild production, but after estimated mortality during down-river migration, approximately 97 million smolts were predicted to enter the estuary in 1998, a typical year (United States Army Corps of Engineers 2000). Terns attracted to East Sand Island were probably former Rice Island breeders, and would consequently have a history of foraging for salmonids in the vicinity of Rice Island. Foraging site fidelity has been demonstrated in other piscivorous larids within a single breeding season (Becker *et al.* 1992; Irons 1998), though not previously for the Caspian Tern (Sirdevan and Quinn 1997).

Other factors, however, suggested that terns attracted to nest on East Sand Island might forage in close proximity to their colony and take fewer juvenile salmonids and favor marine prey. Although relative abundance was unknown, previously published surveys indicated a greater diversity of forage fish species lower in the estuary (Bottom and Jones 1990), including marine fish such as Northern Anchovy (*Engraulis mordax*), Pacific Herring (*Clupea pallasi*), Smelt (Osmeridae), and Surfperch (Embiotocidae). Comparisons of diets of the Double-crested Cormorant (*Phalacrocorax auritus*) and Glaucous-winged/Western Gull (*Larus glaucescens* × *L. occidentalis*) nesting on both Rice Island and East Sand Island indicated less reliance upon salmonids by these bird species nesting on East Sand Island (Collis *et al.* 2002). Additionally, Caspian Terns returning to Rice Island from foraging locations down-river relied less on salmonids than did those returning from up-river locations (Collis *et al.* 2002). Finally, diet composition of Common Terns (*Sterna hirundo*) nesting on various islands within a large bay in the German Wadden Sea strongly reflected the location of the colony within the freshwater/marine spectrum (Frank 1992).

The primary objective of this study was to compare and contrast the spatial distribution of foraging and the resulting patterns of colony attendance and diet composition for Caspian Terns nesting at the two colonies in the Columbia River estuary. Specific hypotheses tested were:

1. Caspian Terns nesting at East Sand Island would forage in the marine/estuarine mixing zones near their colony site, as opposed to the freshwater zone closer to Rice Island.
2. Seasonal declines in availability of juvenile salmonids would be associated with less foraging in the freshwater zone for terns nesting on both Rice Island and East Sand Island.
3. Diet composition of terns would reflect the habitats in which they foraged; marine forage fishes would be more prevalent in the diet of terns that foraged in the marine or estuarine mixing zones of the estuary, while salmonids would be more prevalent in the diet of terns that foraged in the freshwater zone of the estuary.
4. Foraging conditions (indirectly quantified using colony attendance rates and foraging distances from the colony) would be as favorable for terns nesting at East Sand Island as for those nesting at Rice Island.

METHODS

Study Area

Caspian Terns nesting in the Columbia River estuary (Fig. 1) were studied at two locations; Rice Island (river km 34) and East Sand Island (river km 8) during the 1999 breeding season. In 1999, an estimated 8,300 breeding pairs of terns initiated nests at the Rice Island colony and approximately 1,400 pairs nested at the new East Sand Island colony (Roby *et al.* 2002). Due to its position farther up the estuary, Rice Island is in the freshwater zone (above river km 29), while East Sand Island is in the middle of the marine zone of the estuary (river km

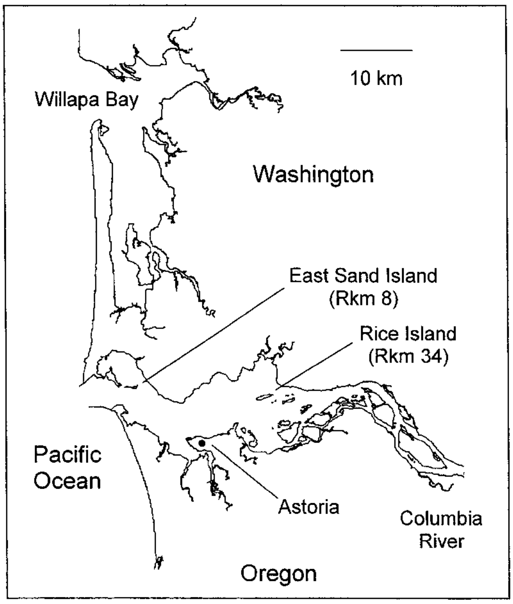

Figure 1. Columbia River estuary, with locations of Rice Island and East Sand Island, and Willapa Bay, the next large estuary to the north.

0-12; Fox *et al.* 1984; Simenstad *et al.* 1990). Tidal amplitudes average 2.4 m at the river's mouth (Fox *et al.* 1984).

Data Collection

Thirty terns were captured at Rice Island during 11-22 May and 22 terns were captured at East Sand Island during 24 May-7 June. All were captured during the middle or late phase of incubation. Radio transmitters (Advanced Telemetry Systems, Inc., Isanti, Minnesota) weighing 9-10 g (~1.5% of body mass) were attached to the central 4-5 retrices of each tern using plastic cable ties and Loctite 404 adhesive (Irons 1998). Subsequent observations of tagged terns indicated no behavioral abnormalities; normal breeding activities, such as courtship feeding and resumption of incubation shifts, were observed within a few hours following tagging and release.

