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Abstract.—We investigated factors affecting chick provisioning by radio-tagged Caspian Terns (*Sterna caspia*) nesting in a large colony on East Sand Island in the Columbia River estuary during 2001. Caspian Tern predation on juvenile salmonids (*Oncorhynchus* spp.) in the estuary prompted resource managers to relocate ca. 9,000 pairs of terns nesting on Rice Island (river km 34) to East Sand Island (river km 8), where terns were expected to consume fewer salmonids in favor of marine forage fishes. This study investigated factors influencing foraging success, diet composition, and overall reproductive success at the managed Caspian Tern colony. Our results indicated that daytime colony attendance by nesting terns averaged 64% and decreased throughout the chick-rearing period, while duration of foraging trips averaged 47 min and increased during the same period; these seasonal changes were more strongly related to date than chick age. Average meal delivery rates to 2-chick broods (0.88 meals h^{-1}) were 2.6 times greater than to 1-chick broods (0.33 meals h^{-1}). Parents delivered more juvenile salmonids to chicks during ebb tides than flood tides, but meal delivery rates to the nest remained constant, suggesting diet composition tracks relative availability of prey species. Foraging trips resulting in delivery of juvenile salmonids averaged 68% longer than foraging trips for schooling marine forage fishes, indicating higher availability of marine prey near the colony. High availability of marine forage fish in the Columbia River estuary during 2001 was apparently responsible for high colony attendance, short foraging trips, high chick meal delivery rates, and high nesting success of Caspian Terns on East Sand Island. *Received 8 June 2004, accepted 20 November 2004.*

Key words.—chick provisioning, Caspian Tern, *Sterna caspia*, salmonids, *Oncorhynchus*, Columbia River.

Caspian Terns (*Sterna caspia*) have nested in the Columbia River estuary since 1984, when a colony of about 1,000 pairs was discovered on a dredged-material disposal site on East Sand Island near the mouth of the Columbia River (G. Dorsey, U.S. Army Corps of Engineers, pers. comm.). Subsequently, the colony moved to Rice Island, a dredge spoil island 26 km up-river, and grew considerably (Roby *et al.* 2002). The colony became the largest for Caspian Terns in North America and comprised 60% of the Pacific Coast population of the species (Suryan *et al.*, 2004). The rapid numerical increase in the Columbia River estuary has been attributed to the availability of hatchery-raised juvenile salmonids (*Oncorhynchus* spp.) as a reliable food source; stable, anthropogenic nesting habitat; and immigration from former colonies along the coast of the Pacific Northwest (Collis *et al.* 2001).

Large aggregations of piscivores may significantly impact the local abundance of forage fishes (Ashmole 1963; Anderson and Ricklefs 1987). Food requirements of piscivorous birds are greatest during chick-rearing (Drent and Daan 1980; Walsberg 1983), and for Caspian Terns nesting in the Columbia River estuary, chick-rearing occurs when juvenile salmonids are migrating through the estuary to the ocean. Twelve of the 20 "evolutionarily significant units" of anadromous salmonids in the Columbia River basin are listed as either endangered or threatened under the U.S. Endangered Species Act (National Marine Fisheries Service 2002). While the number of listed salmonid smolts consumed by Caspian Terns in the estuary is not known, total smolt consumption was estimated as between 9.1 and 15.7 million in 1998 (Roby *et al.* 2003).

In 1999, regional natural resource managers (National Oceanic and Atmospheric Administration Fisheries, U.S. Fish and Wildlife Service, U.S. Army Corps of Engineers, Oregon Department of Fish and Wildlife,

Washington Department of Fish and Wildlife, Idaho Department of Fish and Game, Columbia River Inter-Tribal Fish Commission, and others) agreed to attempt restoration of the colony on East Sand Island in the hopes that Caspian Terns nesting closer to marine environments would consume more marine fishes and fewer salmonids (Roby *et al.* 2002). By 2001, the entire colony had been relocated to East Sand Island, and the proportion of salmonids in the diet of nesting birds was 33%; down from 77% salmonids at the Rice Island tern colony in 1999 (Roby *et al.* 2002).

Foraging distances by birds are restricted by the need to deliver food to the nest (central-place foraging; Orians and Pearson 1979). The parental effort required to meet chick food demands depends on a number of factors, including food availability (Jodice *et al.* 2002), weather conditions (Dunn 1973, Sagar and Sagar 1989), tidal fluctuations (Irons 1998), brood age (Klaassen *et al.* 1989, Wiggins 1989), and brood size (Drent and Daan 1980). Energy requirements at the nest are inexorably tied to the number of nestlings (brood size) and to the increasing energy requirements of nestlings as they grow (brood age). Energy requirements of Common Tern (*S. hirundo*) chicks increase until approximately 20 days post-hatch, after which requirements decline slightly until fledging at about 24 days post-hatch (Klaassen *et al.* 1989). Caspian Terns have a 37 day pre-fledging period (Cuthbert and Wires 1999) and, consequently, peak energy requirements of Caspian Tern chicks likely occurs after 20 days post-hatch.

