AN ABSTRACT OF THE THESIS OF

<u>Scott K. Anderson</u> for the degree of <u>Master of Science</u> in <u>Wildlife Science</u> presented on <u>October 9, 2003</u>.

Title: <u>Foraging Ecology, Colony Attendance, and Chick Provisioning of Caspian Terns (*Sterna caspia*) in the Columbia River Estuary</u>

Abstract appro‌

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Daniel D. Roby

This study was designed to enhance understanding of factors influencing foraging distribution, diet composition, and overall reproductive success of Caspian terns (*Sterna caspia*) nesting on East Sand Island in the Columbia River estuary. This colony of nearly 10,000 breeding pairs is of concern to regional resource managers because Caspian terns consume large numbers of juvenile salmonids (*Oncorhynchus* spp.) listed under the Endangered Species Act. In addition, Caspian terns at this colony consume marine forage fishes, the abundance of which fluctuates on annual and decadal scales. I found that average foraging distance from the colony was 6.6 km (38%) greater in 2000 compared to 2001, associated with lower availability of marine forage fishes in the estuary and lower prevalence of marine prey in tern diets. Also, colony attendance was much lower (37.0% vs.

62.5% of daylight hours), average foraging 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.

In 2001, average meal delivery rates to 2-chick broods (0.88 meals hour^{-1}) was 2.6 times greater than to 1-chick broods (0.33 meals hour^{-1}). Parents delivered more juvenile salmonids to their young during ebb tides than during flood tides, suggesting diet composition reflected short-term changes in relative availability of prey near the colony. Foraging trips resulting in delivery of juvenile salmonids took 68% longer than foraging trips resulting in delivery of schooling marine forage fishes, indicating higher availability of marine prey. High proportion of salmonids in the diet was associated with high use of the freshwater zone of the estuary by radio-tagged terns, suggesting that diet composition also reflected the distribution of foraging terns in the estuary.

High availability of marine forage fish in 2001 was apparently responsible for high colony attendance, relatively brief foraging trips close to the colony, high food delivery rates to young, and high nesting success of Caspian terns on East Sand Island. 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. The foraging behavior and nesting success of Caspian terns at the East Sand Island colony is apparently highly dependent on the fluctuating availability of marine forage fishes in the Columbia River estuary. Diet studies indicate that the primary alternative prey for this tern colony are out-migrating juvenile salmonids from throughout the Columbia River basin.

Foraging Ecology, Colony Attendance, and Chick Provisioning of
Caspian Terns (*Sterna caspia*) in the Columbia River Estuary

by
Scott K. Anderson

A THESIS

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APPROVED:

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Scott K. Anderson, Author

ACKNOWLEDGMENTS

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DEDICATION

To the memory of Christopher Cecil Sharp

FORAGING ECOLOGY, COLONY ATTENDANCE, AND CHICK PROVISIONING OF CASPIAN TERNS (*STERNA CASPIA*) IN THE COLUMBIA RIVER ESTUARY

CHAPTER 1

GENERAL INTRODUCTION

Scott K. Anderson

The population of Caspian terns (*Sterna caspia*) nesting in the Columbia River estuary has increased dramatically since 1984, and now comprises approximately 67% of the Pacific Coast population (Suryan et al., in review). In 1997 and 1998, the diet of Caspian terns nesting on Rice Island in the Columbia River estuary consisted primarily of juvenile salmonids (*Oncorhynchus* spp.; Collis et al. 2002a, Roby et al. 2003). Twelve of the 20 evolutionarily significant units of anadromous salmonids that originate in the Columbia River basin are listed as either endangered or threatened under the U. S. Endangered Species Act (NMFS 2002). While the exact number of listed salmonid smolts consumed by Caspian terns in the estuary is not known, total smolt consumption was between 9.1 and 15.7 million in 1998 (Roby et al. 2003). As part of an effort to reduce predation on juvenile salmonids by Caspian terns nesting on Rice Island (in the freshwater zone of the estuary), the colony was relocated to East Sand Island (in the marine zone of the estuary) during 1999 – 2001 (Roby et al. 2002).

The level of consumption of salmonids by Caspian terns nesting on East Sand Island was about half that of the colony when it was on Rice Island (Roby et al. 2002; D. E. Lyons, unpubl. data), due to the presence of marine forage fishes at the new location. Nevertheless, there is still concern among fisheries managers over the impact of the

East Sand Island tern colony (which now numbers about 10,000 pairs; CBR 2002) on survival of listed salmonids in the estuary. The East Sand Island Caspian tern colony is currently the largest colony for this species in North America (Cuthbert and Wires 1999; Suryan et al., in review) and apparently the world, and comprises approximately 25% of the North American population (Wires and Cuthbert 2000). The high concentration of breeding Caspian terns at one colony site is of conservation concern to managers because a local weather event, disease outbreak, or oil spill could devastate a large proportion of the population. Studies are currently underway to investigate the necessity and feasibility of dispersing part of this colony to several smaller colonies to reduce threats to both Columbia Basin salmonids and Caspian terns.

In 2000 and 2001, I investigated how foraging distribution reflects seasonal and between-year differences in diet composition of Caspian terns nesting on East Sand Island. The location of this colony near the mouth of the Columbia River allows breeding adults to prey upon a wide variety of forage fishes with different salinity requirements (Roby et al. 2002). Changes in flow rates and salinity associated with tidal fluctuations within foraging range of Caspian terns breeding on East Sand Island can alter the spatial distribution and abundance of

prey over short time scales (Bottom and Jones 1990), while changes in ocean conditions and snow pack between breeding seasons can alter the relative abundance of marine forage fishes and anadromous juvenile salmonids that enter the estuary (Brodeur et al. 2003; R. Emmett, NOAA Fisheries, pers. comm.). I sought to relate changes in the spatial distribution of foraging terns (i.e., foraging distribution) within and among breeding seasons to observed changes in the type and number of prey consumed to better understand limitations on nesting success.

In 2001, I investigated the chick provisioning behavior of Caspian terns nesting on East Sand Island in relation to several intrinsic and extrinsic factors. Reproductive effort is highest for most seabirds during chick-rearing, when energy demands at the nest are greatest and foraging areas can be at considerable distance from the nest (Drent and Daan 1980). The parental effort required to meet chick food demands depends on a number of factors, including food availability (Jodice et al. 2002), brood age (Klaassen et al 1989, Wiggins 1989), brood size (von Haartman 1954, cited in Drent and Daan 1980), weather conditions (Dunn 1973, Sagar and Sagar 1989), and tide stage (Irons 1998). I measured changes in foraging trip duration and frequency throughout the chick-rearing period to test for the influence

of these factors and to better understand which factors most limit reproductive output.

This research was designed to 1) quantify seasonal and annual differences in foraging distribution, foraging range, and colony attendance, and 2) determine intrinsic and extrinsic factors influential to chick provisioning by Caspian terns nesting at East Sand Island. The results will enhance understanding of factors that influence the foraging behavior, diet composition, and nesting success of the largest colony of this species in the world.

CHAPTER 2

FORAGING PATTERNS OF CASPIAN TERNS NESTING IN THE
COLUMBIA RIVER ESTUARY

Scott Anderson

ABSTRACT

The prevalence of juvenile salmonids (*Oncorhynchus* spp.) and
marine forage fishes in the diet of Caspian terns (*Sterna caspia*) nesting
on East Sand Island in the Columbia River estuary has been well
established, but the spatial distribution of these birds when foraging
has thus far received little attention. I used radio-telemetry to relate
changes in diet composition and nesting success to the foraging
distribution and colony attendance of adults nesting at the East Sand
Island colony during 2000 and 2001. Average foraging distance from
the colony was 6.6 km (38%) greater in 2000 compared to 2001,
associated with lower availability of marine forage fish in the estuary
and lower prevalence of marine prey in tern diets. Colony attendance
was much lower (37.0% vs. 62.5% of daylight hours), average foraging
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. A high proportion of salmonids in the diet was
associated with relatively high use of the freshwater zone of the estuary
by radio-tagged terns, suggesting that diet composition reflects the
distribution of foraging terns in the estuary. I detected no evidence for
foraging site fidelity, suggesting that prey availability in the study area
was variable and unpredictable across the breeding season. 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.

INTRODUCTION

Nesting Caspian terns (*Sterna caspia*) in the Columbia River estuary consume juvenile salmonids (*Oncorhynchus* spp.; Collis et al. 2002a, Roby et al. 2002, Roby 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), 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, the proportion of salmonids in the diet of nesting terns declined by about half and the proportion of marine forage fish increased (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), and prompted questions about Caspian tern foraging behavior. Although Caspian tern diet composition in the Columbia River estuary is well studied (Collis et al. 2002a, Roby et al. 2002, Roby et al. 2003), little is known about where prey are captured and how foraging locations may shift in relation to changes in diet composition. In addition, an understanding of foraging behavior may help explain how prey availability affects the nesting success of Caspian terns at this location.

I studied the foraging distribution of Caspian terns nesting on East Sand Island in the Columbia River estuary to investigate how foraging behavior reflects seasonal and between-year changes in diet composition. 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. Flow rates and salinity levels within the foraging range of Caspian terns breeding on East Sand Island are highly dynamic, altering the distribution of prey over short time scales (Bottom and Jones 1990). Longer-term changes in ocean conditions and snow pack can alter the abundance of marine forage fish entering the estuary during the tern breeding season (Brodeur et al. 2003; R. Emmett, NOAA Fisheries, pers. comm.).

Colony attendance can also be used as an indicator of prey availability (Cairns 1987, 1992). Parents provisioning chicks must divide time between foraging and protecting chicks on the colony from predation and exposure. Thus, when prey conditions are poor, parents must spend more time foraging to meet the energy demands of chicks at the expense of time spent attending the colony.

Previous studies of the spatial distribution of foraging terns (i.e., foraging distribution) using radio-telemetry have focused on the chick-rearing period because birds are difficult to capture and radio-tag prior to late incubation (Wiggins and Morris 1987, Wagner and Safina 1989, Sirdevan and Quinn 1997). I was able to radio-tag adults at a roost site prior to the onset of egg-laying, allowing the comparison of foraging distributions among the incubation, chick-rearing, and post-fledging stages of the nesting cycle. These data were combined with data from Roby et al. (2002) on diet composition and productivity to investigate how foraging distribution changed with food availability and nesting success.

My objective was to characterize how breeding Caspian terns use foraging habitats near a breeding colony in a highly dynamic and variable estuarine environment and how foraging patterns change temporally. Specifically, I sought to answer the following questions:

1. Do foraging range and distribution of nesting Caspian terns change with stage of the nesting season?

2. Do foraging range and distribution of nesting Caspian terns reflect changes in relative prey availability?

3. Do the foraging range and distribution of Caspian terns differ between the sexes?

4. Do individual Caspian terns nesting in the Columbia River estuary exhibit fidelity to particular foraging sites?

METHODS

Study Area

I conducted this study on Caspian terns nesting on East Sand Island (46°15'45"N, 123°58'06"W) in the Columbia River estuary during the 2000 and 2001 breeding seasons (Figure 2.1). I partitioned the available foraging habitat for this tern colony into 3 zones. The Columbia River estuary was divided into 2 zones: a predominantly marine zone (down-river of the Astoria Bridge) and a predominantly freshwater zone (up-river of the Astoria Bridge; from descriptions in 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. The third zone included areas outside of the estuary: a near-shore coastal zone, Willapa Bay, and Grays Harbor (Figure 2.1).

Capture Methods

Adult Caspian terns were captured for radio-tagging on two islands: East Sand Island and Rice Island (46°14'58"N, 123°42'56"W). Adults were caught pre-laying using a rocket net at a roost site on Rice
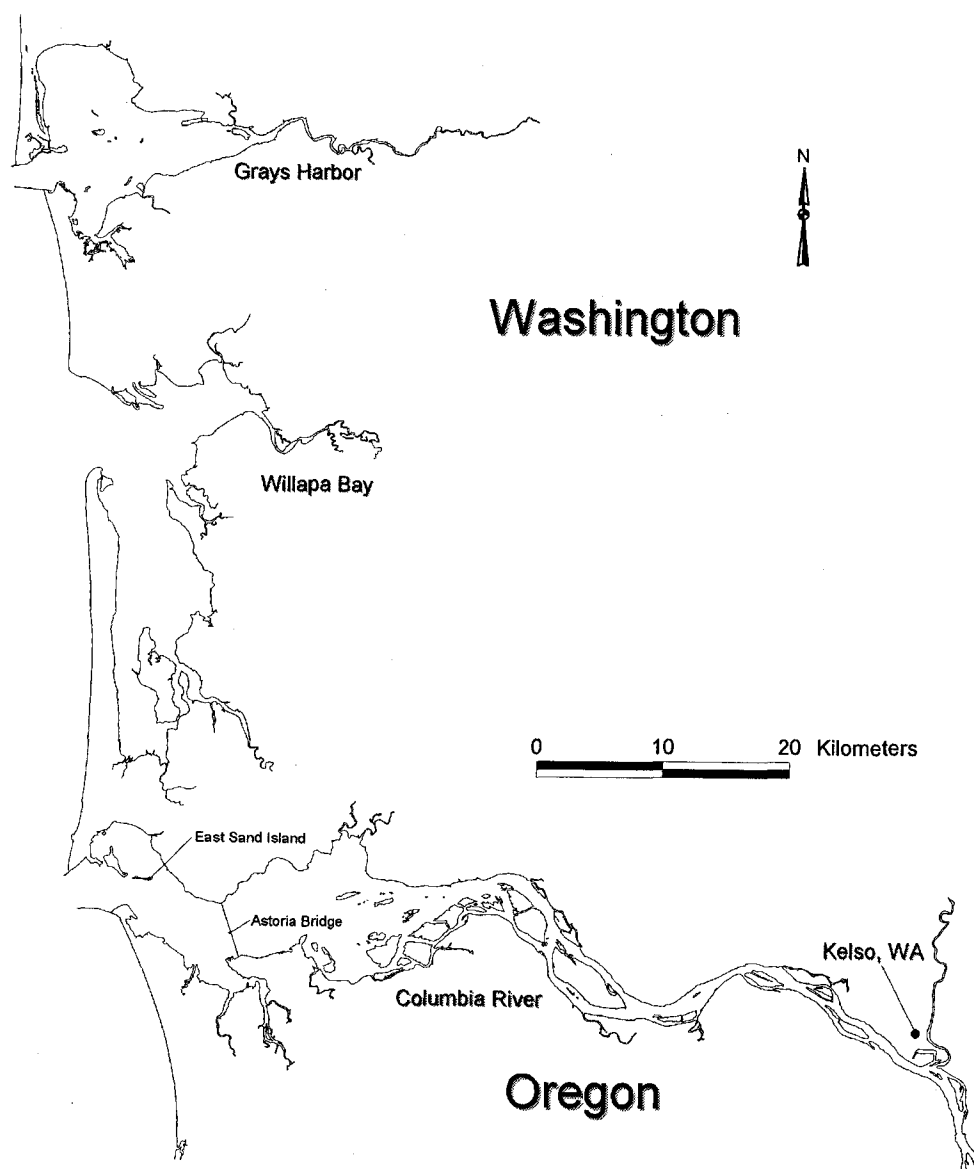
Figure 2.1. Map of study area showing the Columbia River estuary, Willapa Bay, and Grays Harbor.