Radio-tagged terns were tracked on 18 occasions during 28 May-13 July using a Cessna 206 fixed-wing aircraft with an antenna mounted to each wing strut on either side of the fuselage. Locations of all radio-tagged terns detected during a flight (usually >95% of all tagged birds) were pinpointed to within approximately 1 km^2 by circling the location of the transmitter signal. Precision of locations was verified through blind tests of tracking personnel, using reference transmitters placed at unannounced locations within the study area. Locations of radio-tracked terns were plotted on maps from which GPS coordinates were later derived. During any particular flight, radio-tagged terns were detected either at one of the two colony sites or away from both colonies (hereafter designated as "off-colony" locations). Flights departed from Kelso, Washington (river km 110) and followed a consistent flight path down-river to the mouth of the river, overland north to Willapa Bay, north to the mouth of the bay, south along the Washington coast, across the mouth of the Columbia River, south to approximately Seaside, Oregon, overland to Astoria, Oregon, and finally back up-river to Kelso. Four flights included side trips to Grays Harbor, Washington, > 65 km to the north of the Columbia River estuary, to investigate tern use of this large, distant estuary.

At each colony site, radio-tagged terns were continuously monitored between 28 May and 11 July using a telemetry receiver and automated data collection computer (Advanced Telemetry Systems, Inc., Isanti, Minnesota). These systems scanned day and night for all radio-tagged terns, with an approximate cycle of 30 minutes. Correct system operation was verified using a reference transmitter located at each colony and by scanning "dummy" frequencies (where no transmitters were in operation) during every cycle, in addition to periodic manual confirmation of correct system function. At both sites, the reference transmitters were correctly detected in > 95% of all cycles and "dummy" transmitters were detected (false positive detections) during <1% of all cycles. On occasions when system functionality was poor or lost (e.g., due to loss of battery power), data for the entire day were omitted from the analysis. During periods of normal system operation, lack of detection by the colony data loggers was interpreted as an absence from the colony area and immediate surroundings, presumably due to the bird engaging in a foraging trip. Terns were classified as breeding at Rice Island or East Sand Island based on continuous nighttime attendance at the respective colony. This classification was confirmed through visual observation of breeding activity by the radio-tagged terns throughout the season. Terns that did not attend either colony at night were assumed to be failed breeders, and were excluded from data analysis.

Diet composition of Caspian Terns nesting at each colony site was assessed using visual identification of fish brought back to the colony in the bills of terns as courtship or chick meals (Collis *et al.* 2002). During each day and for each tide cycle (i.e., one high and low tide), approximately 25 fish were identified to family using binoculars and spotting scopes from blinds adjacent to the colony (Roby *et al.* 2002). Prey identification at high tide occurred from 90 minutes before the actual high tide until 90 minutes after, and similarly for low tides. Diet composition during ebb and flood tide periods was assumed intermediate between high and low tide periods, so that averaging diet composition of high and low tide periods provided an adequate representation of diet for all time periods.

Statistical Analyses

Distributions of off-colony detections were categorized into five spatial areas, three within the Columbia River (after Simenstad *et al.* 1990) and two outside: (1) the estuary freshwater zone (river km 30 and above), (2) the estuarine-mixing zone (river km 13-29), (3) the estuary marine zone (river km 0-12), (4) Willapa Bay to the north, and (5) coastal Oregon and Washington. Repeated off-colony detections across the season for an individual bird are not independent, so a single detection for each bird was randomly selected and used to compare the spatial distributions of detections for terns nesting at each island (White and Garrott 1990). Because one or the other group of birds seldom visited some regions, Fisher's Exact Test was used to make comparisons to allow for small sample sizes (< 5) in some spatial categories.

Distance from colony for all off-colony detections throughout the time periods of interest (early chick-rearing period [28 May-18 June], late chick-rearing period [19 June-13 July], entire chick-rearing period) were first averaged for each tern, then pooled to make within-season and between-colony comparisons of foraging range. Between colony means and equal variance two-sample t-test comparisons included birds breeding during any portion of the study period. Within-season means and paired t-test comparisons included only birds breeding in both the early and late chick-rearing periods.

To analyze patterns of colony attendance of breeding Caspian Terns, presence/absence data at each colony (as measured by the automated data loggers) were examined at two temporal scales. To investigate diurnal patterns of attendance, data for each bird was divided into one-hour time blocks across daytime hours (dawn to dusk) and pooled for all days in the sampling period. The proportion of all data logger cycles when the bird was detected during each daylight hour block was used as the measure of colony attendance. As the distribution of this proportion was approximately normal for all birds, multiple linear regression was used to investigate daily attendance patterns for each bird separately (PROC REG; SAS Institute, Inc., Cary, North Carolina). Models investigating linear, quadratic, and cubic relationships between time of day and colony attendance were tested and the most appropriate model for each bird was selected using extra-sum-of-squares F-tests (Ramsey and Schafer 1997), with complex models tested against all simpler models. Possible serial correlation was tested using the Durbin-Watson test statistic (DW); if serial correlation was detected or could not be ruled out, regressions were recalculated using first-order autoregressive corrections.