Parents can compensate for increasing energy demands of chicks by delivering larger prey (Wiggins and Morris 1987) or more lipid-rich prey (Anthony *et al.* 2000), but higher demands may also be met by delivering chick meals more frequently. In general, terns provision their young by delivering a single fish held in the bill. Common Terns and Roseate Terns (*S. dougalli*) have been shown in some studies to meet higher demands solely by delivering larger prey (Wiggins and Morris 1987, Burger and Gochfeld 1991). However, nesting Caspian Terns tend-

ing larger broods also exhibit higher provisioning rates to the nest (Quinn 1980). In a study of Common Terns, provisioning rates were sufficient to maintain constant per-chick meal delivery rates (Wiggins 1989).

Although it may be more energetically efficient for Caspian Terns to deliver larger prey, adults must provision young chicks with smaller fish until the young are large enough to ingest the full range of prey sizes consumed by adults (Quinn 1990). Thus, tern parents with larger broods of young chicks must either deliver meals more frequently or deliver meals with a higher energy density in order to maintain per-chick provisioning rates.

Weather and tides can also influence the frequency and duration of foraging trips in seabirds. Irons (1998) found that Black-legged Kittiwakes (*Rissa tridactyla*) foraging in inshore areas are more likely to forage during outgoing (ebb) tides. East Sand Island is located near the mouth of the Columbia River, so the diet of Caspian Terns nesting there includes both marine and freshwater prey (Roby *et al.* 2002), the relative availability of which may change with tidal stage. Fish capture success for the Common Tern and Sandwich Tern (*Sterna sandvicensis*) was positively correlated with wind speed (Dunn 1973). Inclement weather also has been implicated in reduced foraging efficiency in the Roseate Tern, Sandwich Tern, and Common Tern (Dunn 1975). In addition to affecting the ability of parents to provision chicks, weather may affect foraging behavior indirectly. Before chicks can thermoregulate, more time is spent brooding (and less time foraging) to protect nestlings during periods of precipitation (Dunn 1975) or extreme temperatures (Burger and Gochfeld 1990).

We investigated factors that influence chick provisioning in Caspian Terns, as reflected in colony attendance, foraging trip duration, and frequency of foraging trips. Specifically, we examined those factors that may limit nesting success and reproductive output of Caspian Terns nesting at East Sand Island as a way to evaluate the suitability of East Sand Island as a colony site for terns, at least in the short term.

METHODS

Study Area

In 2001, Caspian Terns nested on East Sand Island (46°15'45"N, 123°58'06"W) in the Columbia River estuary, Oregon, USA. East Sand Island is located near the mouth of the estuary at river kilometer 7, well within the marine zone of the estuary (Simenstad *et al.* 1990). Adult Caspian Terns were captured and ratio-tagged on two islands, East Sand Island and Rice Island (46°14'58"N, 123°42'56"W), in the Columbia River estuary. Rice Island, located at river kilometer 34, was a roost site for Caspian Terns, but no nesting occurred there in 2001.

Radio Tagging

Thirty adult terns were caught for radio-tagging using a rocket-propelled net on Rice Island in mid-April, prior to the onset of egg-laying at East Sand Island. Twenty-four adult terns were captured for radio-tagging on the East Sand Island colony in mid-May by placing monofilament noose mats around active nests. In addition, each adult was fitted with a federal numbered metal leg band and a unique color combination of five plastic leg bands.

Male Caspian Terns have been shown to provision their young more than females (Quinn 1990), and studies of other larids suggest that sexual asymmetry in provisioning duties may differ among colonies (Wiggins and Morris 1987; Wagner and Safina 1989; Uttley 1992). Therefore, blood was collected from the brachial vein of each radio-tagged adult for sex determination (Avian BioTech International, Tallahassee, Florida) and accounted for in statistical analyses (see below).

Radio transmitters from Advanced Telemetry Systems (ATS - Isanti, Wisconsin) were attached to the four central retrices, using plastic ties and quick-setting Loctite© epoxy (see Anderson and Ricklefs [1987] and Irons [1998] for details). The transmitters weighed 10 g (1.6% of average adult body mass), had an 80-day battery life expectancy, and emitted 40 pulses min^{-1} with a double-beep every 10 pulses. Irons (1998) found that tail-mounted radio transmitters 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 non-effects of radio tags on Caspian Tern behavior. Radio-tagged terns were marked on the neck, back, and upper wing coverts with picric acid or rhodamine-B dye to assist with behavioral observations when the individual was in the colony.

