

Foraging patterns of male and female Double-crested Cormorants nesting in the Columbia River estuary

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Abstract: The nesting colony of Double-crested Cormorants, *Phalacrocorax auritus* (Lesson, 1831), on East Sand Island in the Columbia River estuary is currently the largest for this species on the Pacific Coast of North America. We used radiotelemetry to investigate the spatial and temporal foraging patterns of nesting cormorants to better understand how this colony of piscivores meets its resource needs. We determined that nesting adults tended to forage >5 km from the colony and foraging distribution was distinctly different between the sexes. On average, males commuted nearly twice the distance to forage compared with females. Females typically foraged in the estuarine mixing zone, reportedly the region of the estuary with the greatest densities of schooling fishes, while males tended to commute more than 15 km to forage in the freshwater zone. Foraging intensity of both sexes varied by time of day, tide stage, and tide series; foraging generally intensified during ebb tides. These gender differences in foraging patterns, combined with the ability to forage at considerable distance from the colony on a wide variety of prey, may allow this large and growing colony to remain productive while potentially competing for food with many thousands of other piscivorous waterbirds that use East Sand Island.

Résumé : La colonie de cormorans à aigrettes, *Phalacrocorax auritus* (Lesson, 1831), qui niche sur l'île East Sand dans l'estuaire du Columbia est actuellement la colonie la plus importante de cette espèce sur la côte pacifique de l'Amérique du Nord. La radio-télémetrie nous a servi à étudier les patterns spatiaux et temporels de recherche de nourriture des cormorans qui y nichent afin de comprendre comment cette communauté de piscivores réussit à combler ses besoins alimentaires. Les adultes qui nichent ont tendance à rechercher leur nourriture à plus de 5 km de la colonie et la répartition des activités de recherche de nourriture est nettement différente en fonction des sexes. Pour se nourrir, les mâles effectuent des navettes en moyenne deux fois plus importantes que celles des femelles. Les femelles se nourrissent ordinairement dans la zone de mélange de l'estuaire, la région qui posséderait les plus fortes de densités de bancs de poissons, alors que les mâles ont tendance à se déplacer sur des distances de 15 km pour se nourrir en eau douce. L'intensité de la quête de nourriture chez les deux sexes varie en fonction de l'heure du jour, l'état de la marée et le cycle annuel des marées; la recherche de nourriture est généralement plus intense durant les marées basses. Les différences dans la recherche de nourriture reliées au sexe, ainsi que la capacité de se nourrir d'une gamme étendue de proies à des distances considérables de la colonie, peuvent permettre à cette grande colonie en expansion de maintenir sa productivité, alors qu'elle fait potentiellement compétition à plusieurs autres milliers d'oiseaux aquatiques piscivores qui utilisent aussi la région de l'île East Sand.

[Traduit par la Rédaction]

Introduction

The nesting colony of Double-crested Cormorants (*Phalacrocorax auritus* (Lesson, 1831)) on East Sand Island near the mouth of the Columbia River is currently the largest for this species on the Pacific Coast of North America (Carter et al. 1995; Collis et al. 2002). In contrast to other Double-

crested Cormorant nesting colonies along the coast of the Pacific Northwest, the East Sand Island colony has grown dramatically. The colony grew from fewer than 100 breeding pairs (R. Lowe, USFWS, 2127 SE OSU Drive, Newport, OR 97365, USA, personal communication) to more than 8 500 breeding pairs in the last 13 years, and now represents a substantial proportion (>30%) of the West Coast population (Anderson 2002). Because the nesting season of these piscivorous waterbirds coincides with peak out-migration of juvenile salmonids (*Oncorhynchus* spp.) from the Columbia River basin (Fish Passage Center 2002), cormorant predation may be a significant source of mortality for migrating smolts, many of which are listed as either threatened or endangered under the US Endangered Species Act (National Marine Fisheries Service 2002).

The impacts of predation by Double-crested Cormorants on commercially important fish stocks have been studied extensively and there is little evidence to suggest that cormo-

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rants seriously deplete commercially valued fish populations (review in Hatch and Weseloh 1999). Cormorants may, however, be a significant source of fish mortality at sites where fish prey are aggregated (e.g., hatcheries or fish farms; Nettleship and Duffy 1995) or when the cormorant population is large compared with their prey resource population (Wires et al. 2001). Recent studies of Double-crested Cormorant diets in the Columbia River estuary revealed that juvenile salmonids were the most prevalent prey type for cormorants nesting on Rice Island in the upper estuary (river km 34), whereas the diet of cormorants nesting on East Sand Island (river km 7) included substantially fewer salmonids (one-third as much by mass; Collis et al. 2002). Presumably, the major differences in diet composition between cormorant colonies reflect differences in foraging distribution within the estuary. Based on these diet differences and central place foraging theory (Mauer 1996), we expected that cormorants nesting on islands in the Columbia River estuary were maximizing foraging efficiency by feeding in proximity to their nesting colonies.

