

Relationship of Caspian tern foraging ecology to nesting success in the Columbia River estuary, Oregon, USA

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Abstract

The prevalence of juvenile salmonids (*Oncorhynchus* spp.) and marine forage fishes in the diet of Caspian terns (*Hydroprogne caspia*) nesting in the Columbia River estuary has been established, but the relationship between diet composition, foraging distribution, and productivity of these birds has received little attention. We used radio-telemetry and on-colony observations to relate changes in off-colony distribution to patterns of colony attendance, diet composition, and productivity of adult terns nesting on East Sand Island during two years of different river and prey conditions. Average distance from the East Sand Island colony (located in the marine zone of the estuary) was 38% (6.6 km) greater in 2000 compared to 2001, associated with lower availability of marine forage fish near East Sand Island and lower prevalence of marine prey in tern diets. Colony attendance was much lower (37.0% vs. 62.5% of daylight hours), average trip duration was 40% longer (38.9 min), and nesting success was much lower (0.57 young fledged pair⁻¹ vs. 1.40 young fledged pair⁻¹) in 2000 compared to 2001. Higher proportions of juvenile salmonids in the diet were associated with relatively high use of the freshwater zone of the estuary by radio-tagged terns, which occurred prior to chick-rearing and when out-migrating salmonid smolts were relatively abundant. Lower availability of marine prey in 2000 apparently limited Caspian tern nesting success by markedly reducing colony attendance and lengthening foraging trips by nesting terns, thereby increasing chick mortality rates from predation, exposure, and starvation.

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1. Introduction

Nesting Caspian terns (*Hydroprogne caspia*) in the Columbia River estuary consume juvenile salmonids (*Oncorhynchus* spp.) (Collis et al., 2001, 2002; Roby et al., 2002, 2003; Ryan et al., 2003) listed as either endangered or threatened under the U.S. Endangered Species Act (NMFS, 2002). As part of an effort to reduce predation on juvenile salmonids by Caspian terns nesting at Rice Island (in the freshwater zone of

the estuary; see Simenstad et al., 1990), regional managers relocated the colony to East Sand Island (in the marine zone of the estuary) during 1999–2001 (Roby et al., 2002). As a result of colony relocation, the proportion of salmonids in the diet of nesting terns declined by about half and the proportion of marine forage fish consumption increased correspondingly (Roby et al., 2002). This dramatic change in diet composition occurred despite moving the colony just 21 km, a fraction of the documented foraging range of nesting Caspian terns (62 km; Gill, 1976). Although Caspian tern diet composition in the Columbia River estuary is well-studied (Collis et al., 2001, 2002; Roby et al., 2002, 2003; Ryan et al., 2003), little is known about where prey are captured and how changes in prey availability may affect foraging patterns of nesting birds.

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We studied the off-colony distribution of Caspian terns nesting on East Sand Island in the Columbia River estuary in 2000 and 2001. The location of this colony near the mouth of the Columbia River allows breeding adults to prey upon a wide variety of forage fishes, including freshwater, euryhaline, and marine species. Roby et al. (2002) listed prey from 10 different fish families in the diet of Caspian terns nesting on East Sand Island during 2000 and 2001. River flows, estuarine currents, and salinities within the foraging range of Caspian terns breeding on East Sand Island are highly dynamic, altering the distribution and abundance of prey over short time scales (Bottom and Jones, 1990). Longer-term changes (e.g., decadal) in ocean conditions and snow pack can also alter the abundance of marine forage fish during the tern breeding season (Brodeur et al., 2003; Emmett, 2003).

Colony attendance has been used as an indicator of prey availability for nesting seabirds (Cairns, 1987, 1992). Parents provisioning chicks must divide time between foraging and protecting their chicks from predation and exposure. When prey availability and foraging conditions are poor, parents spend more time foraging to meet the energy demands of chicks, at the expense of time spent attending their nests.

Previous studies of the spatial distribution of foraging terns (i.e., foraging distribution) using radio-telemetry have focused on the chick-rearing period because terns are difficult to capture and radio-tag prior to late incubation (Wiggins and Morris, 1987; Wagner and Safina, 1989; Sirdevan and Quinn, 1997). We radio-tagged adult terns at a roost site prior to egg-laying, allowing the comparison of off-colony distributions among the incubation, chick-rearing, and post-fledging stages of the nesting cycle. These data were combined with diet composition and productivity data from Roby et al. (2002) to investigate the relationship between food availability, foraging distribution, diet, and productivity of Caspian terns nesting on East Sand Island in 2000 and 2001.

2. Materials and methods

2.1. Study area

This study was conducted on Caspian terns actively nesting on East Sand Island (46°15'45"N, 123°58'06"W) in the Columbia River estuary (Fig. 1) during the 2000 and 2001 breeding seasons. The available tern foraging habitat for this colony was divided into three zones: two zones in the Columbia River estuary and one outside the estuary (i.e., the near-shore coastal zone, including Willapa Bay and Grays Harbor — Fig. 1). The two zones in the Columbia River estuary were a predominantly marine zone (down-river of the Astoria-Megler Bridge, river kilometer 21) and a predominantly freshwater zone (up-river of the Astoria-Megler Bridge) (see Simenstad et al., 1990). East Sand Island is located near the mouth of the Columbia River estuary at river kilometer 7, placing it near the center of the marine zone of the estuary.