Island during April of 2000 (N = 50) and 2001 (N = 30) and during late incubation using monofilament noose mats on the East Sand Island colony in mid-May of 2000 (N = 19) and 2001 (N = 24). On-colony trapping was conducted during late incubation to minimize nest abandonment due to disturbance (Sirdevan and Quinn 1997). Each adult was fitted with a federal numbered metal leg band and a unique color combination of five plastic leg bands. I attached Advanced Telemetry Systems (ATS - Isanti, Wisconsin) radio-tags (40 pulse min^{-1}, double-beep every 10 pulses, 80-day battery life expectancy) weighing 10 g (1.6% of average adult body mass) to the four central retrices using plastic ties and quick-setting Loctite© epoxy (see Anderson and Ricklefs [1987] and Irons [1998] for details). 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 I 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, adults were sexed opportunistically by observing copulation behavior on-colony after release. In 2001, adults were sexed genetically from blood samples analyzed by Avian BioTech International (Tallahassee, Florida).

Aerial Surveys

I conducted 22 aerial surveys in 2000 and 21 aerial surveys in 2001 to locate radio-tagged nesting Caspian terns. I conducted aerial surveys from a Cessna 205 aircraft with a single dipole antenna mounted on each wing. Proper equipment operation was verified at the beginning of each flight by listening for a transmitter placed at the airport. 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 or both simultaneously. While scanning for birds, both antennae were used to provide the greatest reception range possible. Reference transmitters located on-colony were often heard at a distance of up to 10 km, indicating that radio-tagged birds were detectable up to 10 km to either side of the flight path. Where this was not sufficient to cover the entire width of the Columbia River estuary, additional passes were flown.

Once a particular radio-tagged adult was detected, its location was pinpointed by comparing signal strengths from each antenna and instructing the pilot to turn the aircraft in the direction of the stronger signal. 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 handheld or dash-mounted GPS

receiver. I tested location accuracy by placing 7 transmitters on the ground for trackers to find, resulting in an average location error of 0.5 $\pm$ 0.1 km. 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 (Figure 2.1). Occasional surveys were flown south of the Columbia River throughout the breeding season, but few Caspian terns were observed foraging, no radio-tagged terns were detected, and there are no major coastal bays in that area, so it was not included in the analysis. Each zone of the study area was covered only once during each survey flight.

Surveys were flown at an altitude of approximately 500 ft (ASL) and required 2.7 to 5.3 hours to complete. Survey flights generally were timed to coincide with low tide (weather permitting) to control for variation in distribution associated with tide stage. Before each flight, the receivers were programmed with all frequencies of radio-transmitters thought to still be attached to live, nesting adults. Once a bird was located, the frequency was deleted from the receiver, for a maximum of one detection bird^{-1} flight^{-1}. Once in the vicinity of the nesting colony on East Sand Island or the roost site on Rice Island, I circled the site and deleted all radio-tagged birds detected at these sites

to maximize the efficiency of locating radio-tagged individuals actively foraging elsewhere. I assumed that radio-tagged Caspian terns located off-colony were engaged in foraging trips.

Nest Monitoring

I partitioned each breeding season into 3 time periods representing major breeding stages of the entire colony (incubation, chick-rearing, and post-fledging). Nesting chronology was similar in the two years of the study, and trapping occurred near the peak of hatching for radio-tagged adults. Therefore, I designated the last day of trapping as the beginning of the chick-rearing period (i.e., estimated hatch date) in both years of the study. The chick-rearing period (the period between hatching and fledging) was designated as the 37 days (Cuthbert and Wires 1999) following trapping (May 21st to June 26th in 2000, May 24th to June 29th in 2001). Incubation was considered to be the 27 days (Cuthbert and Wires 1999) prior to hatching (April 24th to May 20th in 2000, April 27th to May 23rd in 2001). I defined the post-fledging period as the 20 days following the chick-rearing period (June 27th to July 16th in 2000, June 30th to July 19th in 2001).

Nesting status of radio-tagged adults was confirmed by observing their behavior while on-colony (see Chapter 3 for details). I considered radio-tagged adults to be nesting if I observed them brooding young

chicks or feeding a chick during chick-rearing. After the first 26 days of chick-rearing, confirmation of breeding status became more difficult due to the increased mobility of chicks. Birds confirmed to have failed were omitted from analysis after the last observation confirming nesting.

The 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). 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 mounted near the edge of the colony (see Chapter 3 for details). Reception range of each DCC setup was determined by placing transmitters at various distances from the colony. 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 average time required for the DCC to scan for each frequency once (cycle time) was longer in 2000 than in 2001. Therefore,

I 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 to 21:30 Pacific Daylight Time, the average of civil twilight times during chick-rearing). For comparison, colony attendance also was estimated by the proportion of radio-tagged terns detected on-colony during survey flights. 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).

Several radio-tagged Caspian terns lost the antenna to their radio-transmitter during the study period, requiring these birds to be omitted from some analyses. Antenna loss was confirmed by direct observation or by reduced DCC reception (consecutive days/nights with no detections). I assumed that the off-colony detection rate of a bird, however, would not be dependent on location within the study area. Therefore, I 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.

Data Analysis

The nature of Caspian tern foraging behavior and method of data collection posed challenges for interpretation of the distribution of off-colony detections. Terns (unlike pursuit-diving species) forage during flight and while commuting to foraging areas (pers. obs.), and the behavior of individual radio-tagged terns detected during survey flights was unknown. Therefore, 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. For this reason, I restricted analyses to comparison of the spatial distribution of detections rather than attempting to interpret foraging habitat use based on the distribution of birds while off-colony.

The procedure for locating radio-tagged terns during aerial surveys was to locate all on-colony individuals before searching for off-colony individuals. In some cases, however, a bird not detected on-colony during the first pass returned to the colony in the time it took to track down other off-colony birds, biasing the data toward on-colony detections. To control for this bias, I included both on- and off-colony detections in comparisons of foraging distribution, unless otherwise noted. While this may not reflect the instantaneous foraging distribution of radio-tagged terns, it allows 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).

I 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 PROC MIXED (Laird and Ware 1982, SAS 1999). Covariance structures explaining variance associated with individuals were selected based on the procedure outlined in Wolfinger (1993) and Littell et al. (2000). Mixed effects models are based on likelihood estimation procedures, so I compared full models with all interaction terms and reduced models with no interaction terms using log likelihood ratio tests (Ramsey and Schafer 1997, SAS 1999).

I 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 chi-square tests (SAS 1999, Ramsey and Schafer 1997). Counts were calculated by randomly selecting one off-colony detection from each radio-tagged bird during each breeding stage, creating a balanced dataset. Mantel-Haenszel chi-square tests allow testing for differences due to one variable while accounting for possible effects of others (Ramsey and Schafer 1997, SAS 1999).

I 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. Colony attendance decreased and trip duration increased with date during chick-rearing in 2001 (see Chapter 3). Therefore, I used multiple linear regression (SAS 1999) to compare the proportion of birds detected off-colony during survey flights while controlling for date. This was not necessary for DCC data because data collection was continuous over the entire chick-rearing period.

To test for fidelity of individual terns to particular foraging sites, I compared off-colony locations of each radio-tagged adult to the population distribution using nearest neighbor distances. Only birds with ≥ 4 off-colony detections were used. Due to small sample sizes, no effect of year could be estimated, so data from the two years were combined. I calculated the nearest neighbor distance to all other off-colony detections for an individual (WITHIN), and to a sample of off-colony detections from other breeding adults in that year (AMONG). The size of the sample from other breeding adults was equal to the number of comparisons made within an individual. This resulted in two values for each bird: the average nearest neighbor distance WITHIN a bird and average nearest neighbor distance AMONG birds.

I compared averaged WITHIN and AMONG bird nearest neighbor distances using a pair-wise t-test (Ramsey and Schafer 1997, SAS 1999).

All tests are considered significant at the $\alpha \leq 0.05$ level. Means are presented ± one standard error unless otherwise noted.

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, post-fledging). Of the 22 survey flights completed in 2000, 5 were during incubation, 8 were during chick-rearing, and 9 were during post-fledging. Of the 21 survey flights completed in 2001, 5 were during incubation, 11 were during chick-rearing, and 5 were 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, 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, 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 radio-tagged (1.7:1, 46 males and 27 females).

Foraging Distance from Colony

I compared a full model including gender, year, breeding stage, and their interactions to a reduced model without interactions using average straight-line distance to the colony as a response. A spatial powers 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 three explanatory variables were not supported by the data (log likelihood ratio test; $\chi_7^2 = 8.2$, p = 0.3153). Diagnostic plots indicated that the frequency distribution of distances from colony did not depart significantly from normality. Distances of male terns were not statistically different from those of female terns (male distances 0.17 ± 2.96 km greater than female distances, p = 0.9532). Gender did not explain a significant proportion of the variation in the model.

To further evaluate the effects of year and breeding stage, I removed gender and included all nesting birds from both years, regardless of whether sex was known. I compared a full model including year, breeding stage, and their interaction 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 and the reduced model. Interactive effects between breeding stage and year were not supported by the data (log likelihood ratio test; $\chi_1^2 = 2.5$, p = 0.2865); therefore a reduced model with no interactions was applied.

Average distance of off-colony detections differed significantly between years and among some breeding stages (Figure 2.2). The frequency distribution of distances to the colony was reasonably normal, so no transformation was applied. Average off-colony distance was 6.63 ± 2.88 km greater in 2000 compared to 2001 (95% confidence interval: 0.85 – 12.42, p = 0.0255), after accounting for breeding stage. Differences in off-colony distance between breeding stages were not significant between incubation and post-fledging (1.02 ± 3.20 km; p = 0.7505), were suggestive between incubation and chick-rearing (4.93 ± 3.18 km; p = 0.1225), and were 5.96 ± 2.72 km greater during post-fledging than during chick-rearing (95% confidence interval: 0.58 – 11.33, p = 0.0300), after accounting for year.