The Double-crested Cormorants nesting on East Sand Island currently share the island with ca. 9900 nesting pairs of Caspian Terns (*Sterna caspia* Pallas, 1770), ca. 6000 nesting pairs of Glaucous-winged/Western Gulls (*Larus glaucescens* Naumann, 1840 × *Larus occidentalis* Audubon, 1839), and thousands of post-breeding Brown Pelicans (*Pelecanus occidentalis* Linnaeus, 1766) (D. Roby, unpublished data). The predation pressure associated with a large and growing colony of cormorants and other piscivores may lead to local forage fish depletion in the vicinity of East Sand Island (Furness and Birkhead 1984, Birt et al. 1987). We predicted that because of density-dependent feedback on food supply, cormorants nesting on East Sand Island would, on average, spend more time foraging and take longer, less frequent foraging trips than reported for Double-crested Cormorants nesting at other colonies. While competition for available forage fish may favor cormorants that forage at a distance from East Sand Island, the diet composition of cormorants that nest on East Sand Island suggests that these adults do not commute upriver to the freshwater zone near Rice Island. Instead, adult cormorants nesting on East Sand Island may commute to foraging areas in the marine zone of the estuary or perhaps outside the Columbia River estuary altogether (e.g., Willapa Bay or coastal areas).

Because of increasing concern over avian predation on juvenile salmonids in the Columbia River estuary, there is a need to understand how this large and growing cormorant colony exploits the available forage fish resources of the estuary. We sought to investigate factors affecting the foraging patterns exhibited by cormorants nesting at the East Sand Island colony to better understand their diet composition and use of forage fish resources.

Sexual differences in foraging patterns are known to occur in several species of seabirds that either exhibit sexual dimorphism (reviewed by Weimerskirch et al. 1994) or do not exhibit sexual dimorphism (Lewis et al. 2002). Diving patterns (Wanless et al. 1995; Kato et al. 1996; Watanuki et al. 1996; Grémillet et al. 1998; Casaux et al. 2001; Ishikawa and Watanuki 2002), prey type (Grémillet et al. 1998; Ishikawa and Watanuki 2002), and prey size (Kato et al. 1996; Casaux et al. 2001) have all been reported to differ between the

sexes in various cormorant species. In the West Coast population, *P. a. albociliatus* males are significantly larger than females, having greater mass (9%), culmen length (9%), and culmen depth (9%; C. Anderson, unpublished data). This suggests that there may be differences in foraging behaviour between the sexes.

In addition to gender differences, numerous environmental factors may influence the foraging activity of cormorants within an estuarine environment (e.g., Richner 1995; Dorfman and Kingsford 2001). The spatial and temporal foraging patterns of cormorants in this estuary are likely influenced by a variety of natural (e.g., tidal flow, salinity, time of day) and anthropogenic processes (e.g., dam-regulated river flow, channel dredging, pile dikes). Tidally induced foraging patterns have been reported for a variety of estuarine predators, including seabirds (van Tets 1959; Dunn 1975; Richner 1995; Irons 1998; Dorfman and Kingsford 2001). Diurnal foraging patterns have also been reported for many species of Pelecaniformes, although several studies suggest that there is considerable variation, both among sites and among species, in the intensity of cormorant foraging activity throughout the day (see review in Johnsgard 1993).

In this study, we used radiotelemetry to investigate the spatial and temporal patterns in foraging by male and female Double-crested Cormorants nesting on East Sand Island in the Columbia River estuary. We sought to answer the following questions:

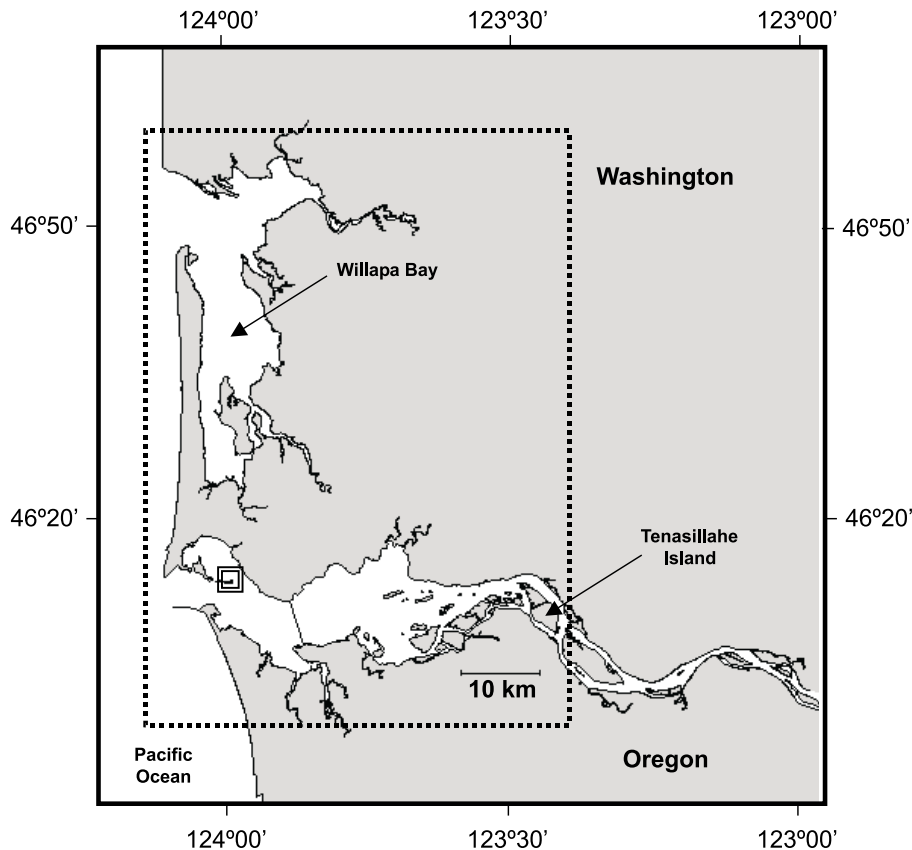
1. Do cormorants nesting on East Sand Island forage predominantly in marine habitats, as suggested by the lower proportion of salmonids in their diet compared with the diet of cormorants nesting in the freshwater zone of the estuary?
2. Is the availability of marine forage fishes near East Sand Island sufficient for cormorants nesting on the island, or are they forced to commute longer distances (e.g., owing to competition with the large numbers of other piscivorous waterbirds on the island)?
3. How is the foraging behaviour of cormorants nesting at East Sand Island influenced by time of day, tidal cycles, seasonal changes, and interannual variability in forage fish availability?

Materials and methods

Study area

We studied the foraging behaviour of Double-crested Cormorants nesting at the large colony on the western end of East Sand Island. East Sand Island (46°15'45"N, 123°57'45"W) is located in Clatsop County, Oregon, near the mouth of the Columbia River estuary (Fig. 1). We monitored the foraging distribution of radio-tagged nesting adults over approximately 396 km² of the Columbia River estuary, between the mouth of the Columbia River and Tenasillahe Island (river km 56), and along the southern coast of Washington up to and including Willapa Bay (Fig. 1). We attempted to include in the survey area all areas potentially used for foraging by cormorants nesting on East Sand Island, based on published records of the maximum foraging range for nesting Double-crested Cormorants (40 km; Custer and Bunck 1992) and previous observations of foraging cormorants in the Columbia River estuary and along the adjacent coastline (D. Roby, unpublished data.).

Fig. 1. Map of the study area showing where aerial telemetry surveys were conducted (dotted rectangle) for foraging radio-tagged Double-crested Cormorants (*Phalacrocorax auritus*) nesting on East Sand Island (double-lined square).



For analysis purposes, we subdivided the estuary into three major zones corresponding to areas of marine (ca. river km 0–12), estuarine mixing (ca. river km 12–29), and freshwater (above ca. river km 29) salinities (sensu Simenstad et al. 1990; Fig. 2). These salinity zones are not static; salinity levels vary with a number of environmental variables including river flow, tide stage, and tide series (i.e., spring versus neap; Jay and Smith 1990; Simenstad et al. 1990). The salinity zones represent, however, large-scale habitats known to strongly influence the distribution of fish assemblages in the Columbia River estuary (Haertel and Osterberg 1967; Bottom and Jones 1990) and likely influence cormorant foraging distribution as well. The cormorant colony on East Sand Island is located within the marine zone, at least 5 km from the estuarine mixing zone, and at least 20 km from the freshwater zone (Fig. 2).