2.2. Capture methods

Adult Caspian terns were captured from East Sand Island and Rice Island (46°14'58"N, 123°42'56"W). On Rice Island in April, roosting adults were caught using a rocket net in 2000 ($n = 50$) and 2001 ($n = 30$) and these birds were monitored once they began nesting on East Sand Island during those same years. On East Sand Island in May, nesting adults were caught using monofilament noose mats placed around active nests in 2000 ($n = 19$) and 2001 ($n = 24$) and were subsequently monitored. Trapping of nesting terns on East Sand Island was conducted during late incubation to minimize nest abandonment due to disturbance (Sirdevan and Quinn, 1997). The last day of tern trapping at East Sand Island coincided with the beginning of the chick-rearing period (i.e., based on estimated hatch date) in both years of the study.

Once captured, each adult was fitted with a federal numbered metal leg band and a unique color combination of five plastic leg bands. We also attached radio-tags (40 pulse min^{-1} , double-beep every 10 pulses, 80-day battery life expectancy) (Advanced Telemetry Systems [ATS], Isanti, Minnesota) weighing 10 g (1.6% of average adult tern body mass) to the four central retrices using plastic ties and quick-setting Loctite[®] epoxy (see Anderson and Ricklefs, 1987; Irons, 1998). Irons (1998) found that tail-mounted radio-transmitters weighing ca. 2.5% of body mass had no detectable effect on behavior or breeding performance of nesting black-legged kittiwakes (*Rissa tridactyla*), so we assumed similar effects on Caspian terns. Radio-tagged terns were marked on the back and upper wing coverts with picric acid or rhodamine-B dye to aid in sighting individuals on-colony.

In 2000, 22 adults were sexed opportunistically by observing copulation behavior on-colony after release. In 2001, 53 adults were sexed genetically from blood samples taken from the brachial vein and analyzed by Avian BioTech International (Tallahassee, Florida; see Griffiths et al., 1998; de Kloet and de Kloet, 2003).

2.3. Aerial surveys

We conducted 22 aerial surveys in 2000 and 21 in 2001 to locate radio-tagged Caspian terns that were confirmed to be nesting on East Sand Island. Aerial surveys were conducted from a Cessna 205 aircraft with a single dipole antenna mounted on each wing. Antennae were connected to an ATS (Model R2100) or Telonics (Mesa, Arizona) receiver through a switch box that allowed the tracker to listen to one antenna at a time (while tracking a single bird) or both simultaneously (while scanning for birds). Once in the vicinity of the bird, the pilot “boxed in” the signal by circling with one wing in the direction of the strongest signal, while the location was marked with a GPS receiver. We tested location accuracy by placing seven transmitters on the ground for trackers to find, resulting in an average location error of 0.5 ± 0.1 km. Once a bird was located, its transmitter frequency was removed from the pool of frequencies to scan, resulting in a maximum of one detection per radio-tagged bird per flight. Reference