Nest Observations

After release, 27 of the 54 radio-tagged terns were located at active nests on East Sand Island. Nineteen of these 27 nesting terns had been radio-tagged on East Sand Island during late incubation, while eight had been radio-tagged pre-laying on Rice Island. A bird was considered nesting if it was observed incubating eggs, feeding another adult tern that was incubating eggs, or feeding a chick. Periodically throughout the season, presence at the colony of the radio-tagged terns was monitored to confirm active nesting and record the number and approximate age of chicks. Chick plumage characteristics were compared to known-age chicks raised in captivity (D. E. Lyons, unpubl. data) to im-

prove the accuracy of brood age estimates and to allow back-calculation of the hatch dates.

Radio-tagged nesting terns were monitored during chick-rearing in two ways: (1) direct observation of radio-tagged terns attending nests from blinds adjacent to the colony for periods of approximately 3 h, coinciding with each of the four tide stages (low, flood, high, ebb) and (2) automated radio telemetry monitoring equipment (see details below) which recorded presence at the colony of each radio-tagged individual at ca. 10-minute intervals.

We observed nests from blinds to measure the effect of tides, time of day, weather, and brood size on meal delivery rates to chicks by pairs of nesting Caspian Terns. During the chick-rearing period (27 May to 5 July), 26 of the 27 located nests with radio-tagged adults were observed during at least one tide stage, and 21 were observed during all four tide stages. Tide stages were determined by centering 3-h time periods on peak high and low tides; flood and ebb tides were defined by the intervening time periods. Nests were randomly selected for observation and randomly assigned to one of three or four complete tide stages that occurred during the daylight period, resulting in a total of 290 hours of nest observations during 101 observation periods. Each nest was observed for no more than one tide stage in the same day to avoid potential autocorrelation. During each nest observation period, the arrival and departure times of parent birds was recorded, as was the size and type of prey fed to the brood.

If a bird returned with a fish, the fish was identified to the family level (Clupeidae [herring/sardine], Engraulidae [anchovy], Cyprinidae [peamouth/pike-minnow], Osmeridae [smelt], *Oncorhynchus* spp. [salmonids], Gadidae [cod], Cottidae [sculpin], Embiotocidae [surfperch], *Ammodytes hexapterus* [Pacific sand lance], and Pleuronectidae [flounder]). Fish lengths (cm) were estimated based on average head-bill length of adult Caspian Terns (13.5 cm). Although the error in fish length estimates was unknown, bias in length estimates should have been constant over the entire sampling period, allowing comparisons within the study. Meal delivery rates (fish h^{-1}) were calculated for each radio-tagged bird to validate the telemetry data, and combined meal delivery rates from both parents was the response variable when testing for brood size, weather, and tide effects.

Daily averages for weather parameters (precipitation, wind speed, and temperature) were obtained from the National Weather Service Station at the Astoria Regional Airport, Oregon (46°09'N, 123°53'W), 14.2 km southeast of the colony site. Tide data (meters of water from mean low water) were acquired from the National Oceanic and Atmospheric Administration tide gauge station at Tongue Point, Oregon (46°11'N, 123°46'W), 17.0 km up-river from the colony site. These data were used to test for associations between meal delivery rate, colony attendance (see below), and environmental variables.

Telemetry

Attendance (presence or absence) of actively-breeding radio-tagged terns at the East Sand Island colony was measured using a fixed receiving station (i.e., combination of an ATS Receiver [Model R2100], ATS Data Collection Computer [DCC II – Model D5041], and an H-antenna) located near the edge of the colony. Radio tag

detections (i.e., sample sizes) were restricted for three reasons. First, accurate determination of brood size and identification of nests became increasingly difficult as chicks became older and more mobile. Consequently, the dataset was restricted to parents of chicks ≤21 days post-hatch. Second, 15 of the 27 radio-tagged nesters whose nest site was known lost their antenna at some point during the breeding season. A significant decline in detection rates occurred after antenna loss, so attendance data for these birds were no longer reliable. Analyses were restricted to radio-tagged nesters that did not lose their antenna in the first 21 days post-hatch. Finally, brood sizes of radio-tagged parents ranged from one to three chicks, but representation of one- and three-chick broods was small, making an estimation of brood size effects difficult with telemetry data. Therefore, we only included telemetry data from those birds raising two-chick broods and estimated brood size effects using nest observations. Using these criteria, 17 radio-tagged nesters had colony attendance monitored.

Nest contents of radio-tagged adults could not be examined immediately after hatching to determine brood size, so the largest brood size observed six to 10 days post-hatch for each nest was used. Data collected after loss of a chick from a nest was removed to avoid confounding brood size effects within a nest with brood size effects among nests.

Prior to the first arrival of terns at the colony, reception of transmitter signals from throughout the 1.6-ha colony was confirmed. Although reception distances vary with transmitter orientation and signal strength, transmitters were detected up to 500 m at an elevation of approximately 2 m. The fixed receiver monitored the frequency of each deployed radio-transmitter for 10 s and recorded the time, date, and number of pulses detected (if any). The DCC searched for each frequency at intervals of approximately 10 min (cycle time) throughout the chick-rearing period.