Trends in colony attendance across the season were investigated by pooling data (proportion of all daytime data logger cycles when the bird was detected) for each bird into five 1-week blocks that covered the duration of the chick-rearing period. Weekly attendance for all birds was considered in a single logistic regression analysis, along with co-variates for tide conditions and colony. Tide conditions during each week were classified as a spring tide series if a majority of days fell on or within three days of a new or full moon, or as a neap tide series if a majority of days fell on or within three days of the first or last quarter phase (half moon). Because consecutive weekly measures of colony attendance for each bird may lack independence, quasi-likelihood generalized estimating equations (GEE; Liang and Zeger 1986; Hardin and Hilbe 2003) were used for the regression (PROC GENMOD; SAS Institute, Inc., Cary, North Carolina), assuming an autoregressive (AR[1]) correlation structure, to more appropriately estimate regression coefficient variances. Interaction terms between week, tide series, and colony were tested for inclusion in the model individually using drop-in deviance χ^2 tests (Hardin and Hilbe 2003). To avoid possible problems associated with missing or incomplete data, temporal analyses were performed using data collected between 7 June (after all birds had been captured and radio-tagged) and 11 July (after which date most tagged birds soon concluded their breeding effort) and using only birds that were actively breeding during this entire period (Rice Island N = 12, East Sand Island N = 17).

The proportion of the diet made up of particular prey types was compared between sites, time periods, and tide stages using approximate tests for equal proportions (Ramsey and Schafer 1997). Other comparisons of overall diet composition data were made using χ^2 tests.

RESULTS

Of the 52 terns trapped and radio-tagged at Rice Island and East Sand Island, 47 were determined to be breeders for at least a portion of the study period; 25 birds nested exclusively at Rice Island, 20 birds nested exclusively at East Sand Island, and two birds first attempted to nest at Rice Island, apparently suffered nest failure there, then renested at East Sand Island.

Off-colony detections of breeding, radio-tagged terns ranged from the mouth of the Columbia River to river km 106, and included many detections along the Oregon or Washington coast (although generally <1 km from the coastline) and in Willapa Bay to the north (Fig. 2). Five radio-tagged terns were detected in Grays Harbor to the north of Willapa Bay, but these detections were only for failed breeders or those that had already fledged young. Terns nesting on Rice Island were more frequently detected in the freshwater portion of the estuary and less frequently in areas outside the estuary than terns nesting on East Sand Island (Fisher's Exact Test N = 45, $P < 0.001$; Fig. 3). In addition, a seasonal shift was observed in the off-colony distribution of Rice Island terns; during the late chick-rearing period, Rice Island terns were more frequently detected in the lower estuary or outside the estuary (Fisher's Exact Test N = 45, $P < 0.01$; Fig. 4A). No significant seasonal shift in the spatial distribution of off-colony detections was seen for terns nesting at East Sand Island (Fisher's Exact Test N = 36, n.s.; Fig. 4B).

Caspian Terns nesting at Rice Island were detected at greater distances (17.3 ± 8.4 km SD; N = 25) from their colony than those nesting at East Sand Island (10.9 ± 5.6 km; N = 21) throughout the chick-rearing period ($t_{44} = 2.98$, $P < 0.01$). For terns nesting at Rice Island, detection distance from the colony increased between the early (14.1 ± 8.2 km; N = 22) and late (19.6 ± 9.9 km; N = 22) chick-rearing periods ($t_{21} = 2.08$, $P < 0.05$; Fig. 5). At East Sand Island there was no sig-