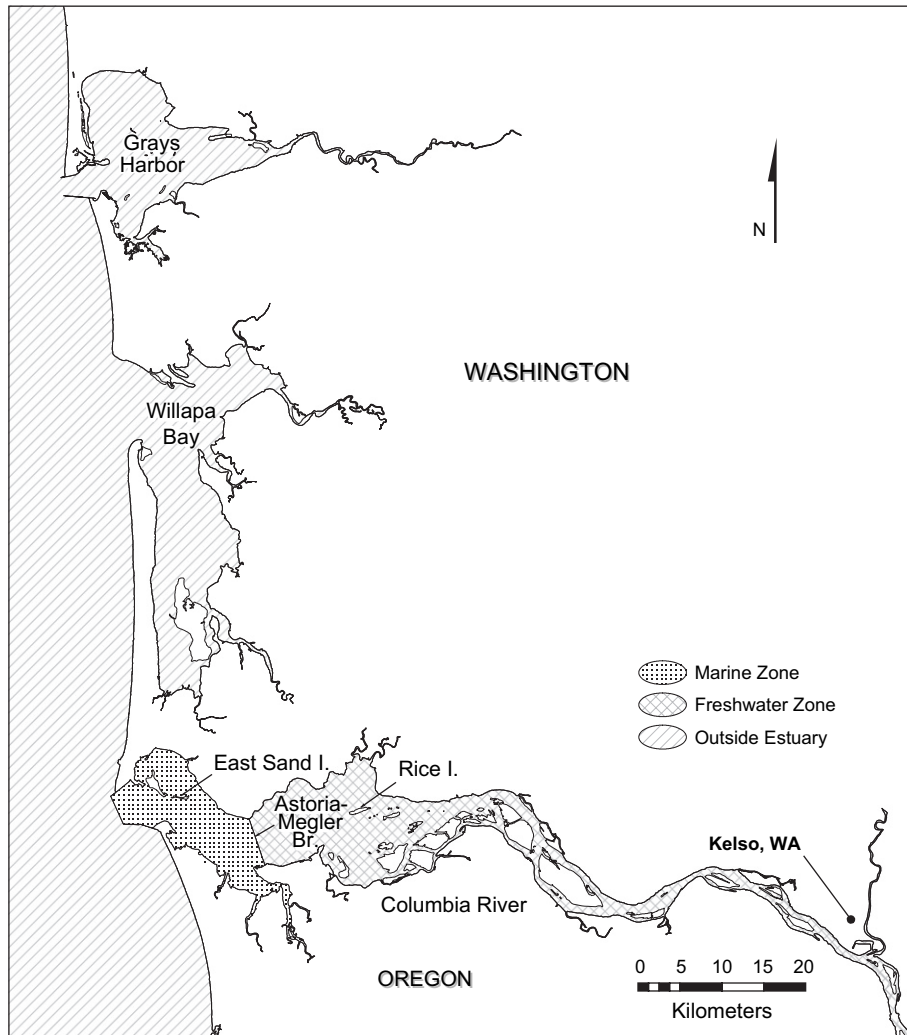


Fig. 1. Map of the study area in northwestern Oregon and southwestern Washington, showing the Columbia River estuary, Willapa Bay, and Grays Harbor.

transmitters located on-colony were often heard at a distance of up to 10 km, indicating that the maximum detection range of a radio-tagged bird was 10 km to either side of the flight path. Where this range was not sufficient to cover the entire width of the Columbia River estuary, additional passes were flown.

The survey route covered all zones of the study area: the Columbia River from Kelso, WA to the mouth, Willapa Bay, Grays Harbor, and the coastline from Grays Harbor to the mouth of the Columbia River (Fig. 1). Each zone of the study area was covered only once during each survey flight. Occasional surveys were flown south of the Columbia River throughout the breeding season, but this area was not included in the analysis because Caspian terns were seldom seen foraging there, nor were any radio-tagged terns detected in that area. Each zone of the study area was covered only once during each survey flight.

Surveys were flown at an altitude of approximately 160 m (above sea level) and required between 2.7 and 5.3 h to complete. Survey flights generally were timed to coincide with low tide (weather permitting) to control the variation in

tern foraging distribution associated with tide stage. We assumed that radio-tagged Caspian terns located off-colony were engaged in foraging trips.

2.4. Nest monitoring

We partitioned the breeding season into three discrete time periods: incubation, chick-rearing, and post-fledging. Incubation was considered to be 27 days (Cuthbert and Wires, 1999) prior to hatching and was April 24th–May 20th in 2000, and April 27th–May 23rd in 2001. The chick-rearing period (the period between hatching and fledging) was designated as 37 days (Cuthbert and Wires, 1999) following trapping and was May 21st–June 26th in 2000, and May 24th–June 29th in 2001. The post-fledging period was 20 days following the chick-rearing period and was June 27th–July 16th in 2000, and June 30th–July 19th in 2001.

Nesting status of radio-tagged adults was confirmed by observing their behavior while on-colony. We considered radio-tagged adults to be nesting if observed brooding young chicks or feeding a chick during chick-rearing. We did not

include observations made after chicks became mobile, when it became more difficult to associate a chick with a parent (>26 days old). Birds confirmed to be failed breeders were omitted from our analysis after the last observation confirming active nesting.

Colony attendance of actively breeding radio-tagged terns on the East Sand Island colony was monitored using a combination of an ATS Receiver (Model R2100) and an ATS Data Collection Computer (DCC II – Model D5041) mounted near the edge of the colony. In 2000, the receiver and DCC were connected to a set of four 6-element Yagi antennae on a 6-m mast, while in 2001 they were connected to an H-antenna (see Anderson, 2003). Reception range of each DCC set-up was determined by placing transmitters at various distances from the antenna array. DCCs were programmed to scan for radio-tags deployed on a bird, radio-tags placed at the edge of the colony (reference transmitters), and two “dummy” frequencies (frequencies not deployed). Reference transmitter detections were used to evaluate reception rates, while “dummy” frequency detections were used to evaluate false detection rates.

The difference in on-colony telemetry set-ups resulted in a greater reception range in 2000 compared to 2001, but reception rates were similar. Testing revealed that transmitters were detected to a range of approximately 0.5 km in 2001, but were detectable up to 7.0 km from the colony in 2000. False detections were not recorded in either year and reference transmitters were detected 95.1% of the time in 2000 and 97.8% of the time in 2001. Of all the radio-tagged terns that were confirmed to be nesting on East Sand Island, nine (in 2000) and 13 (in 2001) kept their antennas and therefore were included in the colony attendance and trip duration analyses. Using the sample of 13 terns in 2001, we sub-sampled every third detection cycle from the DCC data so that detection cycles would be similar in the two years (30.9 min in 2000 and 30.3 min in 2001). This allowed comparison of colony attendance and trip duration between years using the DCC data.