To evaluate reception accuracy, two reference transmitters were placed at the colony periphery and two false frequencies (not deployed on a bird) were programmed into the DCC. Reference transmitters were detected 97.8% of the time, and the false frequencies were never detected, indicating that reception was reliable. Furthermore, DCC records and visuals of parental attendance during observation periods were cross-checked to confirm the accuracy of periods when radio-tagged adults were recorded as on-colony.

Due to the 10-min cycle time of the DCC, off-colony excursions shorter than 5 min were not likely to be detected, trips lasting 5-15 min were likely to be recorded as a single missed detection, trips lasting 15-25 min were likely recorded as two missed detections. We used the number of consecutive missed detections to estimate the duration of off-colony excursions in multiples of 10 min. DCC data were also used to estimate daily colony attendance (proportion of scans resulting in detection), and frequency of foraging trips (number of off-colony excursions day^{-1} resulting in provisioning of the brood with a fish). Telemetry data were compiled over the entire daytime period (see below), controlling for possible effects of tide stage or time of day.

For the purposes of this study, we assumed Caspian Terns foraged solely during daylight hours because they locate prey visually (Bijlsma 1985). Therefore, colony attendance and provisioning trip frequency and duration were restricted to detections from complete scan cycles recorded between 05.00 h and 21.30 h Pacific Daylight Time, the average of civil twilight times during the chick-rearing period.

Data Analysis

Telemetry data were used to investigate the effect of date and brood age on the frequency and duration of foraging trips for chick provisioning. Hatching was not synchronous among our sample of 17 radio-tagged nesters, producing a range of brood ages on the same date. However, brood age and date are not independent factors, and therefore cannot be included in the same statistical analysis. To determine the most influential of these two measures of time without violating the assumption of independence, we averaged values over one factor (e.g., chick age), while testing for the influence of the other factor (e.g., date).

To test for a brood age effect independent of date, data were sampled on trip duration and frequency from each nest on 9 June (near the middle of the chick-rearing period), when the sample of nests with a radio-tagged parent was greatest (N = 14). These data were regressed on brood age and gender of the radio-tagged parent to test for a brood age effect. Similarly, data on trip duration and frequency were sampled from each nest at 8 days post-hatch (N = 17 nests) to test for an effect of date independent of brood age. Again, these data were regressed on Julian date and gender of the parent. Once either brood age or date was determined to explain more of the variation in parental provisioning behavior, it was included in all subsequent analyses to account for changes in provisioning behavior over the chick-rearing period. For the final analysis of telemetry data, daily values of trip duration and frequency were averaged over the least influential of the two variables (date or brood age), and regressed on gender of the parent, brood size, and the most influential of the two variables date or brood age.

We investigated associations between meal delivery rate and tide stage/weather using the nest observation data, after accounting for effects of time of day and brood size. Meal delivery rates were calculated as the total number of fish delivered by both parents to the brood divided by the total observation time for each nest. Only nests observed during all four tide stages were used (N = 21). A mixed effects model was used to test for differences in meal delivery rates with respect to the following fixed effects; time of day, brood size, temperature (daily average), wind speed (daily average), precipitation, and tide stage; while accounting for the random effect associated with individual nests using PROC MIXED (Laird and Ware 1982, SAS 1999). Time of day was categorized into three time periods reflecting the range of observation times: morning (03.30-09.30 h), midday (09.30-15.30 h), and evening (15.30-21.30 h). Covariance structures to account for variation associated with individuals were selected based on the procedure outlined in Wolfinger (1993) and Littell *et al.* (2000).

The effect of brood size on meal delivery rate was estimated using data from nests observed at least once (N = 26). This included five nests with one-chick broods, 19 nests with two-chick broods, and two broods with three chicks. Each nest was observed between one and seven times, and meal delivery rates were calculated by dividing the number of fish delivered to the nest by the total hours of observation time. Differences between each brood size category were tested using regression weighted by the minutes of observation per nest.

We used chi-square (SAS 1999) to test for differences in the ratio of salmonids to marine prey types (i.e., anchovy [Engraulidae], herring/sardine [Clupeidae], and smelt [Osmeridae]) for each pair-wise comparison of tide stage (i.e., ebb to low, ebb to flood, ebb to high, low to flood, low to high, and flood to high). A regression was used to test for a trend in the size of prey (cm) delivered to the nest over time.

To test for differences in foraging trip duration in relation to prey type, we randomly selected four observation periods (one for each tide stage) for each radio-tagged adult and its mate. Only those birds that delivered at least one marine fish and one salmonid during the four observations were included to allow a pair-wise comparison of trip duration by prey type within each nesting pair. Average trip durations for marine and salmonid species for each bird were compared using a paired t-test (Ramsey and Schafer 1997). Means are presented ± one SE unless otherwise noted.