Foraging Distribution

The distribution of radio-tagged terns (both on- and off-colony) among the three zones did not differ between the sexes, after
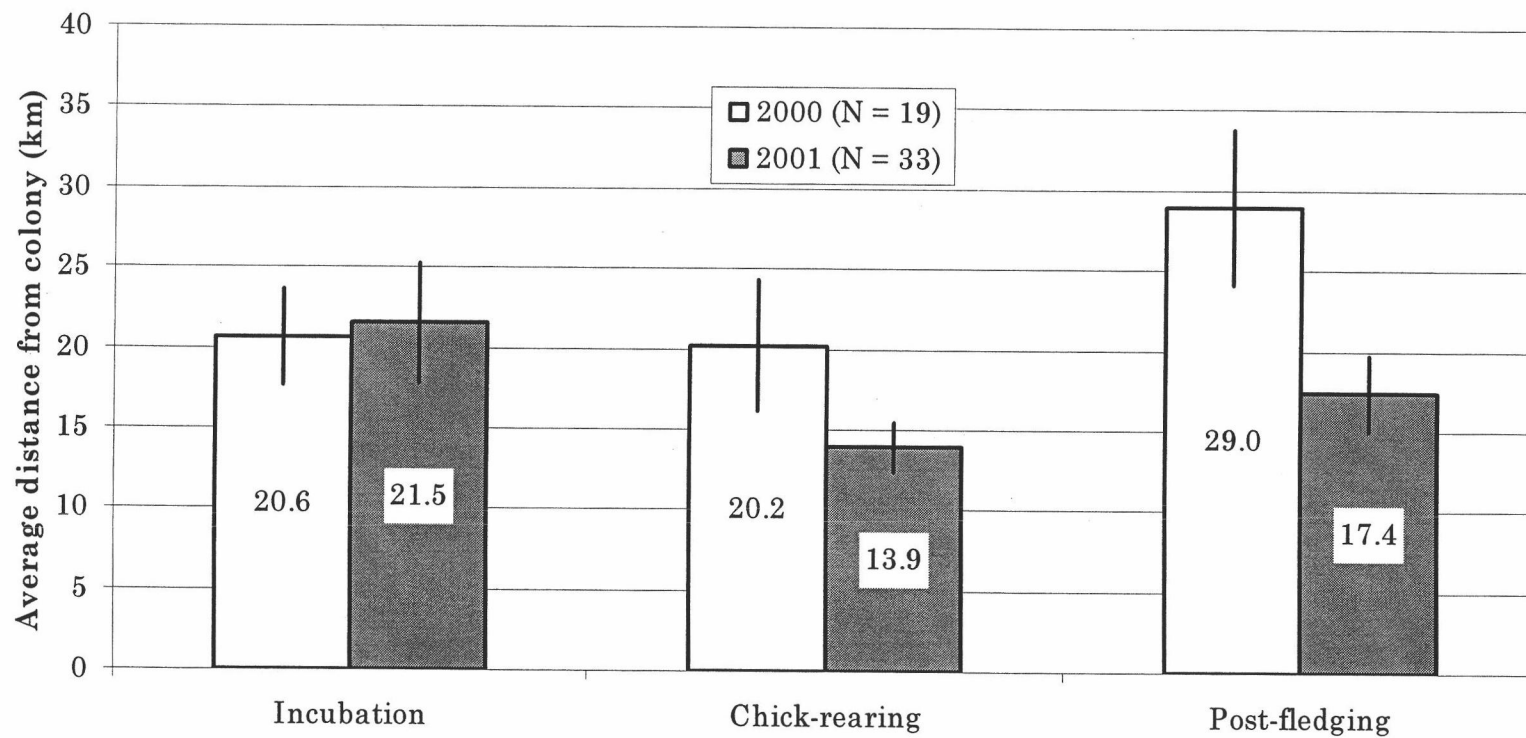
Figure 2.2. Average distance from the colony of off-colony detections of Caspian terns nesting on East Sand Island in the Columbia River estuary during incubation, chick-rearing, and post-fledging in 2000 and 2001.

accounting for year and breeding stage (χ^2_2 = 1.1545, p = 0.5614).

Therefore, subsequent analyses on detections included all radio-tagged

nesters, regardless of sex. The distribution of breeding birds (on- and

off-colony combined) was significantly different among breeding stages,

after accounting for year (χ^2_4 = 11.3829, p = 0.0226; Figure 2.3). 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. Although a greater proportion of birds were consistently

detected in the marine zone of the estuary during 2001 compared to

2000 (Figure 2.3), the differences (after accounting for breeding stage)

were not statistically significant (χ^2_4 = 1.1462, p = 0.5638).

Colony Attendance and Trip Duration

On-colony telemetry set-ups were different between the two

years, and the set-up in 2000 exhibited greater range and similar

reception rates compared to the set-up in 2001. Testing revealed that

transmitters were detected to a range of approximately 0.5 km in 2001,

a) Incubation
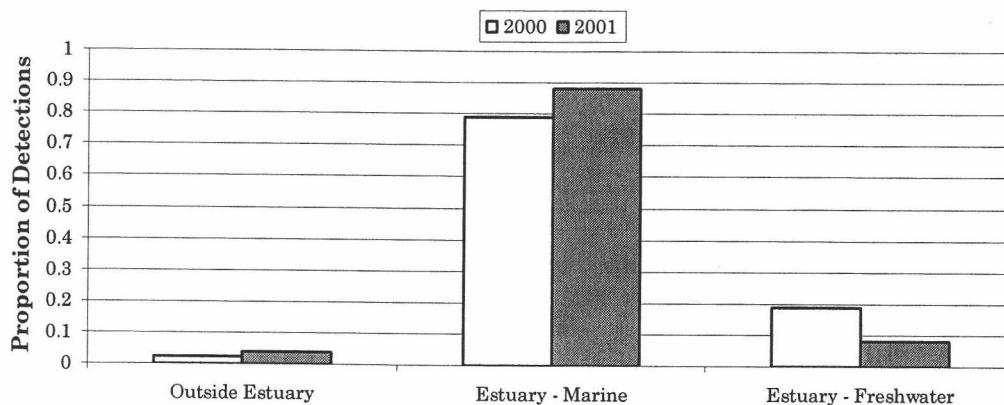
b) Chick-rearing
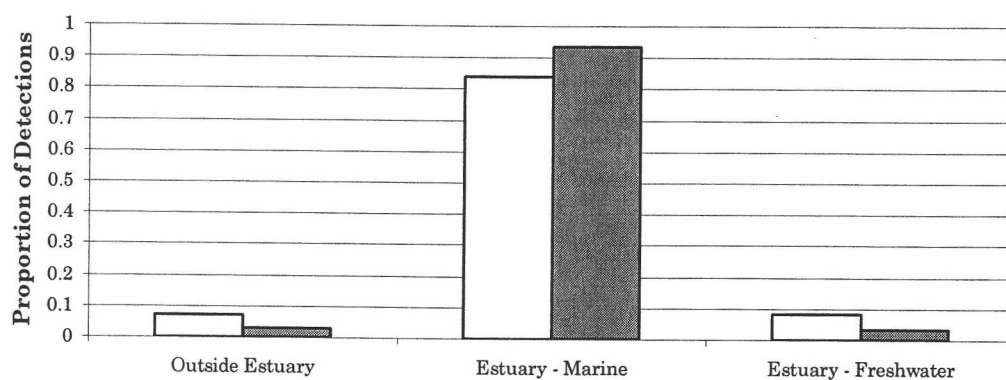
c) Post-fledging
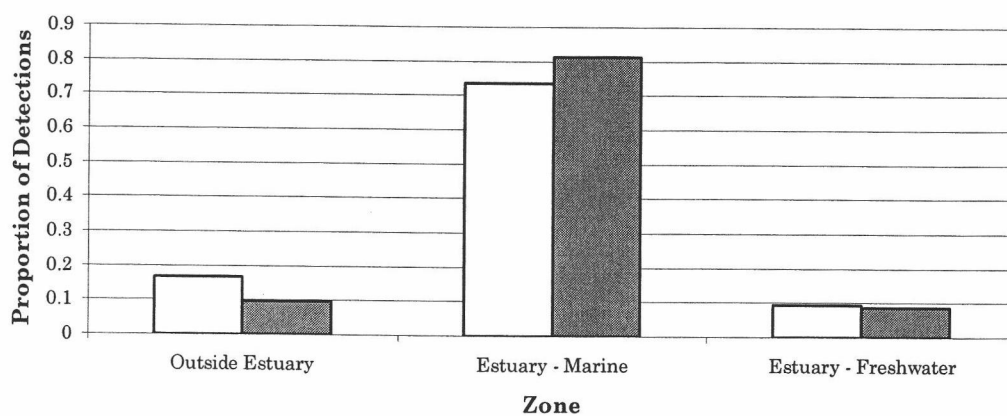
Figure 2.3. Average proportion of all detections in each zone of the study area during (a) incubation, (b) chick-rearing, and (c) post-fledging for each radio-tagged Caspian tern nesting on East Sand Island (N = 19 birds in 2000 and N = 33 birds in 2001).

but were detectable up to 7.0 km from the colony in 2000. False

detections were never 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 radio-tagged, nesting terns, 9 in 2000 and 13 in

2001 consistently attended the colony during the day and night,

indicating transmitter antenna loss had not occurred. Using the

sample of 13 terns in 2001, I 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 daytime colony attendance was much higher in 2001

(62.5%) than in 2000 (37.0%; Welch's t-test, 95% confidence interval:

difference of 18.2 – 32.8 percentage points, t_{15} = -7.417, p < 0.0001;

Figure 2.4). This 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 difference in colony attendance between the two years was

at least partly due to a difference in the duration of foraging trips. Off-

colony trips were significantly longer on average in 2000 (136.4 ± 5.15
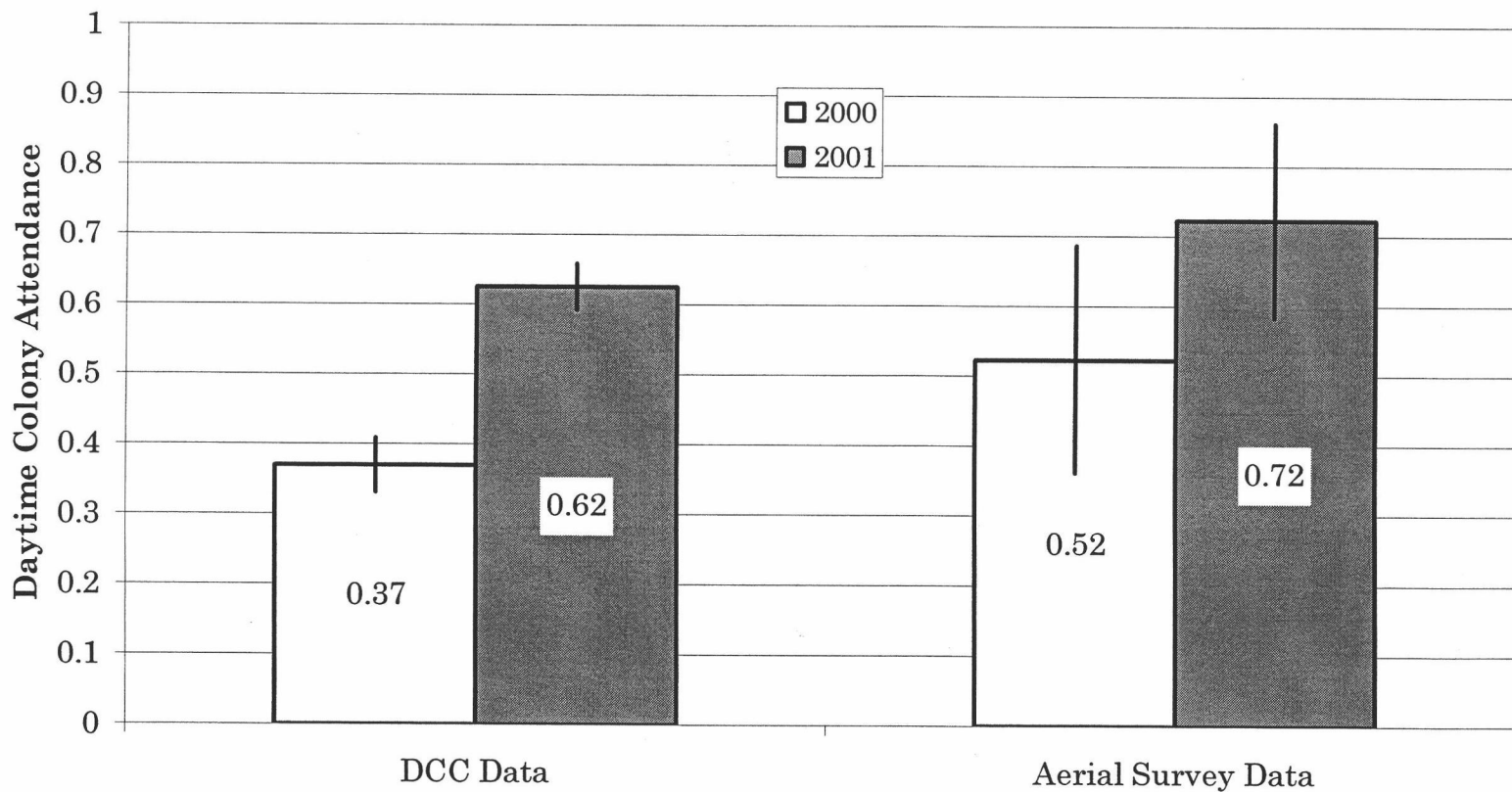
Figure 2.4. Two measures of colony attendance for Caspian terns nesting on East Sand Island during chick-rearing ($\leq$ 37 d post-hatch). See text for methods of estimation of colony attendance from the two data sets. Error bars indicate 95% confidence intervals.

min) than in 2001 (97.5 ± 2.29 min; Welch-modified t-test, $t_{11.2}$ = 6.8901, p < 0.0001). The proportion of on-colony detections from aerial surveys during chick-rearing was significantly higher in 2001 (72.2%, 95% confidence interval: 58.3 – 86.1%) than in 2000 (52.3%, 95% confidence interval: 36.0 – 68.5%), after accounting for date (multiple linear regression; $F_{2,16}$ = 13.45, r^2 = 0.6271, p < 0.0001).

Foraging Site Fidelity

The sample size of radio-tagged, nesting terns detected at least 4 times off-colony was 11 birds in 2000 and 9 birds in 2001. Average nearest neighbor distance WITHIN birds was not significantly different from average nearest neighbor distance AMONG birds (paired t-test; t_{19} = -0.6855, p = 0.5013). This indicates that individual terns did not exhibit season-long tendencies to frequent particular foraging areas and provides no evidence for fidelity to foraging sites.

DISCUSSION

Gender Differences

Male Caspian terns have been reported to contribute more to chick provisioning than females by delivering both larger and more frequent chick meals, suggesting gender differences in temporal and

spatial patterns of foraging. (Quinn 1990). In 2001, male Caspian terns nesting at East Sand Island took more frequent foraging trips than did females (see Chapter 3). Nevertheless, the spatial distribution of birds in this study did not differ between the sexes during any of the three breeding stages. Foraging trip duration also was similar between the sexes during 2001. Taken together, these results suggest that although males took more frequent foraging trips, foraging distribution was similar between the sexes.