The average time required for the DCC to scan for each frequency once (cycle time) was longer in 2000 than in 2001. To compare colony attendance between years, we sub-sampled cycles in 2001 to approximate the average cycle time in 2000. The proportion of time on-colony (colony attendance) during chick-rearing was expressed as the number of DCC scan cycles a bird was detected divided by the number of scans performed during daylight hours (05:00–21:30 Pacific Daylight Time, the average of civil twilight times during chick-rearing). Colony attendance was also estimated by the proportion of radio-tagged terns detected on-colony during survey flights, to check accuracy. Trip duration was estimated by averaging the number of DCC scan cycles skipped on each trip during the entire chick-rearing period and multiplying by the average cycle time (30.6 min).

Some radio-tagged Caspian terns lost the antenna to their radio-transmitter during the study period, requiring these birds to be omitted from analyses of colony attendance and trip duration. Antenna loss was confirmed by direct observation or by reduced DCC reception (consecutive days/nights with

no detections). However, we assumed that the off-colony detection rate of a bird would be independent of location within the study area. Therefore, we included birds that lost their transmitter antenna for comparison of detections during aerial surveys, but not for comparison of colony attendance calculated from DCC detections.

2.5. Data analysis

The nature of Caspian tern foraging behavior and method of data collection posed challenges for interpreting the distribution of off-colony detections. Terns (unlike pursuit-diving species) forage during flight and while commuting to and from the colony, and the behavior of individual radio-tagged terns detected during survey flights was unknown. An off-colony detection may represent a foraging site, a point on the flight path to or from a foraging site, or a roost site near a foraging area, although actively nesting terns are seldom seen roosting off-colony during the nesting season (authors, personal observation). Therefore, estimates of distance from colony are presented as an index of foraging distance. For this reason, we restricted these analyses to compare the spatial distribution of detections, rather than attempting to interpret foraging habitat use based on the distribution of birds while off-colony.

During aerial surveys, we first determined which radio-tagged individuals were on-colony before searching for radio-tagged terns that were off-colony. In some cases, however, a tern not detected on-colony during the first flight pass returned to the colony in the time it took to locate other off-colony birds, biasing the data toward on-colony detections. To control for this bias, both on- and off-colony detections were included in comparisons of off-colony distributions, unless otherwise noted. While this may not reflect the instantaneous off-colony distributions of radio-tagged terns, it allows the detection of differences in the proportion of time spent in each of the three zones associated with each factor of interest (i.e., gender, year, and breeding stage).

2.5.1. Distance from colony

We used a mixed effects model to test for differences in detection distance from the colony (for off-colony detections only) with respect to the year, breeding stage, parent gender, and their interactions (fixed effects), while accounting for variation associated with individual birds (random effect) using a procedure in the statistical program SAS called PROC MIXED (Laird and Ware, 1982; SAS, 1999; see Table 1). Covariance structures explaining variance associated with individuals were selected based on the procedure outlined in Wolfinger (1993) and Littell et al. (2000). Mixed effect models are based on likelihood estimation procedures, so we compared full models with all interaction terms and reduced models with no interaction terms using log likelihood ratio tests (Ramsey and Shafer, 1997; SAS, 1999).

A spatial power covariance structure was chosen to account for variation associated with each individual in both the full model and the reduced model. Interactive effects among these

Table 1

A summary of the different analyses used in this study including the dependent and independent variables, criteria for inclusion of birds in each analysis, and the sample sizes (i.e., number of radio-tagged terns) in 2000 and 2001

Dependent	Independent	Criteria for inclusion	No. of birds	
			2000	2001
Distance from colony	year, sex, breeding stage	nested during all three time periods, sex known, detected off-colony	7	33
Distance from colony	year, breeding stage	nested during all three time periods, detected off-colony	19	33
Off-colony distribution	year, sex, breeding stage	nested during all three time periods, sex known, detected off-colony	7	33
Off-colony distribution	year, breeding stage	nested during all three time periods, detected off-colony	19	33
Colony attendance	year, sex	nested during chick-rearing, sex known, no antenna loss	6	13
Colony attendance	year	nested during chick-rearing, no antenna loss	9	13
Trip duration	year, sex	nested during chick-rearing, sex known, no antenna loss	6	13
Trip duration	year	nested during chick-rearing, no antenna loss	9	13

three explanatory variables were not supported by the data (log likelihood ratio test: $\chi^2_7 = 8.2$, $P > 0.05$). Diagnostic plots indicated that the frequency distribution of distances from colony did not depart significantly from normality.

To further evaluate the effects of year and breeding stage, we removed gender and included all nesting birds from both years, regardless of sex. A full model including year, breeding stage, and their interaction was compared to a reduced model without interactions using average straight-line distance to the colony as a response. A compound symmetric covariance structure was chosen to account for variation associated with the individual in both the full model and the reduced model. Interactive effects between breeding stage and year were not supported (log likelihood ratio test: $\chi^2_1 = 2.5$, $P = 0.2865$); therefore a reduced model with no interactions was applied.