RESULTS

Of the 17 radio-tagged parent terns used in the telemetry analysis, six (35%) were female. This ratio matched the sex ratio in the original sample of 54 radio-tagged individuals.

Chick provisioning frequency from telemetry data collected by the on-colony DCC was cross-validated using nest observations. Eighty percent of trips less than 15 min in duration were non-provisioning trips (parent did not return with a fish), while 87% of trips greater than 15 min were provisioning trips (parent returned with a fish; Fig. 1). This suggests that the great majority of absences recorded by the DCC as one missed detection were not provisioning trips. Consequently, absences consisting of at least two consecutive missed detections during daylight hours were assumed to represent provisioning trips by a parent.

Nest observations and telemetry data captured foraging trips equally well. The frequency distribution of observed foraging trip durations and of trips captured from DCC data showed close agreement (Fig. 2), indicating that DCC data provided a reasonably unbiased and accurate measure of the duration of chick provisioning trips greater than 15 min.

The use of DCCs allowed us to detect foraging trips greater than the 3-h duration of observation periods. The available data, however, indicated that provisioning trips greater than 3 h rarely occurred. Average trip duration based on data from the DCC
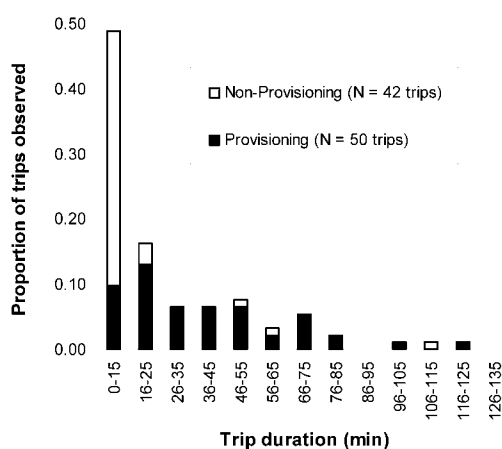

Figure 1. Frequency distribution of off-colony trip durations based on observations of Caspian Terns nesting on East Sand Island in the Columbia River estuary. Provisioning trips were trips resulting in delivery of a fish to the nest and non-provisioning trips were trips not resulting in delivery of a fish.

was 45.8 ± 2.8 min, compared to 40.4 ± 3.2 min based on direct observations (Fig. 2). For all trips recorded as at least two consecutive detections missed by the DCC, trip frequency averaged 6.1 ± 0.31 trips day^{-1} bird^{-1}.

Date and Brood Age

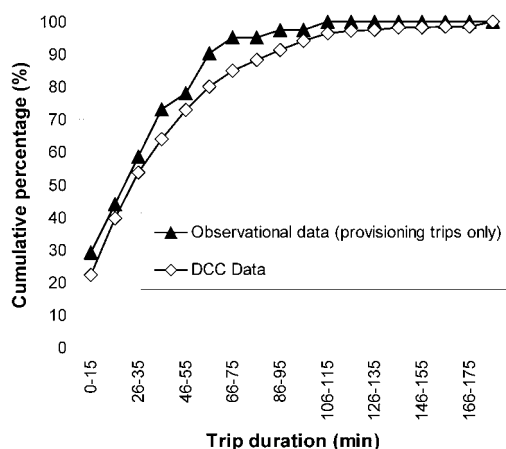Changes in average trip duration were more strongly associated with date than brood

Figure 2. Cumulative frequency distributions of the duration of daytime off-colony excursions recorded by the telemetry Data Collection Computer (DCC) and provisioning trips recorded during nest observations of Caspian Terns on East Sand Island, Columbia River estuary. N = 92 for observed trips and N = 786 for trips.

age, while average trip frequency did not have a strong association with either date or brood age. Based on telemetry data from all nests on 9 June (N = 14), brood age had no significant effect on trip duration (1.12 ± 0.84 min day^{-1} decrease; n.s.) or trip frequency (0.19 ± 0.09 trips day^{-1} decrease, n.s.) after accounting for effects of adult gender (multiple linear regression). Data from all nests at 8 d post-hatch (N = 17), indicated that date had a stronger association with trip duration (1.46 ± 0.33 min day^{-1} increase, $P < 0.001$), after accounting for effects of adult gender (multiple linear regression; $F_{2,14} = 10.36$, $P < 0.01$). However, the effect of date on trip frequency was small and insignificant (0.05 ± 0.07 trips day^{-1} decrease, n.s.), after accounting for adult gender.

Because the duration of provisioning trips was strongly influenced by date but not by brood age, we averaged trip duration and trip frequency values available during 21 days post-hatch for each radio-tagged parent. Multiple linear regression was then used to simultaneously estimate the effects of adult gender and hatch date for each parent bird (see below), weighted by the number of days when data were available. Hatch date represented the timing of chick-rearing (i.e., date) because averaged values represented the same range of brood ages for each nest.