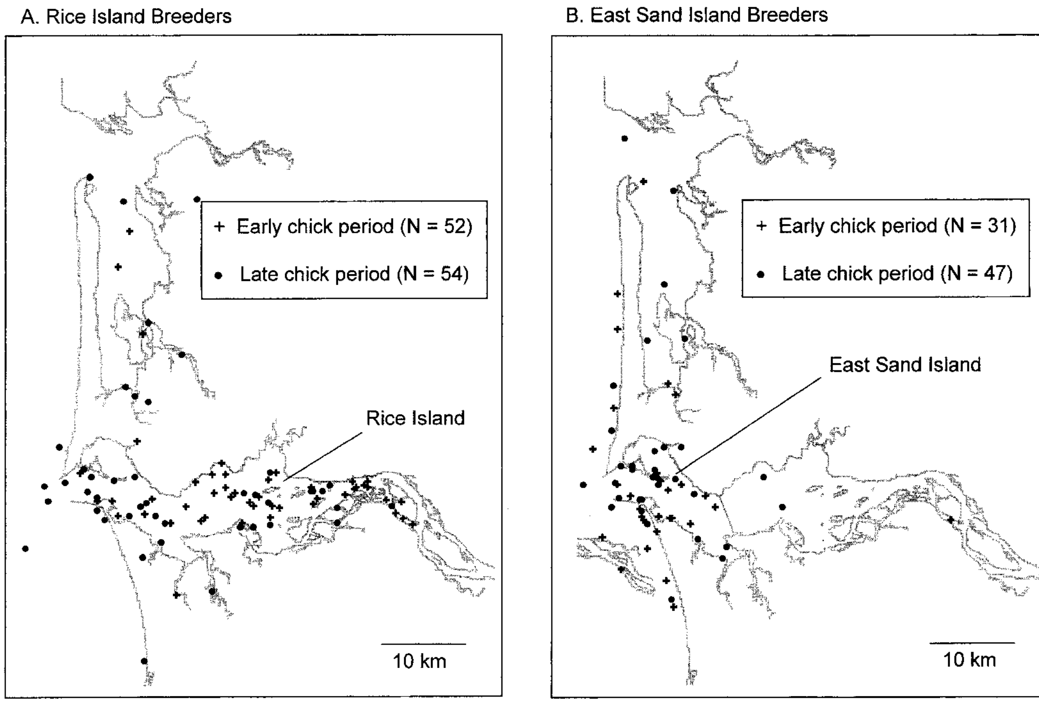

Figure 2. Location of all off-colony detections of radio-tagged Caspian Terns nesting on (A) Rice Island and (B) East Sand Island in 1999, each divided into detections made during the early chick-rearing period (28 May-18 June) and the late chick-rearing period (19 June-13 July).

nificant difference in detection distance between early and late chick-rearing adults (10.7 ± 6.7 and 11.2 ± 7.4 km, respectively; N = 16; $t_{15} = 1.47$, n.s.; Fig. 5).

Radio-tagged terns were detected at their breeding colonies an average of 51% of daytime data logger cycles (range of individual means: 37%-64%) between 7 June and 11 July. Individual birds displayed a variety of attendance patterns across daytime hours: no detectable trend (N = 9), a significant linearly increasing trend (N = 5), a single period of low attendance in the middle of the morning (09.00-10.00 h, N = 2), or lowest attendance early in the morning (before 09.00 h) followed by generally increasing attendance throughout the day, except for a second period of lower attendance in late afternoon (15.00-18.00 h, N = 13). Data for all birds averaged together exhibited the pattern of reduced attendance twice per day (cubic model was significant when compared to quadratic, linear, and null models: $F_{1,13} = 27$, $P < 0.001$; $F_{2,13} = 13$, $P < 0.01$; $F_{3,13} = 11$, $P < 0.01$; no evidence of serial correlation, DW = 1.8; Fig. 6).

Terns nesting at the two colonies were equally likely to be at their respective colonies in early June, and the terns generally exhibited lower colony attendance as the breeding season progressed (Fig. 7). The seasonal decline in colony attendance was greater for Rice Island terns than for East Sand Island terns. The regression model indicated that during a given week, after accounting for other factors, Rice Island terns were 17% less likely to be present at the colony than during the previous week (95% CI: 12-22%; P < 0.001; Table 1). In contrast, East Sand Island terns were 7% less likely to be present at their colony each week, after accounting for other factors (95% CI: 3-11%; P < 0.01; Table 1). Tide conditions (spring or neap tide series) also had a significant effect on weekly colony attendance (P < 0.001; Table 1). Colony attendance was generally greater during spring tide series weeks than during neap tide series weeks (Fig. 7).

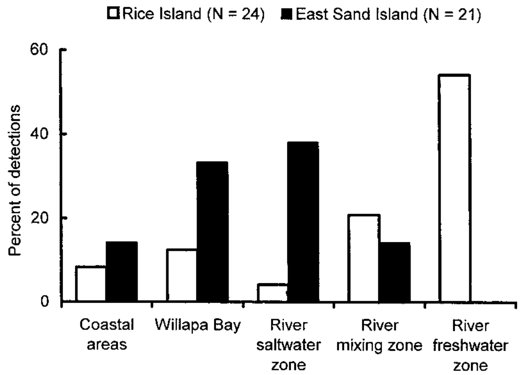

Figure 3. Distribution of off-colony detections of radio-tagged Caspian Terns nesting at Rice Island (N = 24) and East Sand Island (N = 21) between 28 May and 13 July, 1999. A single detection for each radio-tagged bird was randomly selected from all detections during this period.