2.5.2. Off-colony distribution

We tested for differences in the distribution of detections among the three zones of the estuary with respect to gender, breeding stage, and year using Mantel-Haenszel (M-H) Chi-square tests (Ramsey and Shafer, 1997; SAS, 1999; see Table 1). Counts were calculated by randomly selecting one off-colony detection from each radio-tagged bird during each breeding stage, creating a balanced data set. Mantel-Haenszel Chi-square tests allow testing for differences due to one variable while accounting for possible effects of others (Ramsey and Shafer, 1997; SAS, 1999).

2.5.3. Colony attendance and trip duration

We estimated differences in colony attendance and trip duration during chick-rearing in both years from the DCC data using Welch-modified *t*-tests (SAS, 1999) to correct for unequal variance. While the number of radio-tagged birds used in these analyses were small (see Table 1), colony attendance values were based on an average of 33 and 36 days bird⁻¹ and trip duration values were based on an average of 132 and 155 trips bird⁻¹ in 2000 and 2001, respectively. Colony attendance decreased and trip duration increased with date during chick-rearing in 2001 (Anderson et al., 2005). Therefore, we used multiple linear regression (SAS, 1999) to compare the proportion of birds detected off-colony during survey flights while controlling for date (after checking for normality). This was

not necessary for DCC data because data collection was continuous over the entire chick-rearing period.

All tests are considered significant when $P \leq 0.05$. Means are presented as \pm SE unless otherwise noted.

3. Results

Of the birds radio-tagged in 2000 and 2001, 19 and 33 terns, respectively, fed young during the chick-rearing period and were detected at least once during each breeding stage (incubation, chick-rearing, and post-fledging). Of the 22 survey flights completed in 2000, five were conducted during incubation, eight were conducted during chick-rearing, and nine were conducted during post-fledging. Of the 21 survey flights completed in 2001, five were conducted during incubation, 11 were conducted during chick-rearing, and five were conducted during post-fledging. This resulted in a total of 71 off-colony detections and 195 on-colony detections in 2000 (average number of detections bird⁻¹ off-colony = 3.7 and on-colony = 10.3) and 87 off-colony detections and 420 on-colony detections in 2001 (average number of detections bird⁻¹ off-colony = 2.6 and on-colony = 12.7).

Of the radio-tagged, known-sex breeders detected off-colony during each breeding stage, 26 were male (3 in 2000 and 23 in 2001) and 13 were female (3 in 2000 and 10 in 2001). This skewed sex ratio (2.0:1) is similar to that of all adults captured and radio-tagged (1.7:1, 46 males and 27 females).

3.1. Distance from colony

The mixed effects model indicated that gender did not explain a significant proportion of the variation in distance from the colony. Off-colony distances of male terns were not statistically different from those of female terns ($P = 0.9532$). Average distance of off-colony detections differed between years and among some breeding stages (Fig. 2). Average off-colony distance was 6.6 ± 2.9 km (ca. 38%) greater in 2000 compared to 2001 (mixed effects model: $P = 0.026$, 95% CI = 0.85–12.42 km), after accounting for breeding stage. After accounting for the effects of year, average off-colony distance was 5.96 ± 2.72 km greater during post-fledging than during chick-rearing (mixed effects model: $P = 0.030$, 95% CI = 0.58–11.33), and was slightly greater during incubation

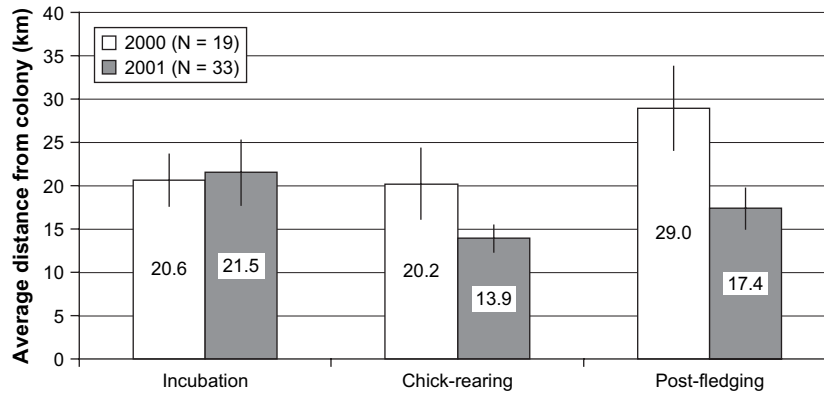


Fig. 2. Average distance from the colony of off-colony detections of Caspian terns nesting on East Sand Island in the Columbia River estuary during incubation, chick-rearing, and post-fledging in 2000 and 2001.

compared to chick-rearing (4.93 ± 3.18 km; $P = 0.123$). Off-colony distance was not significantly different between incubation and post-fledging (mixed effects model: $P = 0.75$).