Foraging Site Fidelity

The distribution of off-colony detections for individuals did not differ from the distribution of off-colony detections for all radio-tagged birds, providing no evidence for season-long fidelity to foraging sites within individuals. Caspian terns raising chicks at a colony in the Great Lakes showed similar high variation in foraging site use by individuals, even on consecutive foraging trips (Sirdevan and Quinn 1997). Black-legged kittiwakes foraging in a marine environment, however, responded to tidal fluctuations in predictable patterns (Irons 1998). Unfortunately, the low frequency of off-colony detections in this study limited inferences about foraging site fidelity in relation to tide stage. In addition, off-colony detections could not be confirmed as foraging sites, further limiting the power to detect foraging site fidelity.

Therefore, although I found no evidence of foraging site fidelity within individuals, further study is required to detect fidelity on smaller temporal and spatial scales.

Seasonal Trends

Several generalizations can be made about the distribution of juvenile salmonids and marine forage fish in the Columbia River estuary during the two years of this study. First, Caspian terns nesting on Rice Island in the freshwater zone of the estuary primarily consumed juvenile salmonids (Collis et al. 2002a, Roby et al. 2003), suggesting that salmonids were the most available forage fish in this zone of the estuary. Second, marine species in the diet of Caspian terns (anchovy, sardine/herring, and smelt) cannot tolerate low salinity (Emmett et al. 1991), and in most years are unlikely to inhabit areas above the Astoria Bridge, the approximate inland limit of saltwater intrusion (Simenstad et al. 1990).

The proportion of salmonids in the diet of Caspian terns nesting on East Sand Island was highest during incubation, and declined throughout the remainder of the breeding season in both 2000 and 2001 (Roby et al. 2002). During the same two years, the number of juvenile salmonids passing Bonneville Dam (the last dam in the Columbia River system) declined throughout the breeding season (FPC 2003).

Together, these data suggest that the prevalence of salmonids in the diet reflected their availability in the Columbia River estuary.

Seasonal changes in the off-colony distribution of Caspian terns nesting on East Sand Island also reflected changes in diet composition. The proportion of birds detected in the freshwater zone was highest during incubation, when the proportion of salmonids in the diet also was highest. Conversely, the proportion of birds detected outside the estuary was highest during post-fledging, when the proportion of juvenile salmonids in the diet was lowest. The distribution of nesting terns was more dispersed during incubation and post-fledging, when chick provisioning duties did not restrict foraging distances, while the distribution of Caspian terns during chick-rearing appeared to be largely confined to the marine zone of the estuary. During incubation and post-fledging, breeding Caspian terns could forage at greater distance from the colony, where prey were presumably more available, because parents were not constrained by the demands of provisioning food to chicks on-colony.

Restrictions on foraging range imposed by chick-rearing duties were also evident in differences in foraging distance from the colony among stages of the nesting cycle. Average distance from the colony during chick-rearing was 6.0 ± 2.7 km (25%) less than during post-

fledging. Although the difference in average foraging distance 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 foraging distances during incubation.

Inter-annual Differences

Diet composition, prey availability, and reproductive success of Caspian terns nesting on East Sand Island were very different between the two years of this study. Productivity was much higher in 2001 (1.40 young fledged pair[-1]) than in 2000 (0.57 young fledged pair[-1]; Roby et al. 2002). The abundance of marine forage fish in the Columbia River estuary and the coastal marine environment was much higher in 2001 than in 2000 (Brodeur et al. 2003; R. Emmett, NOAA Fisheries, unpubl. data). In 2001, Caspian terns nesting on East Sand Island relied less on juvenile salmonids and more on high quality marine forage fishes (anchovy, herring/sardine, and smelt) than in 2000 (Roby et al. 2002), suggesting that annual differences in tern diet composition and productivity reflected differences in prey availability in the Columbia River estuary. The association between seabird productivity and prey availability has been shown in other studies (Kitaysky et al. 2000, Jodice et al. 2002), most notably by Cairns (1987, 1992), who suggested

that measures of seabird productivity can be indicators of the health of marine fish stocks.

One mechanism whereby lower prey availability causes lower nesting success is through brood reduction. Brood reduction theory states that the size of the brood is adjusted to the parents' ability to provision food to the brood (Lack 1954, Ricklefs 1965). Brood reduction may occur primarily through starvation in Caspian terns (Quinn 1980, Cuthbert and Wires 1999). When prey availability is low, provisioning rates to younger chicks tend to be much lower than those to older chicks (Quinn 1990).

I recorded greater average foraging distance from the colony, longer average trip duration, and lower colony attendance during chick-rearing in 2000 compared to 2001, suggesting that terns were required to spend more time foraging to provision their broods. While low chick provisioning rates can lead to lower productivity through starvation of chicks, low adult colony attendance can also affect productivity through higher chick mortality due to predation and exposure. Aggression from conspecific adults also can be an important source of mortality for unattended Caspian tern chicks (Bent 1921, Cuthbert and Wires 1999).

Predation on tern chicks by glaucous-winged/western gulls (*Larus glaucescens* X *L. occidentalis*) can have a significant impact on

tern nesting success in the Columbia River estuary (Roby et al. 2002). For example, predation by glaucous-winged/western gulls had a major negative impact on productivity of Caspian terns nesting on Rice Island in 2000, but at the tern colony on East Sand Island, gulls that were observed depredating tern chicks were selectively removed to ensure success of the colony relocation effort (Roby et al. 2002). Gull control at the East Sand Island colony was discontinued in 2001, but gull predation on tern chicks was rarely observed (pers. obs.). This suggests gull predation rates on chicks also were linked to forage fish availability. If glaucous-winged/western gull parents feeding young on East Sand Island can meet the energy demands of their broods by preying on forage fishes, this may decrease predation pressure on tern chicks at the nearby Caspian tern colony. The effects of reduced forage fish availability on both lower provisioning of tern chicks and higher gull predation on tern chicks may have contributed significantly to lower chick survival in 2000.

Exposure to inclement weather also contributed to lower productivity in 2000. A severe wind and rain storm occurred on June 11th, early in chick-rearing, killing an estimated 1,000 chicks (D. D. Roby, pers. comm.). Although there were no major storms during chick-rearing in 2001, the mortality associated with the storm in 2000 was

likely exacerbated by the lower colony attendance of parent terns in that year.

CONCLUSIONS

The greater abundance of marine forage fishes in the Columbia River estuary in 2001 compared to 2000 resulted in high prey availability near the East Sand Island tern colony. In addition, marine forage fish may be more susceptible to repeated exploitation than salmonids because of their schooling behavior and vulnerability to coarse-level local enhancement (see Chapter 3).

Seasonal changes in the foraging distribution of Caspian terns nesting at East Sand Island reflected changes in diet composition and availability of prey within the Columbia River estuary. Foraging distances were more restricted during chick-rearing, suggesting chick provisioning duties limit the foraging habitats available to parent Caspian terns. Consequently, high nesting success of Caspian terns at the East Sand Island colony is likely dependent on high prey availability near the colony during chick-rearing.

Relatively low prey availability near the East Sand Island colony in 2000 apparently resulted in lower productivity compared to 2001. When prey were more difficult to locate, nesting terns were required to take longer foraging trips, forage farther from the colony, and reduce

colony attendance. This not only resulted in lower provisioning rates to broods and consequent brood reduction, but chicks were unattended for a greater proportion of the day, increasing mortality due to predation, exposure, and aggression from conspecific adults.

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CHAPTER 3

FACTORS AFFECTING CHICK PROVISIONING BY CASPIAN
TERNS NESTING IN THE COLUMBIA RIVER ESTUARY

Scott K. Anderson

ABSTRACT

I investigated factors affecting chick provisioning by radio-tagged

Caspian terns (*Sterna caspia*) nesting at a large colony on East Sand

Island in the Columbia River estuary during 2001, when abundance of

marine forage fishes was high. Caspian tern predation on threatened

juvenile salmonids (*Oncorhynchus* spp.) in the estuary has prompted

management action to reduce smolt losses, resulting in a greater

reliance on marine forage fishes. This study was designed to enhance

understanding of factors influencing foraging success, diet composition,

and overall reproductive success at a colony of conservation concern for

both the predator and its prey. Daytime colony attendance by parent

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 hour^{-1}) were 2.6 times greater than to 1-chick broods (0.33

meals hour^{-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. 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.

INTRODUCTION

Caspian terns (*Sterna caspia*) have been nesting 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, USACE, pers. comm.). Subsequently, the colony shifted to Rice Island, a dredge spoil island 25 km up-river, and grew considerably (Roby et al. 2002). The colony became the largest for Caspian terns in North America and comprised 67% of the Pacific Coast population of the species (Suryan et al., in review). The rapid population 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 such as Caspian terns may significantly impact 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), and for Caspian terns nesting in the Columbia River estuary, chick-rearing occurs during out-migration by juvenile salmonids. 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 (NMFS 2002). While the number of listed salmonid smolts consumed by Caspian terns in the estuary is not known, total smolt consumption was between 9.1 and 15.7 million in 1998 (Roby et al. 2003).

In 1999, regional natural resource managers (NOAA 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).

High prey availability is most crucial for nesting success during chick-rearing. Reproductive effort is highest for most seabirds during chick-rearing, when energy demands at the nest are greatest (Drent and Daan 1980) and foraging distances 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 (von Haartman 1954 cited in 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 (*Sterna 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 longer pre-fledging period than common terns (37 days; Cuthbert and Wires 1999) and, consequently, peak energy requirements of Caspian tern chicks likely occurs at about 30 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 meals more frequently. Terns, which provision their young by delivering single fish held in the bill, have been shown in some studies to meet higher demands solely by delivering larger prey

(Wiggins and Morris 1987, Burger and Gochfeld 1991). However, parent terns tending larger broods also exhibit higher provisioning rates to the nest (Quinn 1980), sufficient to maintain per-chick meal delivery rates in one study (Wiggins 1989).

Although it may be more energetically efficient 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 Caspian tern adults (Quinn 1990). Thus, tern parents with larger broods of young chicks may be forced to deliver meals more frequently, or meals with a higher energy density.

Male Caspian terns have been shown to provision their young more than females (Quinn 1990), but 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, parent gender may be a significant factor influencing the frequency or duration of foraging trips by nesting Caspian terns.

Weather and tides can also influence the frequency and duration of foraging trips in seabirds. Irons (1998) found that black-legged kittiwakes (*Rissa tridactyla*) 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 tide stage. Fish capture success for common and Sandwich terns (*Sterna sandvicensis*) was positively correlated with wind speed, presumably because it requires more effort and wing movement to hover in calm winds compared to moderate winds, making a foraging tern more obvious to potential prey (Dunn 1973). Inclement weather also has been implicated in reduced foraging efficiency in roseate (*S. dougallii*), Sandwich, and common terns (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).

I sought to determine factors that influence chick provisioning, as reflected in colony attendance, foraging trip duration, and frequency of foraging trips by answering the following questions:

1. Do Caspian tern parents of larger or older broods exhibit higher provisioning rates than parents of smaller or younger broods?

2. Do male and female parents respond in similar ways to different energy demands at the nest?

3. Do environmental factors such as wind speed, precipitation, temperature, and tide stage affect parental provisioning of chicks?

4. Does prey type affect parental provisioning of chicks?

Answers to these questions will elucidate the factors limiting chick survival and the reproductive output of Caspian terns nesting at East Sand Island.

METHODS

Study Area

I conducted this study during the 2001 breeding season at the Caspian tern colony 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). I radio-tagged breeding adult Caspian terns to monitor the colony attendance and chick provisioning of individual adults. To attach radio transmitters on breeding Caspian terns, I captured adults on two islands in the Columbia River estuary: East Sand Island and Rice Island (46°14'58"N, 123°42'56"W). Rice Island, located at river kilometer 34, was a roost site for Caspian terns, but no nesting occurred there in 2001.

Capture Methods

Thirty adult terns were caught for radio-tagging using a rocket net apparatus on Rice Island in mid-April, prior to the onset of egg-laying at East Sand Island. I also captured 24 adult terns for radio-tagging on the East Sand Island colony in mid-May by placing monofilament noose mats around active nests. I used this capture technique during late incubation to minimize nest abandonment due to disturbance (Sirdevan and Quinn 1997). I collected blood from the brachial vein of each radio-tagged adult for sex determination (Avian BioTech International, Tallahassee, Florida). I banded each adult with a federal numbered metal leg band and a unique color combination of five plastic leg bands (double-wrap, Darvic™ plastic bands from A.C. Hughes Ltd.).

I attached radio transmitters from Advanced Telemetry Systems (ATS - Isanti, Wisconsin) 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, so I assumed similar effects on Caspian terns. Radio-tagged terns were marked on the neck, back, and upper wing coverts with picric acid or rhodamine-B dye to assist with observations when the individual was on the colony.

After release, I located 27 of the 54 radio-tagged terns at active nests on East Sand Island. Nineteen of these 27 nesting terns (70%) had been radio-tagged on East Sand Island during late incubation, while the remainder (30%) had been radio-tagged pre-laying on Rice Island. A bird was considered actively nesting if it was observed incubating eggs, feeding another adult tern that was incubating eggs, or feeding a chick. Periodically throughout the season, I checked the on-colony behavior of radio-tagged terns to confirm active nesting and to record the number and approximate age of chicks. I compared characteristics of chick plumage to known-age chicks raised in captivity (D. E. Lyons, unpubl. data) to improve the accuracy of brood age estimates and back-calculated hatch dates.

I monitored radio-tagged nesting terns during chick-rearing in two ways: (1) nests of radio-tagged terns were directly observed from blinds adjacent to the colony for periods of approximately 3 hours, coinciding with each of the four tide stages (low, flood, high, ebb) and (2) on-colony presence of each radio-tagged individual was recorded

about every 10 minutes using automated radio telemetry monitoring equipment (see details below).