Hatch Date and Parent Gender

There was an increase in average trip duration with hatch date, after accounting for adult gender (weighted multiple linear regression: $F_{2,14} = 14.59$, $r^2 = 0.68$, $P < 0.001$, N = 17). Average foraging trip duration for all birds was 47.2 min $\pm$ 2.9 min. Nests that hatched one week later in the season were associated with an increase in provisioning trip duration of 10.3 min $\pm$ 1.9 min (21.9% of overall average; $P < 0.001$; Fig. 3). There was no effect of gender on average duration of chick provisioning trips (n.s.).

Foraging trip frequency was affected by adult sex but not hatch date (weighted multiple linear regression: $F_{2,14} = 4.80$, $r^2 = 0.41$, $P < 0.05$, N = 17). Average foraging trip frequency was 6.20 ± 0.33 trips day^{-1}. On average, males made 6.8 trips per day and
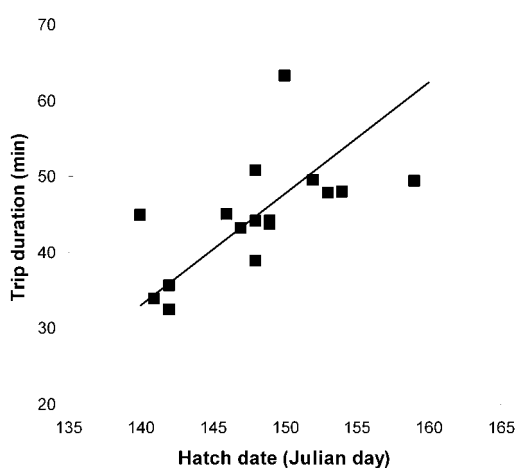

Figure 3. Average provisioning trip duration as a function of hatch date for parent Caspian Terns raising broods. Line represents least squares linear regression.

females took 5.1 trips per day (a difference of 1.7 ± 0.58 more trips per day; $P < 0.02$). Differences in colony attendance were associated with both adult sex and hatch date (multiple linear regression: $F_{2,14} = 6.89$, $r^2 = 0.50$, $P < 0.01$, N = 17). Females attended the colony 8.5% $\pm$ 3.0% more of the day than did males ($P < 0.02$), and parents attended the colony 3.8% $\pm$ 1.5% less of the day ($P < 0.05$) for each week delay in hatch date.

Weather and Tide Stage

The mixed effects model detected no effects of tide stage, weather, or time of day on chick meal delivery rates, after accounting for date and brood size using a compound symmetric covariance matrix. Tide stage had no effect on meal delivery rates to the nest (n.s.). Precipitation, wind speed, and temperature did not explain a significant proportion of the variation in meal delivery rates. The 2001 breeding season was notable, however, for the absence of severe storms. Precipitation throughout the sampling period ranged from 0.0 to 14.2 cm per day ($\overline{x}$ = 0.23 cm), average daily wind speeds ranged from 7.7 to 31.8 knots ($\overline{x}$ = 15.7 knots), and daily temperatures ranged from 8.9 to 17.8°C ($\overline{x}$ = 13.5°C). In addition, nests were not observed on the most extreme weather days because of limited access to the island. Consequently,

extreme weather may affect the foraging be-havior of breeding Caspian Terns, but such effects were not demonstrable in this study.

Brood Size

Nests with larger broods were associated with a higher rate of meal delivery (weighted multiple linear regression: $F_{2,23}$ = 13.78, r^2 = 0.55, P < 0.001). Meal delivery rates to one-, two-, and three-chick broods were 0.33 ± 0.03 (N = 5), 0.88 ± 0.06 (N = 19), and 1.25 ± 0.09 (N = 2) meals h^{-1}, respectively. Meal delivery rates to two-chick broods were 0.54 ± 0.12 meals h^{-1} greater than to one-chick broods (P < 0.001), or 2.6 times the rate to one-chick broods.

Prey Composition

The taxonomic composition of fish deliv-ered by radio-tagged adult to their broods was similar to that of the colony as a whole (χ^2_4 = 8.24, n.s.; D. D. Roby, unpubl. data), suggesting that the sample of fish delivered by radio-tagged terns was not biased. The proportion of salmonids delivered to the brood (compared to marine forage fish) was lowest during flood tides, highest during ebb tides, and intermediate during low and high tides (N = 22 nests; Fig. 4). The proportion of salmonids delivered to the brood during ebb tides was 24 percentage points higher than during flood tides (Pearson chi-square: χ^2_1 = 5.82, P < 0.05). No other pair-wise com-parisons were significant.

The average length of fish delivered to the colony increased with date during the chick-rearing period. Estimated lengths of fish delivered to the colony averaged 0.54 ± 0.03 cm longer for each subsequent week of the chick-rearing period (P < 0.02), after ac-counting for fish type (multiple linear re-gression; $F_{11,191}$ = 6.51, r^2 = 0.27, P < 0.001).