3.2. Off-colony distribution

The distribution of radio-tagged terns (on- and off-colony combined) among the three zones did not differ between the sexes, after accounting for year and breeding stage (M-H: $\chi^2_2 = 1.2$, $P = 0.5614$). Therefore, subsequent analyses of detections included all radio-tagged nesters, regardless of sex. The distribution of breeding terns (on- and off-colony combined) was different among breeding stages, after accounting for year (M-H: $\chi^2_4 = 11.4$, $P = 0.02$; Fig. 3). The proportion of birds detected in the freshwater zone of the estuary was highest during incubation and lowest during chick-rearing, while the proportion of birds detected outside the estuary was highest during post-fledging. Most detections occurred in the marine zone of the estuary, where East Sand Island is located, regardless of breeding stage. Greater proportions of terns were detected in the marine zone of the estuary during 2001 compared to 2000 (Fig. 3), these differences (after accounting for breeding stage) were not statistically significant (M-H: $\chi^2_4 = 1.15$, $P = 0.56$).

3.3. Colony attendance and trip duration

The average daytime colony attendance during chick-rearing was higher in 2001 (62.5%) than in 2000 (37.0%; Welch's t -test: $t_{15} = -7.42$, $P < 0.0001$; Fig. 4). The large difference in colony attendance suggests that in 2001 chicks were attended by at least one parent most of the time, whereas in 2000 chicks were left unattended for about a third of the day. The proportion of on-colony detections from aerial surveys during chick-rearing was much higher in 2001 (72.2%, 95% CI = 58.3–86.1%) than in 2000 (52.3%, 95% CI = 36.0–68.5%), after accounting for date (multiple linear regression: $r^2 = 0.63$, $P < 0.0001$).

This difference in colony attendance between the two years appears at least partly due to a difference in the duration of trips. Off-colony trips were longer, on average, in 2000 ($136.4 \pm$

5.15 min) than in 2001 (97.5 ± 2.29 min; Welch's t -test: $t_{11} = 6.89$, $P < 0.0001$).

4. Discussion

4.1. Distribution, diet, and breeding chronology

Our index of foraging distribution of breeding terns in the study area differed between the breeding stages. The proportion of radio-tagged terns detected in the freshwater zone of the estuary was highest during incubation (May), when the proportion of salmonids in the diet also was highest (Roby et al., 2002). This time period generally coincides with peak out-migration of juvenile salmonids through the Columbia River estuary based on detections of out-migrating smolts at Bonneville Dam, the lowermost dam on the Columbia River (FPC, 2006a). Conversely, the proportion of radio-tagged terns detected outside the estuary was highest during post-fledging (July), when the proportion of juvenile salmonids in the diet was lowest (Roby et al., 2002). Thus, the distribution of Caspian terns while chick-rearing was largely confined to the immediate vicinity of East Sand Island (the marine zone of the estuary), regardless of diet composition. Although we observed an interannual difference in overall distance from the colony, the seasonal pattern of distribution across the zones of the study area was generally similar between years.

Restrictions on range imposed by chick-rearing duties were also evident in differences in our index of foraging distance from the colony among stages of the nesting cycle. Average distance terns were detected from the colony during chick-rearing was 25% (6.0 ± 2.7 km) less than during post-fledging. Although the difference in average tern distance from the colony between chick-rearing and incubation was not significant, the magnitude of the difference was large (4.9 ± 3.2 km), and the trend was toward greater distances from the colony during incubation. These results are consistent with those from other seabird studies, which suggest that the time constraints imposed by chick-rearing requires breeding adults to forage nearer the colony than at other stages of the breeding cycle (Weimerskirch et al., 1993; Ojowski et al., 2001; Barlow and Croxall, 2002).