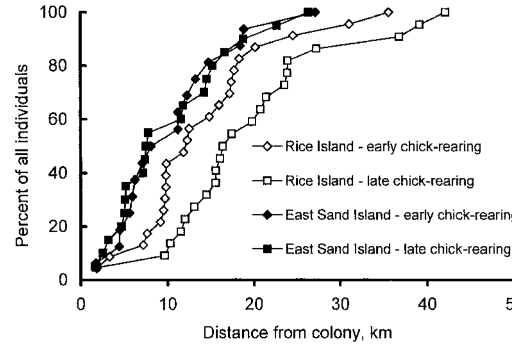

Figure 5. Cumulative distribution of distance from colony for off-colony detections of Caspian Terns breeding at Rice Island (N = 22) and East Sand Island (N = 16). Average distances for each bird in each time period were used to assemble the cumulative distribution, including only birds detected in both time periods. For each distance interval from colony, the graph indicates the percentage of all birds that were detected at this distance or closer to their respective colony.

Across the study period, 58% (±2%) of the identified prey of Caspian Terns nesting at Rice Island consisted of salmonids, substantially more than the 28% (±2%) salmonids in the diet of East Sand Island terns (equal proportions test: $z = 21$, $P < 0.001$; Fig. 8). High proportions of Anchovy ($z = 15$, $P < 0.001$), clupeids (primarily Herring; $z = 11$, $P < 0.001$), Surfperch ($z = 14$, $P < 0.001$), and other alternative prey partially replaced salmonids in the diet of East Sand Island terns ($\chi^2_4 = 743$, $P < 0.001$; Table 2). Significant differences in diet composition were observed between the early chick-rearing period and the late chick-rearing period at both Rice Island ($\chi^2_6 = 238$, $P < 0.001$) and at East Sand Island ($\chi^2_6 = 273$, $P < 0.001$), with the prevalence of salmonids declining and the prevalence of anchovies and surfperches

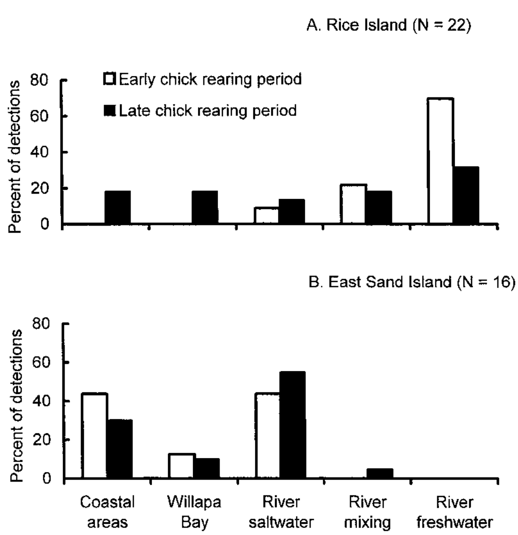

Figure 4. Distribution of off-colony detections during the early chick-rearing period (28 May-18 June) and the late-chick rearing period (19 June-13 July) for radio-tagged Caspian Terns nesting at (A) Rice Island (N = 22) and (B) East Sand Island (N = 16) in 1999. One detection from each bird from each time period was randomly selected for analysis, including only birds detected during both time periods.

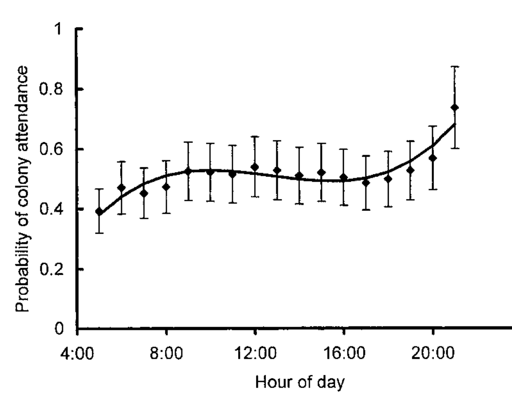

Figure 6. Colony attendance of nesting, radio-tagged Caspian Terns across daylight hours. Data are averages (±1 SE) of birds nesting at Rice Island and East Sand Island during the 1999 chick-rearing period. The curve is the best-fit model to the average hourly attendance for all radio-tagged birds; see text for details.

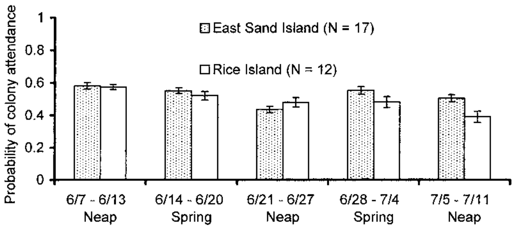

Figure 7. Weekly colony attendance (means ± 1 SE) of radio-tagged Caspian Terns nesting at East Sand Island (N = 17) and Rice Island (N = 12) in the Columbia River estuary across five weeks of the 1999 chick-rearing period (7 June to 11 July), separated by colony. Tide conditions during each week were classified as a spring tide series (the majority of days fell on or within three days of a new or full moon), or as a neap tide series (the majority of days fell on or within three days of the first or last lunar quarter phase).

increasing at both colonies (Table 2). Diet composition also differed significantly between high and low tides at both islands (Rice Island: $\chi^2_6 = 32$, $P < 0.001$, East Sand Island: $\chi^2_6 = 72$, $P < 0.001$), with the proportion of salmonids and sculpins in the diet being higher at low tides, and the proportion of anchovies being higher at high tides (Table 3).