Foraging trip duration was associated with the prey type delivered to the nest. We compared foraging trip durations from adult terns that delivered at least one marine and one salmonid prey item to the colony during each of the four tide stages in the analysis (N = 12 birds). Foraging trips resulting in the
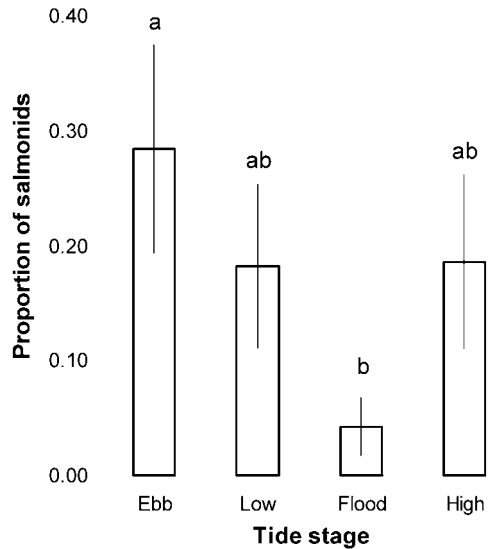

Figure 4. Proportion of juvenile salmonids (and SE) de-livered to broods as a function of tide stage for Caspian Terns nesting on East Sand Island in 2001. Bars with dif-ferent letters are significantly different. Only salmonids and schooling marine prey (anchovy, herring/sardine, and smelt) are shown.

delivery of marine forage fish were 22.4 ± 8.74 min shorter on average than foraging trips resulting in delivery of a salmonid (av-erage trip durations for marine forage fish and salmonids were 32.6 and 54.9 min, re-spectively; paired t-test; t_{11} = 2.56; P < 0.05).

DISCUSSION

Caspian Tern productivity on East Sand Island in 2001 was the highest so far record-ed in the Pacific Northwest (1.40 young fledged per nesting pair; Roby et al. 2002). Exceptionally high productivity was likely due to high food availability in the Columbia River estuary, a reflection of increased stocks of marine forage fishes due to favorable ocean conditions compared with previous years (Brodeur et al. 2003; R. Emmett, NOAA Fisheries, pers. comm.). A further indication of high food availability in 2001 was high productivity of the Double-crested Cormo-rants (*Phalacrocorax auritus*) nesting on East Sand Island (Anderson 2002), and greater use of the island as a post-breeding roost site by Brown Pelicans (*Pelecanus occidentalis*) (Wright 2004). Concurrently, high-lipid ma-

rine forage fishes were more prevalent in the diet of terns than in previous years (Roby *et al.* 2002). This suggests that parents may have experienced less difficulty provisioning chicks during 2001 as compared to previous years and that productivity and colony attendance were both positively associated with prey availability (Anderson 2003).

Seasonal Changes

The seasonal increase in duration of chick provisioning trips was mostly due to date, rather than age of the brood, implicating seasonal changes in prey availability as a cause. Relative availability of various salmonids (FPC 2001) and other prey types (R. Emmett, NOAA Fisheries, pers. comm.) apparently changed during the chick-rearing period. The proportion of salmonids in the diet of Caspian Terns nesting on East Sand Island declined throughout the chick-rearing period (Roby *et al.* 2002). Foraging trips that resulted in the capture of salmonids took more time than foraging trips for marine forage fishes, so a decline in salmonids in the diet should result in shorter foraging trips. Longer average duration of foraging trips may instead reflect an overall decline in prey availability. The increase in trip duration was concurrent with an increase in the average length of fish delivered to the colony, suggesting that terns may have invested more time to obtain larger prey.

Alternatively, younger, less productive adults tend to nest later in the season (Nisbet *et al.* 1984; Coulson *et al.* 1985), suggesting that later nesting parents may be less efficient foragers. If provisioning trip duration reflects parental age and experience, parents initiating nests later in the season would be expected to take longer provisioning trips. A combination of prey availability and parental quality may be responsible for the increasing duration of foraging trips as the chick-rearing period progresses.

Brood Size and Age

Energy demands at the nest are dependent primarily on brood size and brood age.

Although brood age did not appear to significantly influence chick provisioning behavior, brood size was associated with major changes in the frequency and duration of provisioning trips. Caspian Terns raising two-chick broods delivered meals at more than twice the rate as parents of one-chick broods. High meal delivery rates to larger broods in the present study are further support for the conclusion that forage fish availability near East Sand Island was high in 2001. Furthermore, parents of two-chick broods delivered more prey without a significant reduction in colony attendance. A decline in colony attendance by parents leaves chicks unattended, increasing the risk of chick mortality due to predation, exposure, and aggression from conspecific adults (Cuthbert and Wires 1999). In years when prey availability is low, parent terns must trade-off attending the brood and provisioning the brood with adequate food. In years of high food availability, however, the combination of high parental attendance and high chick-provisioning rates favors high nesting success.