Nest Observations

I observed nests from blinds to measure the effect of tides, time of day, weather, and brood size on the rate of meal delivery to chicks by pairs of nesting Caspian terns. Twenty-six of the 27 located nests with radio-tagged adults were observed at least once, and 21 were observed at all four tide stages during the chick-rearing period (May 27th to July 5th). Tide stages were determined by centering 3-hour time periods on peak high and low tides; flood and ebb tides were defined by the intervening 3-hour 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. Nests were not observed for more than one tide stage in the same day to avoid potential autocorrelation. During each nest observation period, I noted arrival and departure of parent birds and the size and type of prey fed to the brood.

If a bird returned with a fish, I identified the fish to the family level (Clupeidae [herring/sardine], Engraulidae [anchovy], Cyprinidae [peamouth/pikeminnow], Osmeridae [smelt], *Oncorhynchus* spp.

[salmonids], Gadidae [cod], Cottidae [sculpin], Embiotocidae [surfperch], *Ammodytes hexapterus* [Pacific sand lance], and Pleuronectidae [flounder]). I estimated fish length (cm) based on average head-bill length of adult Caspian terns (13.5 cm). Although the error in fish length estimates was unknown, any bias in length estimates should have been constant over the entire sampling period, allowing comparisons within the study. I calculated meal delivery rates (fish hour^{-1}) for each radio-tagged bird to validate the telemetry data, and combined meal delivery rates from both parents when testing for brood size, weather, and tide effects.

I obtained daily averages for weather parameters (precipitation, wind speed, and temperature) 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, and tide data (meters of water from mean low water) from the NOAA tide gauge station at Tongue Point, Oregon (46°11'N, 123°46'W), 17.0 km up-river from the colony site. I used these data to test for associations between meal delivery rate, colony attendance (see below), and environmental variables.

Telemetry

I monitored the attendance (presence or absence) of actively-breeding radio-tagged terns at the East Sand Island colony using a

combination of an ATS Receiver (Model R2100) and an ATS Data Collection Computer (DCC II – Model D5041) connected to an H-antenna mounted near the edge of the colony. 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, I restricted the dataset 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 were no longer reliable. I restricted analyses to radio-tagged nesters that did not lose their antenna in the first 21 days post-hatch. Third, brood sizes of radio-tagged parents ranged from 1-3 chicks, but representation of 1- and 3-chick broods was small, making an estimation of brood size effects difficult with telemetry data. Therefore, I only included telemetry data from those birds raising 2-chick broods and estimated brood size effects using nest observations. Using these criteria, 8 radio-tagged nesters were omitted, leaving 17 radio-tagged nesters whose colony attendance was monitored using radio-telemetry.

I could not examine the contents of most nests of radio-tagged adults immediately after hatching to determine brood size, so I used the

largest brood size observed 6-10 days post-hatch for each nest. I removed data after loss of a chick from a nest to avoid confounding brood size effects within a nest with brood size effects among nests.

Prior to the first arrival of terns on the colony, I confirmed reception of transmitter signals from throughout the 1.6-ha (4-acre) colony. Although reception distances can vary with transmitter orientation and signal strength, I estimated a range of 500 m at an elevation of approximately 2 m based on field tests. The fixed receiver monitored the frequency of each deployed radio-transmitter for 10 seconds 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) continuously throughout the chick-rearing period.

To evaluate reception accuracy, I placed two reference transmitters at the colony periphery and programmed two false frequencies (not deployed on a bird) 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, I compared DCC records and visuals of parental attendance during observation periods 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, etc. I 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). By compiling telemetry data over the entire daytime period, I controlled for the possible effects of tide stage or time of day.

For the purposes of this study, I assumed Caspian terns forage solely during daylight hours because they locate prey visually (Bijlsma 1985). Therefore, I restricted analyses of colony attendance and provisioning trip frequency and duration to detections from complete scan cycles recorded between 05:00 and 21:30 Pacific Daylight Time, the average of civil twilight times during the chick-rearing period.

Data Analysis

I investigated the effect of date and brood age on the frequency and duration of foraging trips for chick provisioning using telemetry data. Hatching was not synchronous among my sample of 17 radio-

tagged nesters, producing a range of brood ages on the same date. Nevertheless, brood age was highly correlated with date. To test for a brood age effect independent of date, I sampled data on trip duration and frequency from each nest on June 9th (near the middle of the chick-rearing period), when the sample of nests with a radio-tagged parent was greatest (N = 14). I regressed these data on brood age and gender of the radio-tagged parent to test for a brood age effect. Similarly, I sampled data on trip duration and frequency from each nest at 8 days post-hatch (N = 17 nests) to test for an effect of date independent of brood age. Again, I regressed these data 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, I averaged daily values of trip duration and frequency over the least influential of the two variables (date or brood age), and regressed these averages on gender of the parent, brood size, and the most influential of the two variables date or brood age.

I investigated associations between meal delivery rate and tide stage/weather using the observational data, after accounting for effects of time of day and brood size. I calculated meal delivery rates 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). I used a mixed effects model 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), midday (09:30-15:30), and evening (15:30-21:30). Covariance structures to account for variation associated with individuals were selected based on the procedure outlined in Wolfinger (1993) and Littell et al. (2000).

I estimated the effect of brood size on meal delivery rate using data from nests observed at least once (N = 26). This included 5 nests with 1-chick broods, 19 nests with 2-chick broods, and 2 nests with 3-chick broods. Each nest was observed between 1 and 7 times, and meal delivery rates were calculated by dividing the number of fish delivered to the nest by the total hours of observation time. I tested for differences between each brood size category using regression weighted by the minutes of observation per nest.

I used the Pearson chi-square statistic (SAS 1999) to test for differences in the ratio of salmonids to marine prey types [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). To test for a trend in the size of prey delivered to the nest over time while accounting for prey type, I regressed date and fish type (an indicator value for each fish type was used) on estimated fish length in cm.

To test for differences in foraging trip duration in relation to prey type returned to the colony, I randomly selected 4 observation periods (one for each tide stage) for each radio-tagged adult and its mate. Only those birds that returned at least one marine fish and one salmonid during the 4 observations were included in the analysis. Average trip durations for marine and salmonid species were compared using a paired t-test (Ramsey and Schafer 1997).

Values were considered significant at the $\alpha \leq 0.05$ level. Means are presented ± one standard error unless otherwise noted.

RESULTS

Of the 17 radio-tagged parent terns used in the telemetry analysis, 6 (35%) were female. This ratio matches the sex ratio in the

original sample of 54 radio-tagged individuals [18 females (34%) in the 53 adults successfully sexed - one adult's blood test inconclusive].

Comparison of Telemetry Data and Nest Observations

I validated the measurement of chick provisioning frequency from telemetry data collected by the on-colony DCC 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; Figure 3.1). This suggests that the great majority of absences recorded by the DCC as one missed detection were not provisioning trips. Consequently, I assumed absences consisting of at least two consecutive missed detections during daylight hours represented 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 (Figure 3.2), indicating that DCC data provided a reasonably unbiased and accurate measure of the duration of chick provisioning trips greater than 15 min.

In addition, nest observations did not miss a large number of provisioning trips that exceeded the 3-hour duration of observation
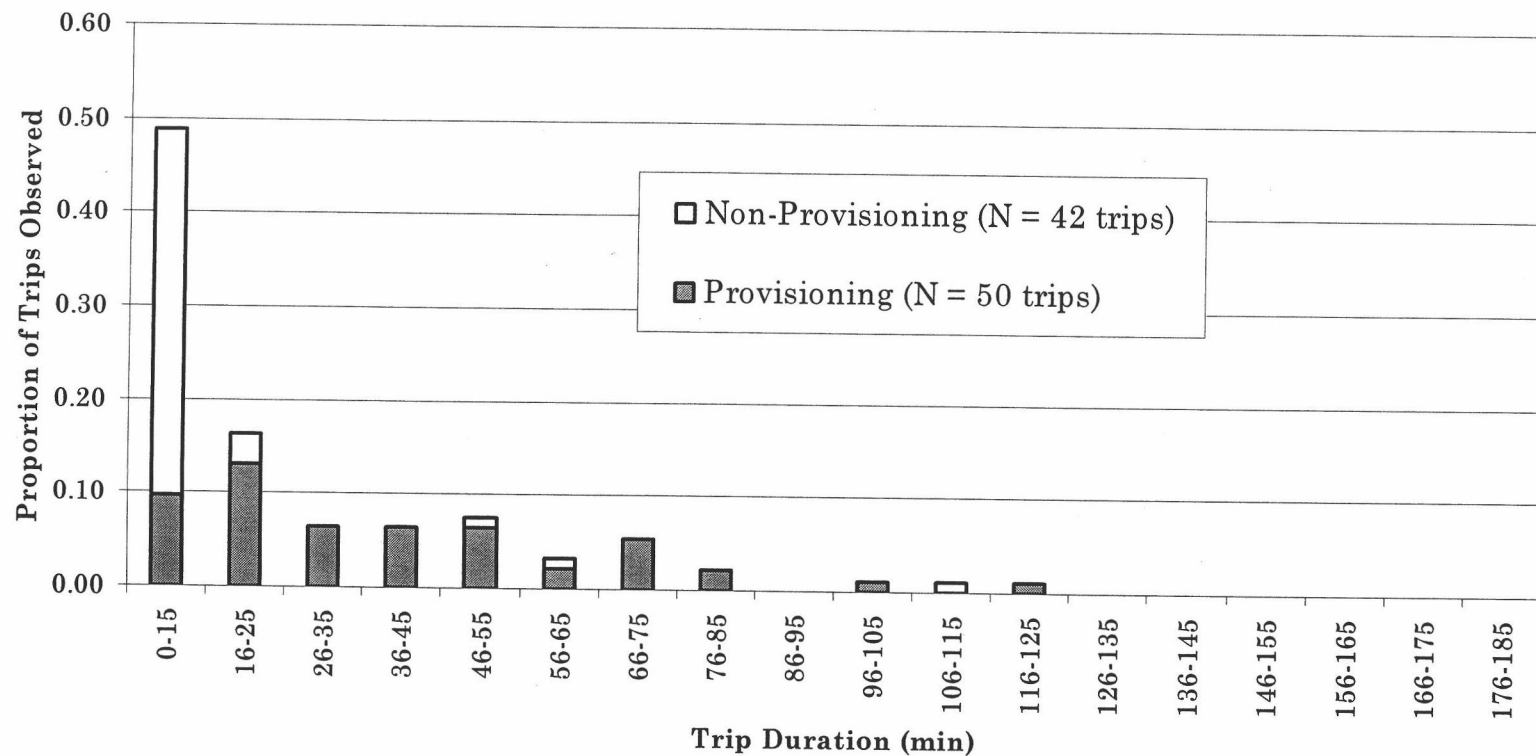
Figure 3.1. Frequency distribution of off-colony trip durations based on observations of Caspian terns nesting on East Sand Island in the Columbia River estuary. Provisioning trips were trips resulting in delivery of a fish to the nest and non-provisioning trips were trips not resulting in delivery of a fish.
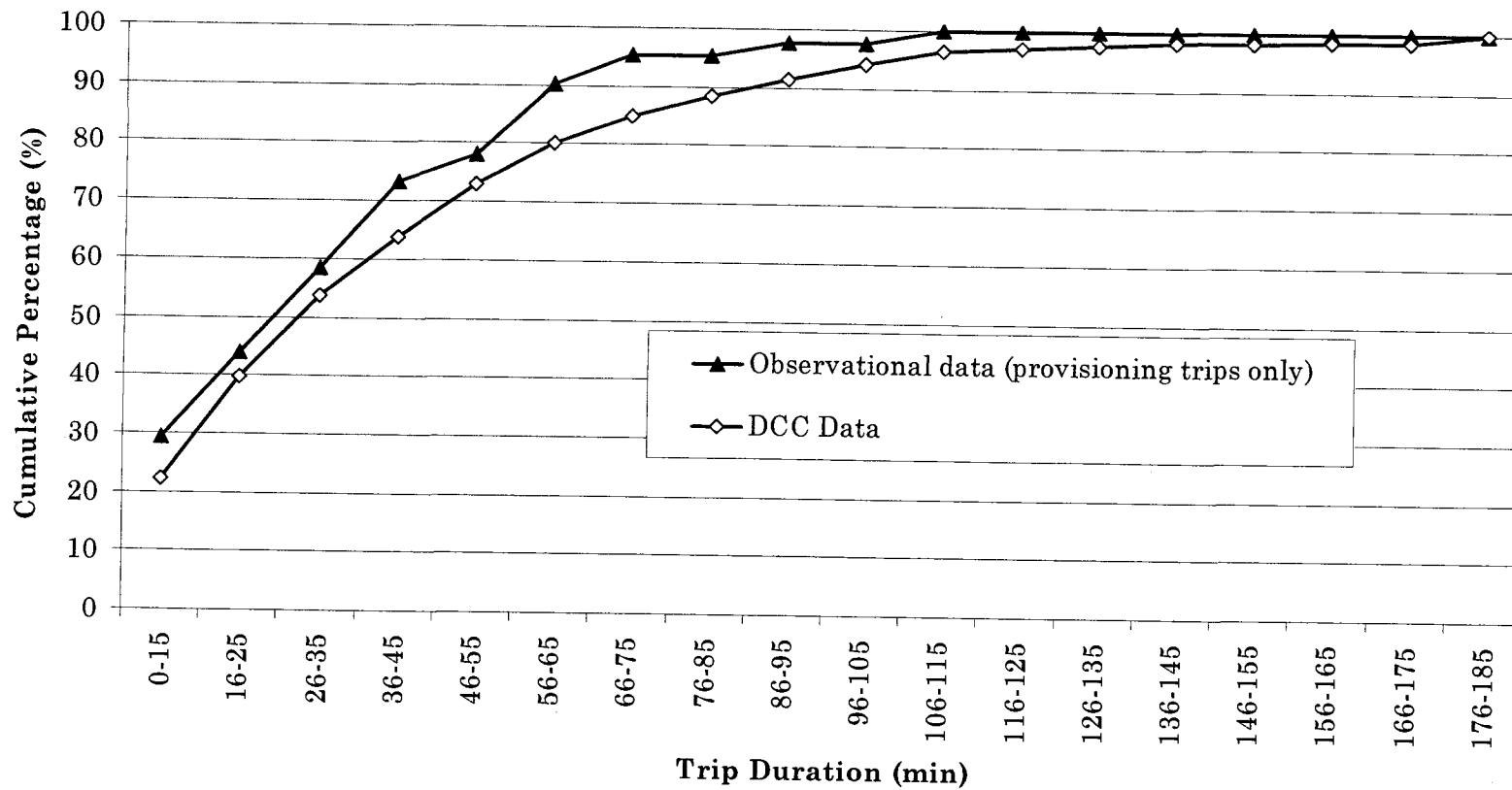
Figure 3.2. Cumulative frequency distributions of the duration of daytime off-colony excursions recorded by the DCC and provisioning trips recorded during nest observations of Caspian terns on East Sand Island, Columbia River estuary. N = 92 for observed trips and N = 786 for trips recorded by DCC.

periods. Average trip duration from DCC data was 45.8 ± 2.8 min, compared to 40.4 ± 3.2 min based on direct observations (Figure 3.2). 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}.