DISCUSSION

Despite the close proximity (21 km straight line separation) of the two colonies of Caspian Terns in our study, substantial differences were observed in the foraging ecology of terns nesting at each site. In particular, the foraging distribution and colony attendance were significantly different between the two colonies and food habits reflected these differences. Even in highly vagile species, such as Caspian Terns, individuals appear to adjust their behavior in relation to their local environment.

The detections of radio-tagged terns at off-colony locations suggested that terns from both sites foraged primarily in the vicinity of their colony during late incubation (immediately following capture) and early in the chick-rearing period. Terns nesting at Rice Island frequently were found in the freshwater zone of the upper estuary, where juvenile salmonids were, presumably, the most available prey. In contrast, terns nesting at East Sand Island only occasionally traveled to the freshwater zone, instead utilizing the estuarine mixing and marine zones for foraging, where marine forage fish species (e.g., anchovy, herring, surfperch) were presumably more available. The diet of birds in each colony was consistent with the observations of foraging in these zones. Rice Island terns relied heavily on juvenile salmonids early in the season, whereas East Sand Island terns did much less so.

Late in the chick-rearing period, radio-tagged terns nesting at Rice Island were more frequently detected in the lower estuary and areas outside the estuary (north or south along the coast or north in Willapa Bay) than they had been during the early chick-rearing period. Concurrently, the proportion of salmonids in the diet of Rice Island terns declined significantly from 71% to 46%. The peak out-migration of juvenile salmonids from the Columbia River basin, particularly the larger species (Steelhead and Coho Salmon) and age classes (yearling Chinook Salmon), occurs during the month of May (Fish Passage Center 2002). Relative-

Table 1. Model coefficients of the generalized estimating equations (GEE) logistic regression model used to assess factors affecting weekly colony attendance by radio-tagged Caspian Terns during the chick-rearing period. Standard errors (SE) are given for all parameters assuming independence (IND) of all observations and assuming an autoregressive (AR[1]) correlation structure; P-values are based on the AR[1] standard errors.

		Model coefficient estimate			
Variable	Parameter range	Mean	IND SE	AR[1] SE	P
Colony site	East Sand Island (1) or Rice Island (0)	-0.08	0.06	0.12	n.s.
Week of season	7-13 June (1)-5-11 July (5)	-0.19	0.01	0.03	<0.001
Tide series	Neap (1) or Spring (0)	-0.15	0.03	0.04	<0.001
Colony × week	0-5	0.11	0.02	0.04	<0.01

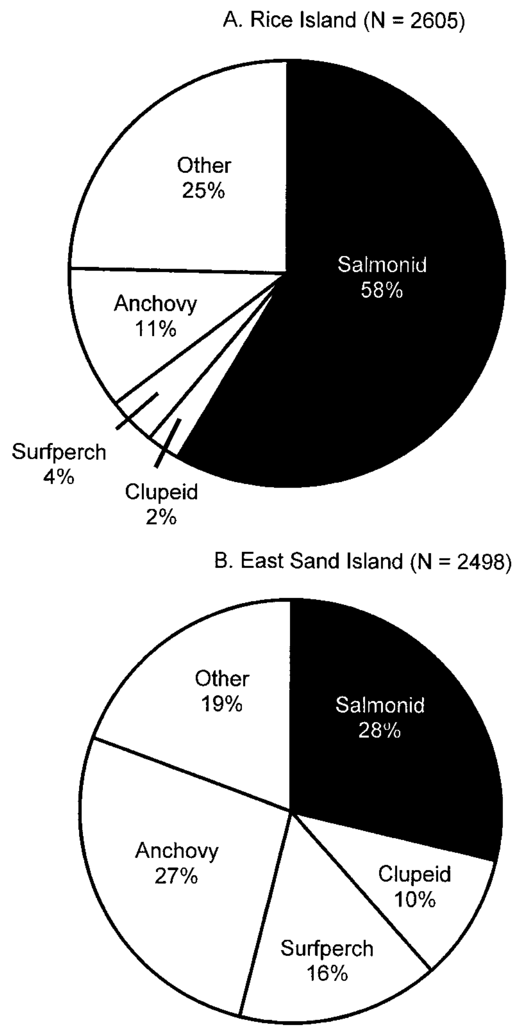

Figure 8. Diet composition (% identifiable prey items) of Caspian Terns nesting on (A) Rice Island and (B) East Sand Island from 28 May-13 July, 1999. For more information on diet composition see Roby *et al.* (2002).

ly high numbers of smolts were still moving through the estuary in early June but the numbers declined throughout the month (Fish Passage Center 2002). The shift in foraging locations and diet composition of Rice Island terns tracked the observed decline in the number of juvenile salmonids entering the estuary as the season progresses.