Gender Differences

The frequency of chick provisioning trips by male Caspian Terns was higher than by females. Both sexes responded similarly to the influence of brood size, so the higher chick provisioning rates of the male parent were maintained even with increased energy demands at the nest. These results are similar to those of Wiggins (1989) working with Common Terns and Quinn (1990) studying Caspian Terns. The magnitude of the gender difference in foraging trip frequency was much greater in the Quinn (1990) study than in the present study. This may be due to differences in foraging conditions between the two studies, or because we monitored Caspian Tern chicks at different ages than in Quinn's study. Kirkham (1996) suggested that the sexual asymmetry in chick provisioning duties is greatest when chicks are young. Caspian Terns in the study by Quinn (1990) were observed until 15 days post-hatch, while the present study included observations until 21 days post-hatch. Therefore, it is possi-

ble that at least part of the difference in magnitude of sexual differences seen between the two studies was due to the difference in brood age.

Tide Stage and Prey Composition

Meal delivery rates did not vary with tide stage. The constancy of meal delivery rates regardless of tide stage may have been due to generally high food availability in 2001, or specifically to the high availability of marine forage fishes on flood tides and juvenile salmonids on ebb tides. In addition, East Sand Island is located in the marine zone of the estuary (Simenstad *et al.* 1990) where marine, euryhaline, and freshwater prey species are all available nearby (Collis *et al.* 2002), allowing terns to exploit a variety of prey types as salinity changes due to tidal fluctuations.

Although chick meal delivery rates did not vary with tide stage, the proportion of salmonids in chick meals changed with tide stage. The prevalence of salmonids was highest during ebb tides, when juvenile salmonids are most likely migrating out to sea (C. B. Schreck, pers. comm.) and passing East Sand Island. Conversely, on flood tides, when more marine water flows into the estuary, we observed a higher proportion of marine forage fishes in chick meals. Previous studies suggest that the Caspian Tern is a generalist forager, feeding on the most available fish of suitable size close to the nesting colony (Roby *et al.* 2002). Tidal fluctuations appear to affect the relative availability of prey taxa near the East Sand Island colony and hence the prey composition provided as chick meals. It is possible, however, that in years with lower availability of marine forage fish, Caspian Terns nesting at East Sand Island may attempt to compensate by capturing more freshwater and anadromous prey species.

The average duration of foraging trips that resulted in delivery of a salmonid to the nest was significantly longer than foraging trips resulting in the delivery of a marine fish, suggesting that availability of marine forage fishes was higher than that of salmonids. One explanation is that schooling marine fish are more vulnerable to repeated exploitation than non-schooling prey (e.g., salmonids; C. Schreck, pers. comm.). Three of the four most common prey types in Caspian Tern diets in this study (anchovy [Engraulidae], herring/sardine [Clupeidae], and surfperch [Embiotocidae]; Roby *et al.* 2002) occur in schools (Emmett *et al.* 1991). Caspian Tern parents may exploit a nearby prey patch (i.e., school of fish) repeatedly until they and their chicks are sated or the patch has dissipated. During survey flights, we observed many multi-species foraging flocks of piscivorous birds in the estuary apparently taking advantage of a productive prey patch. Self-feeding takes less time where prey are concentrated and search time is avoided by returning to the same prey patch, thereby reducing the average duration of foraging trips for schooling marine prey compared to non-schooling prey.

The prey-dependent difference in duration of foraging trips by Caspian Terns is also consistent with coarse-level local enhancement, as defined by Pöysä (1992). Coarse-level local enhancement predicts that the presence of predators using a productive prey patch increases the delectability of that prey patch, thereby attracting more predators. Schooling marine forage fish would be more susceptible to detection (and therefore predation) through coarse-level local enhancement than out-migrating juvenile salmonids. Further investigation is needed to determine if this is a factor influencing trip duration.

The results of this study support previous evidence that Caspian Tern nesting success on East Sand Island is highly dependent on marine forage fish. Caspian Tern diet composition reflects changes in local prey availability, suggesting reliance on prey most available and proximal to the nesting site. Foraging trip distance and duration are most restricted during chick-rearing by the need to attend the nest and protect chicks (Anderson 2003). Lower availability of marine forage fish in other breeding seasons would likely have a significant negative impact on the productivity of the East Sand Island colony, a large proportion of the Pacific Coast population of Caspian Terns.

Marine forage fish comprise the largest component of the diet of Caspian Terns at East Sand Island (Roby *et al.* 2002), and appear to be more available than the primary alternative prey, juvenile salmonids (this study). However, the local abundance of marine forage fishes is subject to dramatic fluctuations associated with regime shifts in offshore conditions (Brodeur *et al.* 2003). Therefore, in addition to affecting Caspian Tern productivity, a significant decline in marine forage fish availability would likely result in a greater reliance on juvenile salmonids, most of which are listed as endangered or threatened under the U.S. Endangered Species Act (National Marine Fisheries Service 2002).

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