Telemetry: Date versus Brood Age

Changes in average trip duration were more strongly associated with date than brood age, while average trip frequency did not have a strong association with either measure of time. Based on telemetry data from all nests on June 9th (N = 14), brood age had no significant effect on trip duration (1.12 ± 0.84 min day^{-1} decrease; p = 0.2053), and a marginal effect on trip frequency (0.19 ± 0.09 trips day^{-1} decrease, p = 0.0625) 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 = 0.0006), after accounting for effects of adult gender (multiple linear regression; $F_{2,14} = 10.36$, p = 0.0017). However, the effect of date on trip frequency was small and insignificant (0.05 ± 0.07 trips day^{-1} decrease, p = 0.4714), after accounting for adult gender.

Because the duration of provisioning trips was strongly influenced by date but not brood age, I averaged all trip duration and trip frequency values available during 21 days post-hatch for each

radio-tagged parent. I then used multiple linear regression to simultaneously estimate the effects of adult gender and date for each parent bird, weighted by the number of days when data were available. I used hatch date to represent the timing of chick-rearing (i.e., date) because averaged values represented the same range of brood ages for each nest.

Telemetry: Hatch Date and Parent Gender

There was a significant increase in average trip duration with hatch date, after accounting for adult gender (weighted multiple linear regression: $F_{2,14} = 14.59$, $r^2 = 0.6757$, $p = 0.0004$). Average foraging trip duration for all birds was 47.2 ± 2.9 min. Nests that hatched 1 week later in the season were associated with an increase in provisioning trip duration of 10.3 ± 1.9 min (21.9% of overall average; $p < 0.0001$; Figure 3.3). There was no effect of gender on average duration of chick provisioning trips ($p = 0.6656$).

Foraging trip frequency was affected by adult sex but not hatch date (weighted multiple linear regression: $F_{2,14} = 4.799$, $r^2 = 0.4068$, $p = 0.0258$). Average foraging trip frequency was 6.20 ± 0.33 trips day^{-1}. Males took an average of 1.70 ± 0.58 more trips per day than did females (27.4% of overall average; $p = 0.0106$; Figure 3.4). Differences in colony attendance were associated with both adult sex and hatch
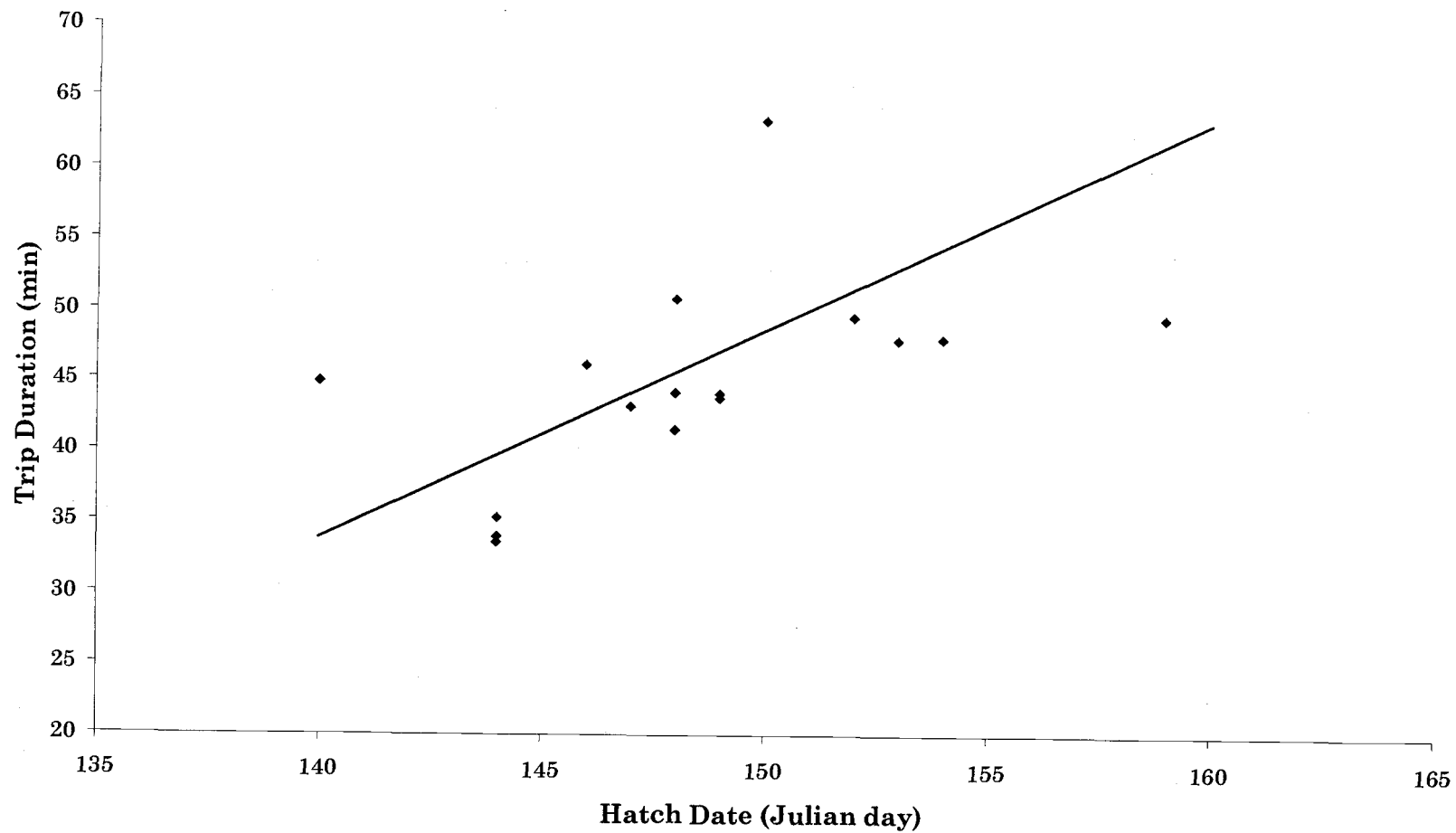
Figure 3.3. Average provisioning trip duration as a function of hatch date for parent Caspian terns raising 2-chick broods. Line represents least squares regression estimate from a linear model.
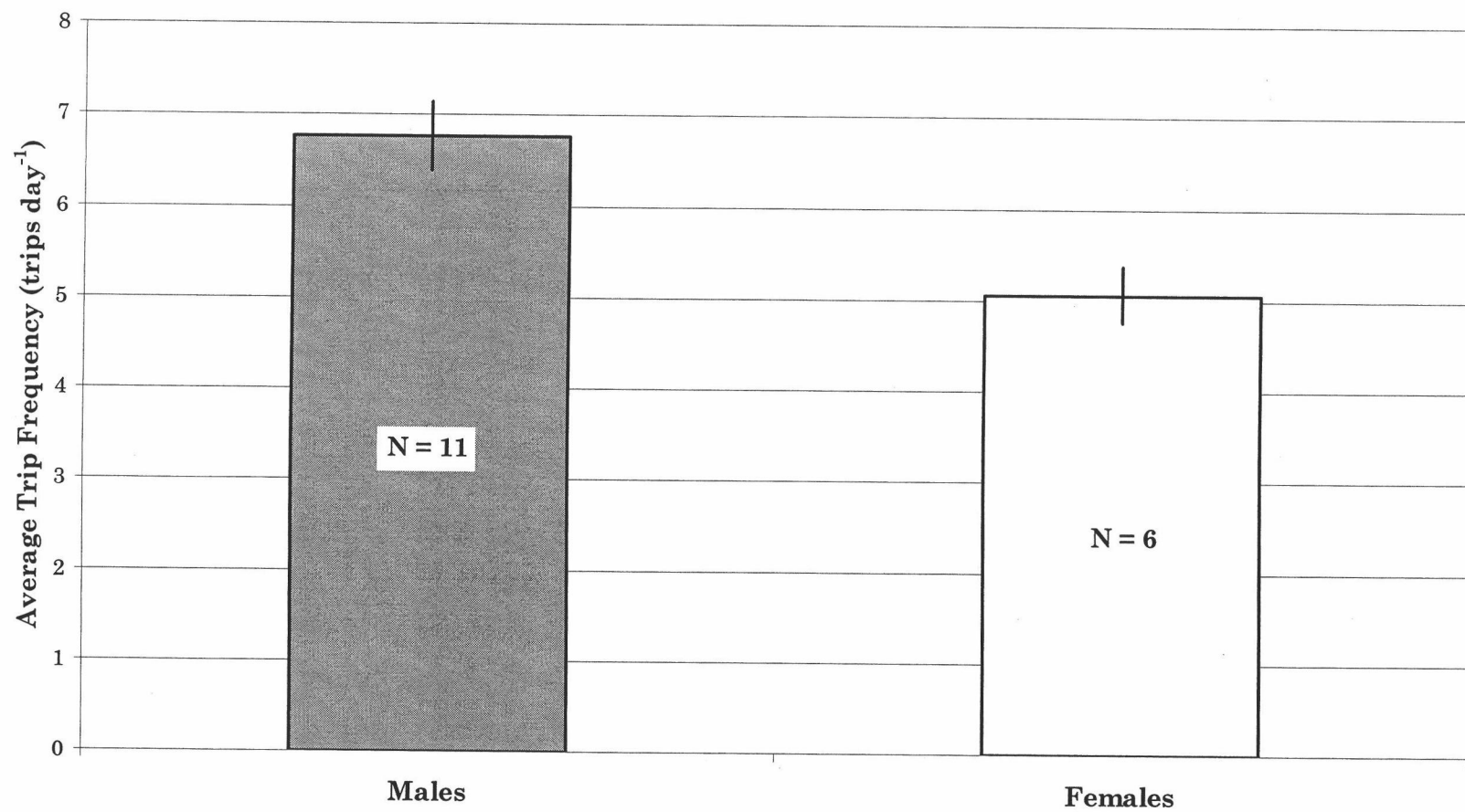
Figure 3.4. Frequency of chick provisioning trips to 2-chick broods by male and female Caspian terns nesting on East Sand Island in the Columbia River estuary in 2001.

date (multiple linear regression: $F_{2,14} = 6.886$, $r^2 = 0.4959$, $p = 0.0083$; Figure 3.5). Females attended the colony $8.5 \pm 3.0\%$ more of the day than did males ($p = 0.0134$), and parents attended the colony $3.8 \pm 1.5\%$ less of the day ($p = 0.0275$) for each week delay in hatch date.