East Sand Island terns foraged in the same areas during the late chick-rearing period as they did during early chick-rearing. Their diet during late chick-rearing, however, included significantly fewer salmonids and more anchovy and surfperch. This also tracks the declining abundance of juvenile salmonids as the chick-rearing period progresses, but may also indicate that substantially more marine forage fish entered the lower estuary and Willapa Bay as the season progressed and were more readily available to terns there. There was no significant difference between distances from the colony for terns nesting on East Sand Island during the late chick-rearing period and the earlier period, so the apparent decline in availability of juvenile salmonids did not cause them to shift to foraging areas farther from the colony, as was the case with Rice Island terns.

In addition to differences in foraging distribution and diet composition, regression analysis indicated that as the season progressed, colony location became a significant factor in colony attendance. Lower adult attendance at the nest can have adverse consequences for chicks. Young chicks initially rely upon parents for thermoregulation and defense against predation by Glaucous-winged/Western Gulls. Unescorted older chicks sometimes suffer displacement from the nest territory, injury, or even death as a result of aggressive encounters with other adult terns. Lower colony attendance and foraging farther from the colony for Rice Island terns might also translate into lower meal delivery rates to the brood, which could hinder chick growth and development and even impact post-fledging survival (Coulson and Porter 1985; Keedwell 2003). Given these scenarios, more frequent colony attendance by East Sand Island terns would seem to be an advantage, potentially allowing greater reproductive success.

While colony site and day of season played critical roles in foraging behavior, our study suggested tidal conditions also affected behavior. During spring tide series, colony attendance at both colonies was higher. Tide cycles within a day have often been shown to influence when other larids visit foraging sites (Burger 1982, 1983; Irons 1998) and ultimately colony attendance (Galusha and Amlaner 1978). Relationships between foraging behavior and tide series on a weekly scale have been shown less often (Anderson

Table 2. Comparison of diet composition (% identifiable prey items) between the early (28 May-18 June) and late (19 June-13 July) chick-rearing periods for Caspian Terns breeding at two sites in the Columbia River estuary. Prey types making up significantly different proportions of the diet for each time period are highlighted in bold type (equal proportions test; P ≤ 0.05).

	Rice Island		East Sand Island	
Prey type	Early	Late	Early	Late
Anchovy[a]	**3.6**	**16.6**	**15.1**	**37.5**
Clupeid[b]	**0.4**	**4.1**	9.9	9.2
Peamouth, Pikeminnow[c]	**0.8**	**3.4**	**0.3**	**1.4**
Salmonid[d]	**70.7**	**46.2**	**42.3**	**16.3**
Sculpin[e]	**0.6**	**2.3**	3.1	4.5
Smelt[f]	**3.2**	**1.0**	7.7	2.2
Surfperch[g]	**1.3**	**5.6**	**11.1**	**19.5**
Other[h]	19.4	20.8	10.5	9.3
N	1198	1407	1188	1310

[a]Engraulidae, [b]Clupeidae, [c]Cyprinidae, [d]*Oncorhynchus* spp., [e]Cottidae, [f]Osmeridae, [g]Embiotocidae, [h]lamprey (*Lampetra* spp.), stickleback (Gasterosteidae), sucker (*Catostomus* spp.), or unidentified non-salmonids.

et al. 2004). Tidal cycles also influenced diet: Anchovy were a larger portion of the diet at high tides, consistent with greater salt water intrusion into the estuary allowing entry farther up-river, perhaps in greater numbers and closer to tern colonies. Diet differences at high and low tide stages have been consistently observed in Caspian Terns nesting in subsequent years at East Sand Island (Anderson *et al.* 2005).

Central place foraging around colony sites appeared to be the leading cause of differences in foraging ecology between terns nesting on Rice Island and East Sand Island; however, two other possible factors should be considered. First, density-dependent effects might have been much more important at Rice Island in 1999, where the tern colony was estimated at 8,300 breeding pairs, compared to 550 pairs on East Sand Island (Roby *et al.* 2002). Localized depletion of available prey in areas near the Rice Island colony might have caused individual terns to forage farther from the colony than terns nesting at East Sand Island (Ashmole 1963). Second, East Sand Island is downstream of Rice Is-

Table 3. Comparison of diet composition (% identifiable prey items) between high and low tide stages for Caspian Terns breeding at two sites in the Columbia River estuary from 28 May to 13 July 1999. Prey identification for high tide periods occurred from 90 minutes before the actual high tide until 90 minutes after, and similarly for low tides. Prey types making up significantly different proportions of the diet for each tide stage are highlighted in bold type (equal proportions test; P ≤ 0.05).