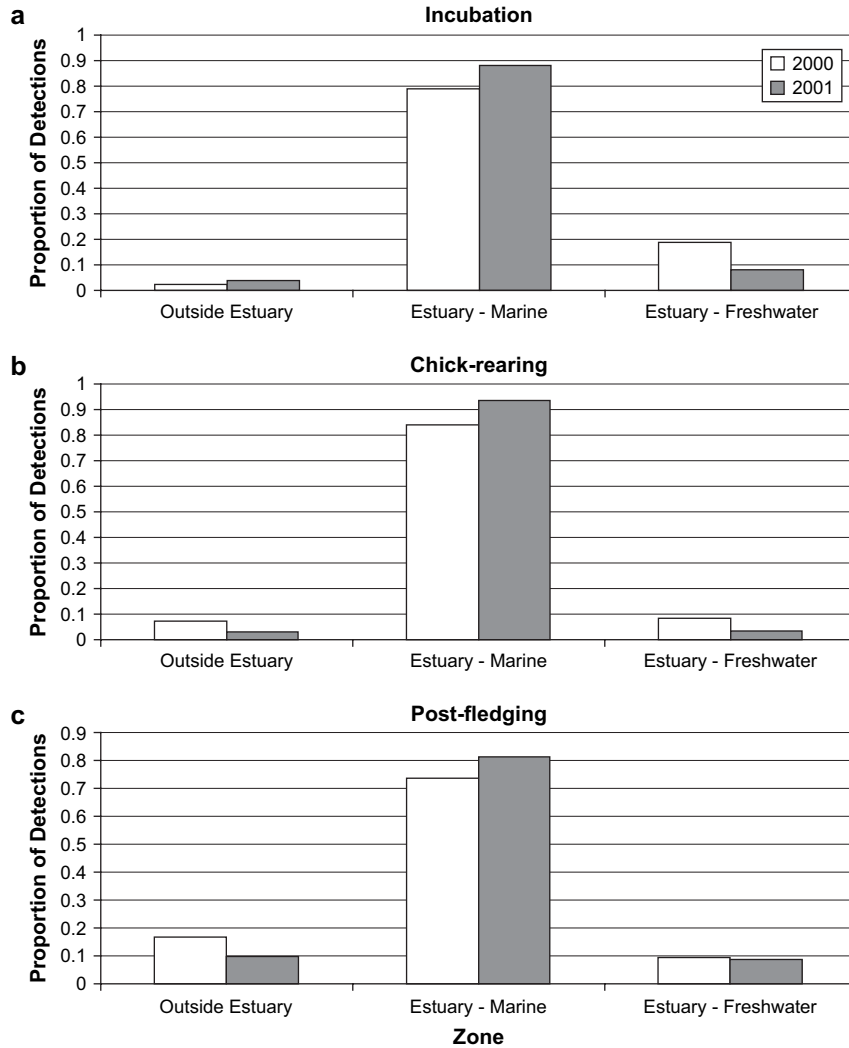


Fig. 3. Average proportion of all detections in each zone of the study area during (a) incubation, (b) chick-rearing, and (c) post-fledging for each radio-tagged Caspian tern nesting on East Sand Island ($n = 19$ birds in 2000 and $n = 33$ birds in 2001).

The observation of greater travel distances by breeding adults during incubation and post-fledging suggests an advantage to foraging farther from the colony. Assuming distance detected from colony is a suitable index of foraging distance, there are several possible explanations for our results. First, prey resources near the colony may become depleted (Ashmole, 1963; Birt et al., 1987) making foraging at more distant locations more favorable when maximizing time on-colony is not an issue. Second, seasonal changes in prey distribution may result in higher prey availability at more distant locations (e.g., peak out-migration of juvenile salmonids through the freshwater portion of the estuary occurs during incubation). Third, the increased mobility of chicks after fledging allows fledglings to follow adults on more extensive excursions from the colony, reducing the need for parents to return to the colony (Soikkeli, 1973).

4.2. Fisheries interactions

Each year 150–200 million juvenile salmonids are released from hatcheries in the Columbia River basin (FPC, 2006b).

Out-migrating juvenile salmonids are the most abundant forage fishes in the freshwater zone of the Columbia River estuary during the spring and early summer (Hinton et al., 1995; Emmett et al., 2006), providing terns with a reliable

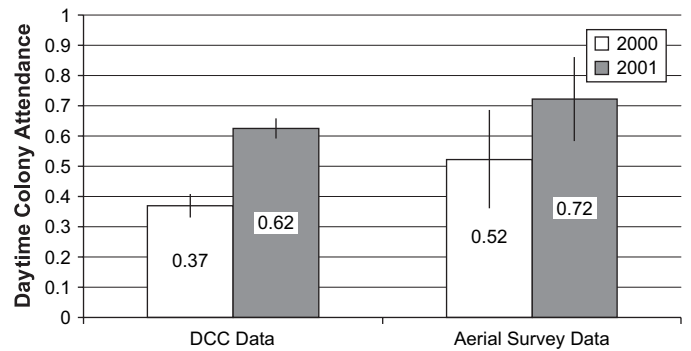


Fig. 4. Two measures of colony attendance during chick-rearing (≤ 37 day post-hatch) for Caspian terns nesting on East Sand Island. See text for methods of estimation of colony attendance from the two data sets. Error bars indicate 95% confidence intervals.

food supply during the early part of the breeding season (i.e., through early chick-rearing; Collis et al., 2001, 2002). Terns that formerly nested in the freshwater zone of the estuary (Rice Island) were highly dependent on smolts as a food source, 77% and 90% of the diet in 1999 and 2000, respectively (Roby et al., 2002). Management actions which lead to the relocation of terns from Rice Island to East Sand Island (located in the marine zone of the estuary) resulted in a sharp drop in the prevalence of juvenile salmonids in the diet of terns, 46%, 47%, and 33% of the diet in 1999, 2000, and 2001, respectively (Roby et al., 2002). This study suggests that the proportion of salmonids in the diet of terns nesting on East Sand Island was positively associated with use of the freshwater zone of the estuary prior to chick-rearing, when juvenile salmonids were relatively abundant in this zone.