Nest Observations: 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 ($p = 0.7680$). Weather conditions (precipitation [$p = 0.3556$], wind speed [$p = 0.8311$], temperature [$p = 0.5029$]) 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 to 14.2 cm per day (mean = 0.23 cm), average daily wind speeds ranged from 7.7 to 31.8 knots (mean = 15.7 knots), and temperatures ranged from 8.9 to 17.8 degrees C (mean = 13.5 degrees C). In addition, I was not able to observe nests on the most extreme weather days because of limited access to the island. Consequently, extreme weather may affect the foraging behavior of breeding Caspian terns, but such effects were not demonstrable in my study.
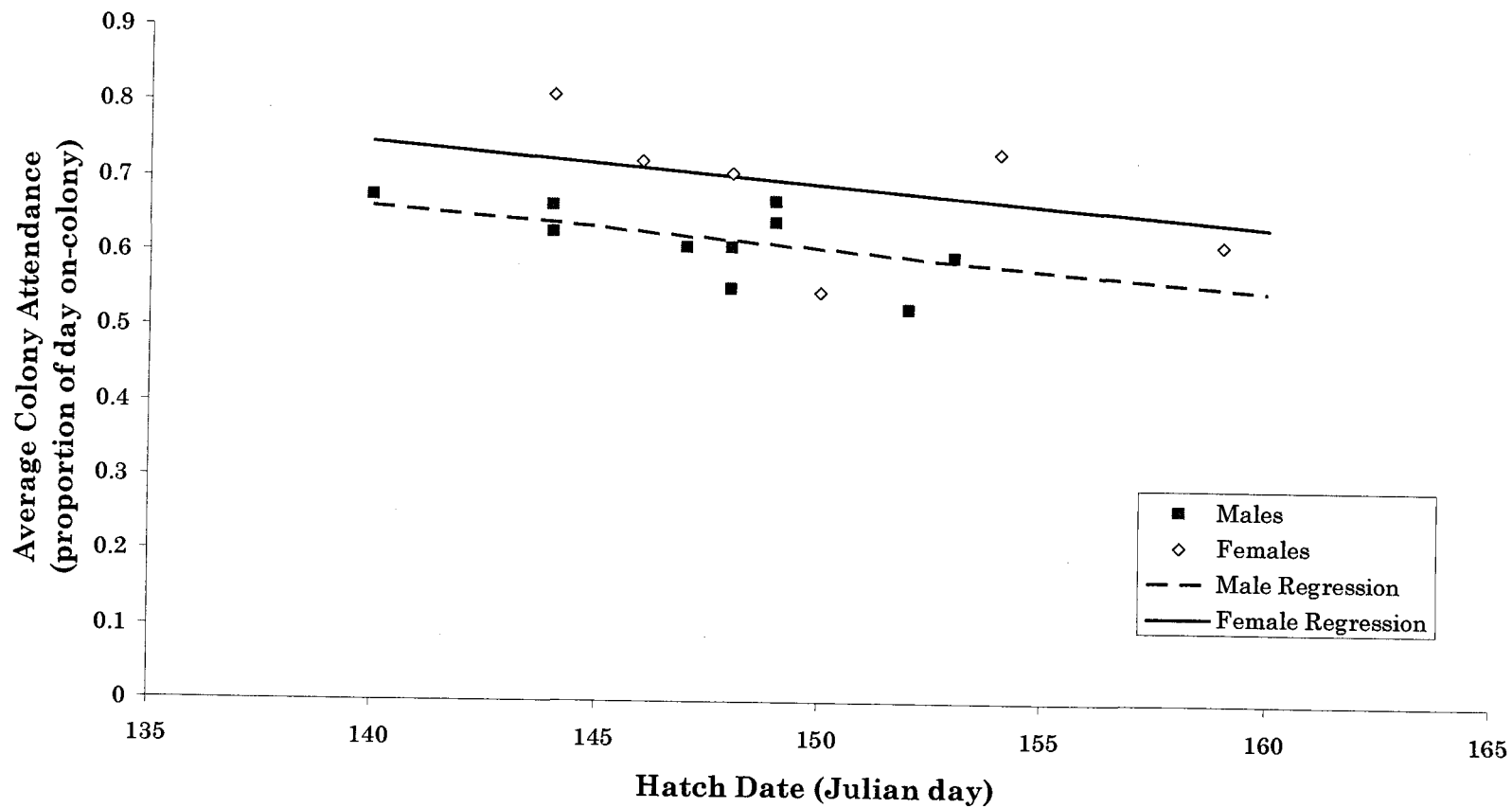
Figure 3.5. Colony attendance of Caspian terns nesting on East Sand Island in the Columbia River estuary as a function of hatch date and sex. Lines represent least squares regression estimates from a multiple linear model with no interactions.

Nest Observations: Brood Size

Nests with larger broods were associated with a higher rate of meal delivery (weighted multiple linear regression: $F_{2,23} = 13.78$, $r^2 = 0.5450$, $p = 0.0001$).   Meal delivery rates to 1-, 2-, and 3-chick broods were 0.33 ± 0.03, 0.88 ± 0.06, and 1.25 ± 0.09 meals hour^{-1}, respectively (Figure 3.6). Meal delivery rates to 2-chick broods were 0.54 ± 0.12 meals hour^{-1} greater than to 1-chick broods ($p < 0.0001$), or 2.6 times the rate to 1-chick broods.

Nest Observations: Prey Composition

The taxonomic composition of fish delivered by radio-tagged adult to their broods was similar to that of the colony as a whole (Pearson's chi-square: $\chi^2_4 = 8.2371$, $p = 0.083$; D. D. Roby, unpubl. data), suggesting that the sample of fish delivered by radio-tagged terns was not biased (Figure 3.7). 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; Figure 3.8). The proportion of salmonids delivered to the brood during ebb tides was significantly higher than during flood tides (Pearson chi-square: $\chi^2_1 = 5.8166$, $p = 0.0223$). No other pair-wise comparisons were significant.
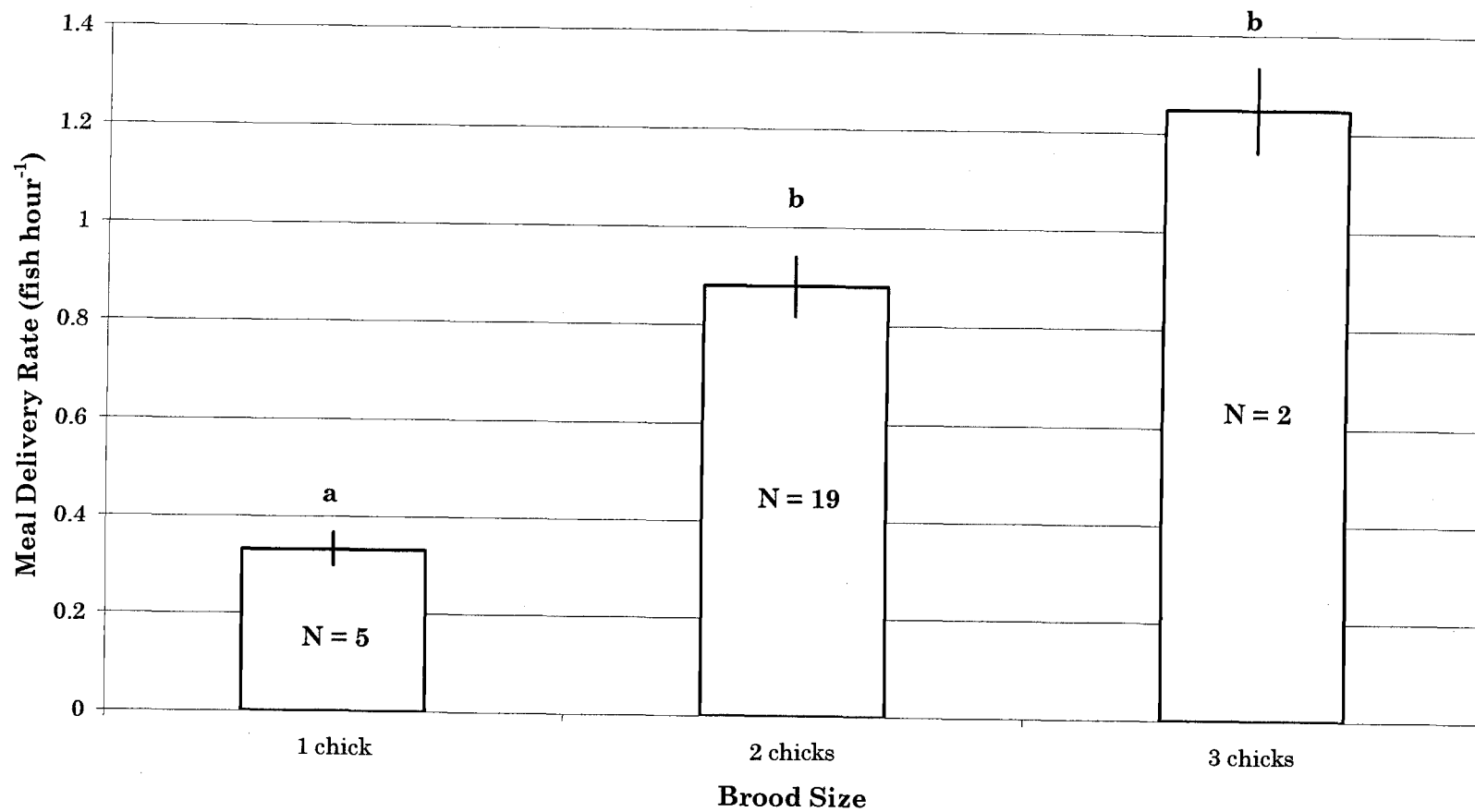
Figure 3.6. Average meal delivery rates by pairs to 1-, 2-, and 3-chick broods from nest observations of Caspian terns nesting on East Sand Island in the Columbia River estuary. Bars with different letters are significantly different.

A. Radio-tagged Caspian terns

Other
14.9%

Salmonid
21.6%

Smelt
9.7%

Anchovy
22.4%

Sardine
31.4%
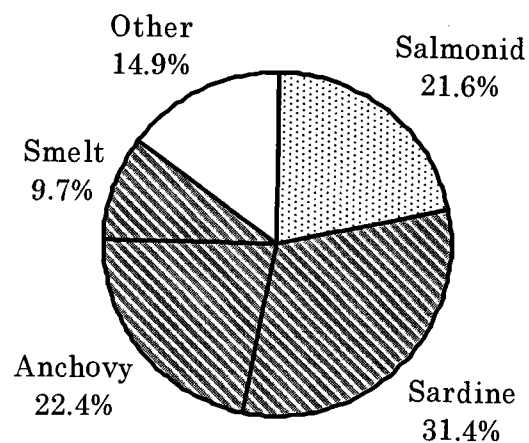
N= 107 Bill Loads

B. Un-tagged Caspian terns

Other
15.4%

Salmonid
32.6%

Smelt
6.0%

Anchovy
22.4%

Sardine
23.7%
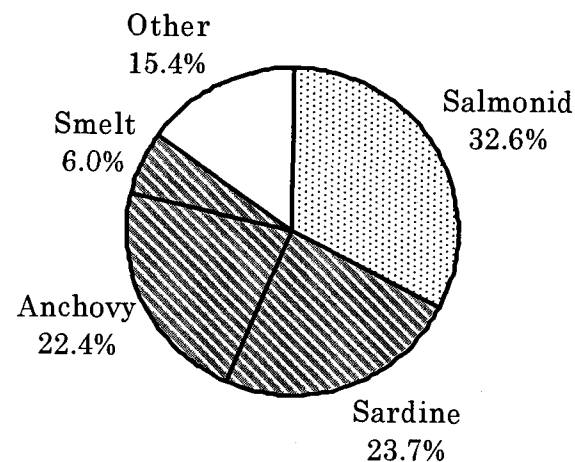
N= 1224 Bill Loads

Figure 3.7. Taxonomic composition of fish delivered to the nest by (a) radio-tagged Caspian terns (this study) and (b) Caspian terns nesting at the same colony on days of nest observations (D. D. Roby, unpubl. data). Diagonal stripes represent marine prey types and stipples represent anadromous prey types.

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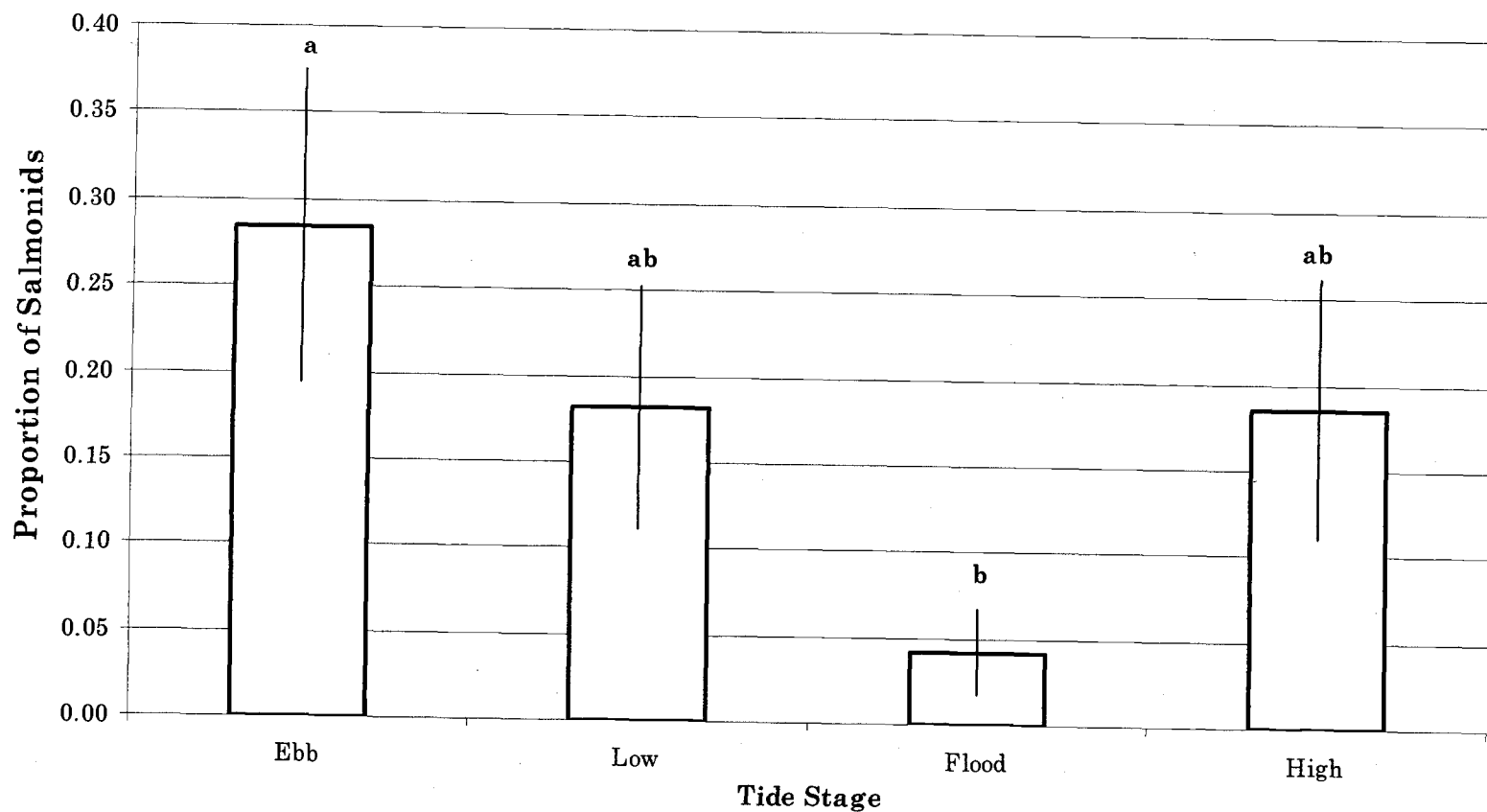
Figure 3.8. Proportion of juvenile salmonids delivered to broods as a function of tide stage for Caspian terns nesting on East Sand Island in 2001. Bars with different letters are significantly different. Only salmonids and schooling marine prey (anchovy, herring/sardine, and smelt) are shown.