	Rice Island		East Sand Island	
Prey type	High	Low	High	Low
Anchovy[a]	**13.7**	**8.6**	**31.2**	**22.3**
Clupeid[b]	1.9	1.5	9.5	9.6
Peamouth, Pikeminnow[c]	2.0	2.0	0.8	0.8
Salmonid[d]	**52.0**	**64.2**	**26.9**	**31.5**
Sculpin[e]	**0.7**	**1.9**	**0.8**	**7.0**
Smelt[f]	2.6	1.8	5.0	5.1
Surfperch[g]	**4.4**	**2.4**	14.8	14.3
Other[h]	**22.6**	**17.5**	11.0	9.4
N	992	1180	1062	1043

[a]Engraulidae, [b]Clupeidae, [c]Cyprinidae, [d]*Oncorhynchus* spp., [e]Cottidae, [f]Osmeridae, [g]Embiotocidae, [h]lamprey (*Lampetra* spp.), stickleback (Gasterosteidae), sucker (*Catostomus* spp.), or unidentified non-salmonids.

land, and Rice Island terns could potentially deplete a significant proportion of the available salmonids migrating down the river, leaving less for East Sand Island terns to utilize. It has been estimated that in 1998 the Rice Island tern colony (8,700 pairs) consumed 9-17% of all salmonids that entered the estuary (Roby *et al.* 2003). In 1999, slightly fewer terns bred at Rice Island than in 1998 (Roby *et al.* 2002), presumably consuming a slightly smaller fraction of all salmonids. It is unknown what proportion of juvenile salmonids is present high enough in the water column to be caught by plunge-diving terns. It is possible that only a fraction of salmonids are actually available to terns—for example, those fish stressed by passage through mainstem dams or predator-naïve due to hatchery rearing. However, if this potential effect of up-stream prey depletion was an important influence on foraging behavior when feeding primarily upon juvenile salmonids, terns nesting at both islands should benefit from foraging in areas up-river of their respective colonies, where densities of available salmonids would presumably be higher. Our results do not suggest any preferential foraging upriver of the colony site by terns from either island, so prey depletion by terns from the upriver colony does not seem likely to be a significant factor affecting foraging behavior.

The foraging metrics examined in this study indicate that the location of East Sand Island in the marine zone was more favorable as a Caspian Tern colony site than the location of Rice Island in the freshwater zone. The position of East Sand Island lower in the estuary allowed terns nesting there to travel shorter distances during foraging trips to abundant and diverse assemblages of marine forage fishes. This advantage was more pronounced later in the chick-rearing period when individual chick energy requirements are high (but when both parents are available to feed chicks), but was present throughout the chick-rearing period. Colony attendance during the chick-rearing period was also higher for terns nesting at East Sand Island. In addition, East Sand Island terns were less reliant on a single prey type, juvenile salmonids, to meet their food requirements, which may have conferred an advantage as the size and abundance of salmon smolts traveling through the estuary declined rapidly during the chick-rearing period (Fish Passage Center 2002).

The apparently enhanced foraging conditions at East Sand Island presumably contributed to higher production of fledglings. Per capita productivity at the East Sand Island colony in 1999 was much higher: 1.20 fledglings/breeding pair compared to 0.55 fledglings/pair at Rice Island (Roby *et al.* 2002). This result is confounded by targeted removal of problem gulls to limit nest predation at East Sand Island and facilitate the restoration of the tern colony there (Roby *et al.* 2002); however, favorable foraging conditions likely contributed to the ability of a significant proportion of East Sand Island breeding pairs to provision and fledge multiple-chick broods. Unknown density-dependent factors (e.g., conspecific interactions at the colony) may have also played a role, but the trend of higher productivity at East Sand Island has been bourn out in subsequent years, regardless of colony size (Roby *et al.* 2002). Similarly, our only observations of radio-tagged terns attempting to re-nest at a new site after presumably failing at one site were moves from Rice Island to East Sand Island. But East Sand Island radio-tagged terns that failed did not attempt to breed at Rice Island. This apparent shift of breeding birds from Rice Island to East Sand Island (and the lack of movement in the opposite direction) again suggests East Sand Island was a more favorable breeding location in 1999.

In 1999, colony location within the Columbia River estuary had a significant effect on the foraging ecology of Caspian Terns, and likely fledgling production. Even on spatial scales that were small relative to the maximum foraging range of the species, significant differences were observed in several measures of foraging behavior. Colony sites in marine zones of coastal estuaries may generally provide benefits for Caspian Terns over sites in freshwater zones in terms of proximity to a more diverse and perhaps more abundant prey base, at least during periods of coastal upwelling. These traits might be of use to resource managers who wish to reduce tern predation on threatened and endangered salmonids from the Columbia River basin, if terns can be attracted to colony sites where alternative prey are available. East Sand Island appears to be such a site, and substantial reductions in tern predation upon Columbia River salmonids are achievable if more or the entire Rice Island Caspian Tern colony was shifted to East Sand Island (Roby *et al.* 2002). Reductions in tern predation on anadromous salmonid species and stocks throughout the region might be achieved if terns were redistributed to colony sites in the marine zone of other estuaries. Further analysis would still be required to assess to what extent reductions in tern predation might potentially increase salmonid population levels (Roby *et al.* 2003).

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