4.3. Food availability and tern productivity

A direct relationship between food availability and seabird nesting success has been demonstrated in other studies (Vermeer et al., 1979; Baird, 1990; Hamer et al., 1993; Kitaysky et al., 2000; Jodice et al., 2002), and hypothesized by Cairns (1987, 1992), who suggested that measures of seabird productivity can indicate the relative abundance of marine fish stocks. During the two years of this study, productivity at the East Sand Island Colony increased from 0.57 young fledged pair⁻¹ in 2000 to 1.40 young fledged pair⁻¹ in 2001 (Roby et al., 2002), while tern diet composition and trawl catch data indicated a large increase in marine forage fish availability from 2000 to 2001.

The prevalence of marine forage fishes (i.e., Pacific herring [*Clupea pallasii*], Pacific sardine [*Sardinops sagax*], anchovies [Engraulidae], and smelt [Osmeridae]) in the diet of Caspian terns nesting on East Sand Island doubled between 2000 and 2001 (Roby et al., 2002), while trawl catches in the Columbia River plume (a probable indicator of estuary fish abundance) also showed a doubling in the density of these same fish species (Emmett et al., 2006). Conversely, the prevalence of juvenile salmonids in the diet of the terns decreased by 14% from 2000 to 2001 (Roby et al., 2002), while the density of juvenile salmonids in the Columbia River plume increased from 2000 to 2001 (Emmett et al., 2006).

It is likely that the presence of salmonids in tern diets did not increase from 2000 to 2001 because salmonid densities in 2001 peaked during May (the incubation period), while salmonid densities in June, July, and August were much lower than in 2000 (Emmett et al., 2006). Additionally, 2001 was a drought year, with Columbia River flows approximately half of the average flow between 1998 and 2003 (Emmett et al., 2006), allowing greater saltwater intrusion into the estuary. Unfortunately, it is not possible to determine the relative contribution of low river flow (and therefore greater saltwater intrusion) and increased offshore productivity to the greater abundance of marine forage fish in the Columbia River estuary during 2001. Regardless, nesting terns spent less time away from the colony (decreased average travel distances, shorter trip durations, and higher colony attendance), suggesting

a mechanism for the relationship between productivity and prey availability.

Decreased prey availability directly causes lower nesting success through brood reduction (i.e., the size of the brood is adjusted to the parents' ability to provide food to the brood; Lack, 1954; Ricklefs, 1965). Brood reduction occurs primarily through starvation in Caspian terns (Quinn, 1980; Cuthbert and Wires, 1999). When prey availability is low, provisioning rates to younger chicks in a brood tend to be much lower than those to older chicks (Quinn, 1990).

Food shortages can also directly affect productivity through chick starvation. However, low forage fish availability and the resulting reduction in colony attendance by breeding adults also indirectly affect nesting success through higher chick mortality due to predation, exposure, and aggression from conspecific adults. Predation on Caspian tern chicks and eggs by glaucous-winged/western gulls (*Larus glaucescens* × *Larus occidentalis*) in the Columbia River estuary is common (authors, personal observation), and was the major proximate cause for poor tern nesting success in some years (Roby et al., 1998). Glaucous-winged/western gulls that nest in the Columbia River estuary also feed on marine fish (Collis et al., 2002). As a result, in years of low forage fish availability, gulls may become more reliant on the chicks and eggs of other seabirds as a way to meet their food requirements, as has been shown in other predatory gull species (Spear, 1993; Regehr and Montevecchi, 1997; Stenhouse and Montevecchi, 1999; Massaro et al., 2000).

Low parental nest attendance in other ground-nesting birds has been shown to increase the vulnerability of chicks and eggs to predation and inclement weather (Yalden and Yalden, 1990; Barrett and Krasnov, 1996; Flemming et al., 1988; Samelius and Alisauskas, 2001). During the 2000 nesting season, a severe wind and rain storm at East Sand Island caused the loss of roughly 1000 Caspian tern chicks (D.D. Roby, unpublished results). This mortality was likely exacerbated by the low colony attendance of parent terns that year. Finally, aggression from conspecific adults has been shown to be an important source of mortality for Caspian tern chicks not attended by their parents (Bent, 1921; Cuthbert and Wires, 1999).

5. Conclusion

Lower chick provisioning rates and lower colony attendance by Caspian terns nesting on East Sand Island were likely associated with lower availability of marine forage fishes in 2000 compared to 2001. Lower provisioning and attendance contributed to lower chick survival through higher vulnerability of chicks to a combination of starvation, predation, exposure, and conspecific aggression.

The large difference in nesting success of Caspian terns at East Sand Island during the two years of our study demonstrates the importance of the availability of marine forage fishes to the productivity of this colony. Because the East Sand Island colony represents the majority of the Pacific Coast population of Caspian terns, a prolonged period of decreased

marine forage fish abundance would likely result in a decline in the regional population of Caspian terns, as well as increased predation rates on juvenile salmonids in the Columbia River estuary.

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