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 ($p = 0.01$), after accounting for fish type (multiple linear regression; $F_{11,191} = 6.513$, $r^2 = 0.2728$, $p < 0.0001$).

Foraging trip duration was associated with the prey type delivered to the nest. A total of 12 adult terns delivered at least one marine and one salmonid prey item to the colony during each of the four tide stages. Foraging trips resulting in the delivery of marine forage fish (32.6 ± 9.6 min) were shorter on average than foraging trips resulting in delivery of a salmonid (54.9 ± 9.6 min; paired t-test; two-tailed $p = 0.027$; Figure 3.9).

DISCUSSION

Caspian tern productivity on East Sand Island in 2001 was the highest so far recorded anywhere 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.).
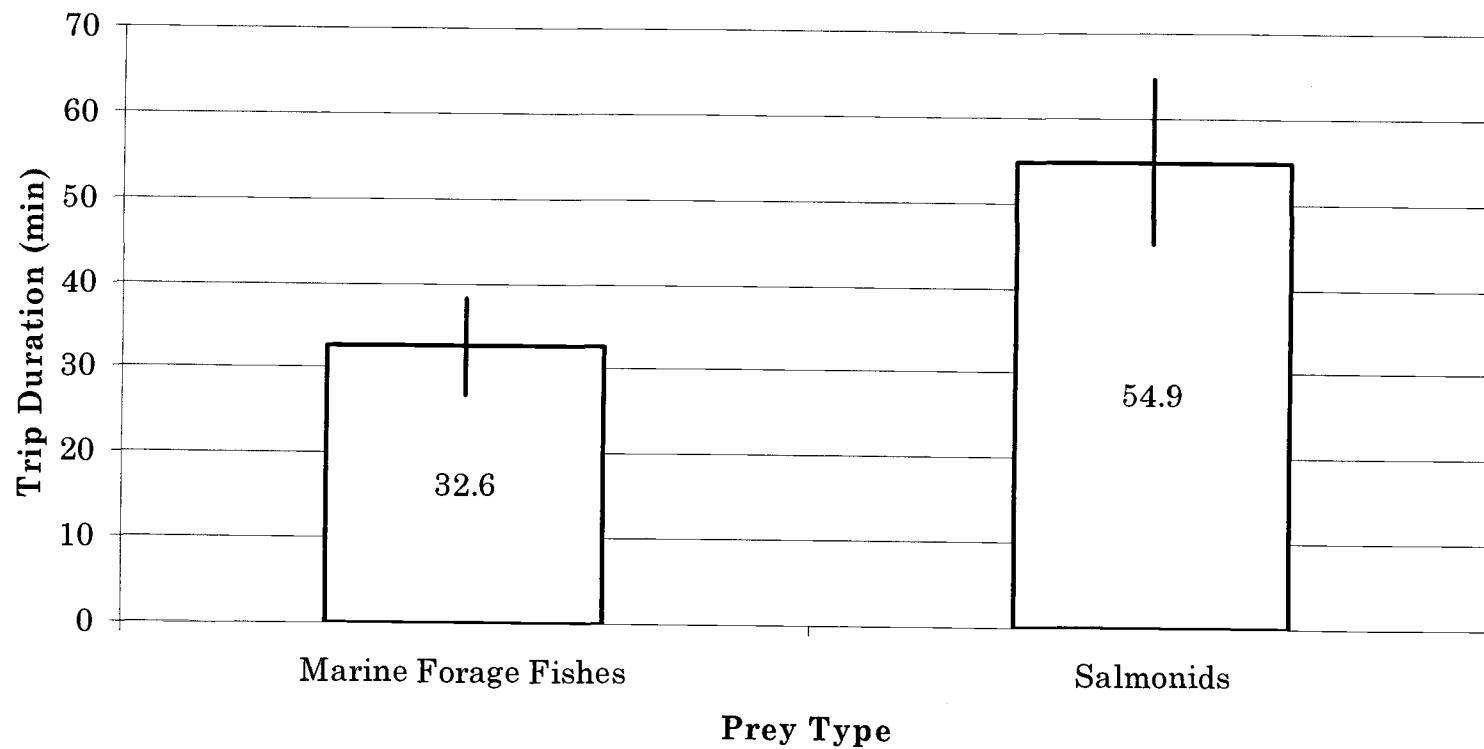
Figure 3.9. Average foraging trip duration for salmonids and marine forage fishes delivered to the nest by Caspian terns nesting on East Sand Island in the Columbia River estuary. Average values are shown inside the bars and error bars represent ± 1 SE.

Concurrently, high-lipid marine forage fishes were more prevalent in the diet of terns than in previous years (Roby et al. 2002). This suggests that parents had much less difficulty provisioning chicks during 2001 and that productivity and colony attendance were both positively associated with prey availability (see Chapter 2).

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 prey types 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 for salmonids, however, 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, one would expect longer provisioning trips from parents initiating nests later in the season. 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 2-chick broods delivered meals at more than twice the rate as parents of 1-chick broods. High meal delivery rates to larger broods in the present study are more support for the conclusion that forage fish availability near East Sand Island was high in 2001. Furthermore, parents of 2-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 was higher for male Caspian terns compared to 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) working with 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. 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 possible that at least part of the difference in magnitude of sexual differences seen between the two studies was due to the difference in average brood age.

Tide Stage

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. 2002a), 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 differed 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, I observed a higher proportion of marine forage fishes in chick meals. Previous studies suggest that Caspian terns are generalist foragers, feeding on the most available fish of suitable size close to the nesting colony (Roby et al. 2002). This suggests that tidal fluctuations affect the relative availability of prey taxa near the East Sand Island colony. In years of

lower marine forage fish availability, Caspian terns nesting at East Sand Island may attempt to compensate by capturing more freshwater and anadromous prey species.

Prey Composition

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 (Figure 3.9), 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 4 most common prey types in Caspian tern diets in the two years of 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 return to a nearby prey patch (i.e., school of fish) repeatedly until sated or the patch has dissipated. During survey flights, I observed many multi-species foraging flocks of piscivorous birds in the estuary apparently taking advantage of a productive prey patch. By returning to the same prey patch, search time is avoided, thereby reducing the average duration of foraging trips for schooling marine prey compared to non-schooling prey.

Foraging Caspian terns also may be influenced by coarse-level local enhancement as defined by Pöysä (1992). Coarse-level enhancement predicts that the presence of predators using a productive prey patch increases the detectibility of that prey patch, thereby attracting more predators. Schooling marine forage fishes would be more susceptible to detection (and therefore predation) through coarse-level local enhancement than out-migrating juvenile salmonids.

CONCLUSIONS

The results of this study support previous evidence that Caspian tern nesting success on East Sand Island is highly dependent on marine forage fishes. 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 (Chapter 2). 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 fishes 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 (NMFS 2002).

Regional managers are currently evaluating the merits of dispersing a portion of the East Sand Island colony to other nesting sites in the Pacific Northwest. The results of this study support redistribution of part of this colony to reduce potential impacts to the regional Caspian tern population, as well as the survival of juvenile salmonids in the Columbia River estuary.

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CHAPTER 4

SUMMARY AND SYNOPSIS

Scott K. Anderson

The research presented here was designed to enhance understanding of factors influencing foraging behavior, diet composition, and overall reproductive success of Caspian terns nesting on East Sand Island in the Columbia River estuary. The main goals were to (1) investigate the relationship between foraging distribution, foraging range, foraging site fidelity, and colony attendance of Caspian terns and (2) determine intrinsic and extrinsic factors influencing the duration and frequency of foraging trips.

Seasonal changes in the foraging distribution of Caspian terns nesting on East Sand Island reflected changes in diet composition. During incubation, when the proportion of birds in the freshwater zone was highest, the proportion of salmonids in the diet was also highest. Conversely, the proportion of birds detected outside the estuary was highest when the proportion of salmonids in the diet was lowest. Caspian terns nesting on East Sand Island foraged closer to the colony during chick-rearing, when foraging range was presumably constrained by chick provisioning.

Diet composition, prey availability, and nesting success were very different between the two years of this study. The abundance of marine forage fishes near East Sand Island in 2001 apparently reduced foraging times by providing a readily available food source. In addition,

marine forage fish may be more susceptible to repeated exploitation by foraging Caspian terns than salmonids because of the schooling behavior of most marine species.

Relatively low prey availability near the East Sand Island colony in 2000 was likely responsible for lower productivity compared to 2001. When marine prey (which comprised the majority of Caspian tern diets) were less available, nesting terns tended to take longer foraging trips to more distant foraging sites, reducing colony attendance. This not only resulted in lower brood provisioning rates and consequent brood reduction, but broods were unattended for a greater proportion of the day, increasing chick mortality due to predation, adult aggression, and exposure.

There is evidently a close relationship between prey availability and nesting success in Caspian terns. In good years, terns deliver chick meals at higher rates, supporting more chicks through fledging. In years of low prey availability, however, parents are forced to spend more time foraging, reducing colony attendance, and increasing the risk of chick mortality. Although the foraging distribution of Caspian terns during incubation and post-fledging periods was extensive, foraging distance was more restricted during chick-rearing, and therefore prey

availability near the colony was a more important constraint on productivity during chick-rearing.

Caspian tern foraging trip frequency in 2001 was highly dependent on brood size. Caspian terns raising 2-chick broods delivered prey at more than twice the rate as parents of 1-chick broods. This may be due to either adjustment of foraging effort, or differences in the foraging efficiency of parents. Foraging trip duration increased with date, regardless of brood age, suggesting that either foraging conditions changed during the season or that higher quality parents (i.e., more efficient foragers) nested earlier in the season.

Meal delivery rates did not vary with tide stage, but diet composition did, suggesting that terns shifted to the most available prey in the vicinity of East Sand Island during each tide stage. The prevalence of salmonids was highest during ebb tide, when juvenile salmonids are likely migrating out to sea (C. B. Schreck, pers. comm.), past East Sand Island. This suggests that during chick-rearing, Caspian terns at this colony are dependent on prey availability very close to the colony. The average duration of foraging trips that resulted in the delivery of a salmonid, however, was significantly longer than foraging trips resulting in the delivery of a marine forage fish; schooling

marine fishes were apparently more available near the colony than non-schooling prey such as salmonids.

Evidence from my study indicates that during chick-rearing, Caspian terns nesting on East Sand Island are particularly sensitive to annual, seasonal, and tidal variation in prey availability close to the colony. This colony is located in habitat supporting a wide variety of prey species, favoring successful breeding despite decreases in the relative availability of one or a few prey type(s). However, the unusually large size of this colony may make it more susceptible to small fluctuations in overall prey availability. Large colonies of birds can deplete food resources close to the colony, exacerbating the effects of low prey availability, and requiring longer foraging trips resulting in higher parental effort (Ashmole 1963).

Marine forage fishes are currently the dominant prey for the East Sand Island tern colony (Roby et al. 2002), but their abundance in the estuary is subject to variable ocean conditions (Brodeur et al. 2003). Ocean productivity along the coast of the Pacific Northwest fluctuates dramatically on annual and decadal scales, affecting the availability of marine forage fish in the Columbia River estuary (Brodeur et al. 2003, R. Emmett, NOAA Fisheries, pers. comm.). This, in addition to the rapid increase in numbers of Caspian terns nesting in the estuary

since 1984 (Suryan et al., in review), sets up an inherently risky situation where the productivity of a large proportion of the Pacific Coast population of Caspian terns is dependent on prey available in a relatively small area near East Sand Island. In addition, other Caspian tern nesting sites along the Pacific coast have been abandoned (Collis et al. 2001), and nesting habitat elsewhere in the Pacific Northwest appears to be limited (Collis et al. 2002b). A decline in marine forage fish availability also may result in a greater reliance on juvenile salmonids listed under the U. S. Endangered Species Act (NMFS 2002). This combination of factors supports proposed management recommendations to redistribute part of this large colony of Caspian terns to several smaller colonies to (1) reduce the impact of tern predation on survival of salmonid smolts from the Columbia River basin and (2) reduce risks to the Pacific Coast population of Caspian terns from localized events.

Future Directions

Further studies with radio-tagged and marked Caspian terns would help refine and expand understanding of the foraging behavior of Caspian terns. Some suggested hypotheses include:

- Do Caspian terns exhibit foraging site fidelity on smaller spatial and temporal time scales?

- What governs foraging choices (e.g., flight direction and foraging location) of breeding Caspian terns?

- Are the prey types captured by Caspian terns in the Columbia River estuary associated with specific habitats?

- How do meal delivery rates and average foraging distance of Caspian terns nesting at East Sand Island compare to other Caspian tern colonies?

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