Radio-tagging

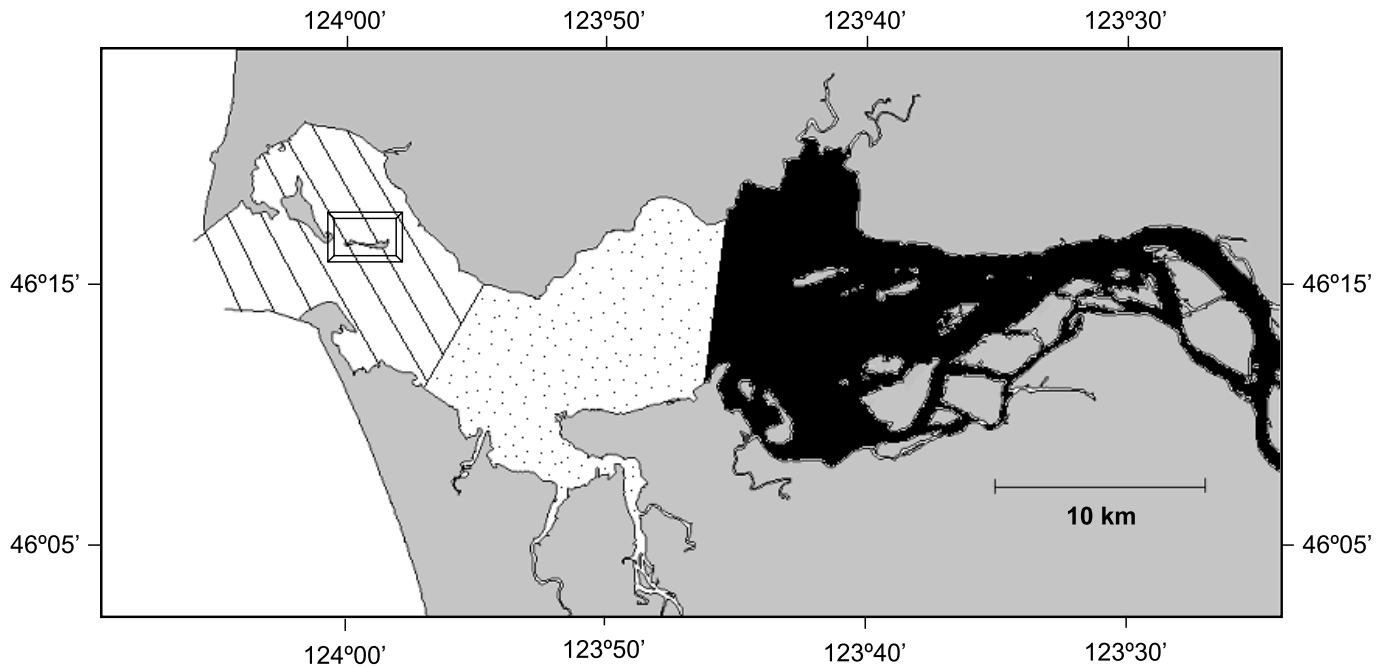
We studied the foraging patterns of radio-tagged Double-crested Cormorants nesting on East Sand Island between 1 June and 26 July in 2000 and 2001. Early in the 2000 and 2001 nesting seasons, we captured and radio-tagged a total of 85 adult Double-crested Cormorants at the East Sand Island colony. We trapped adults on dark (i.e., moonless or cloudy), cool, dry nights from mid- to late May, when cormorants were attending nests during egg laying and early incubation. Adult cormorants were spotlighted on the colony using water-resistant, hand-held spotlights (12 V, 1×10^6 candlepower) and captured using aluminum, hand-held fish landing nets

(1.5-m extendable pole with 0.75-m hoop). Captured individuals were immediately placed in cotton bags and transported to holding crates located at an off-colony location, where they were held until processing.

Radio transmitters (150–152 MHz, 45 pulses/min; Advanced Telemetry Systems (ATS), Insanti, Minnesota) weighing 10 g (0.4% of average adult cormorant body mass) were attached to 35 cormorants in 2000 and 50 cormorants in 2001. Transmitters had an estimated battery life of 80 d and were equipped with a mortality switch. Transmitters were affixed ventrally at the base of the four central rectrices using two cable ties and Loctite® superglue, after Anderson and Ricklefs (1987). Radio-tagged cormorants were then marked with a patagial tag made of brightly coloured vinyl-coated fabric (fluorescent orange in 2000 and bright pink in 2001) and numbered with a unique two-digit number to aid in behavioural observations from blinds located on the periphery of the cormorant colony to verify nesting status. All procedures and protocols involving live cormorants as part of this research were approved by the Institutional Animal Care and Use Committee at Oregon State University.

In 2000, radio-tagged cormorants were sexed using a discriminant function model incorporating culmen length, culmen depth, and flattened wing length of known-sex birds (cf. Glahn and McCoy 1995); the model predicted sex with >95% accuracy (C. Anderson, unpublished data). In 2001, radio-tagged cormorants were sexed using blood samples ($\leq 250 \mu\text{L}$) collected from the tarsal vein. Blood was stored in cryogenic tubes containing a buffer solution (100 mM

Fig. 2. Major salinity zones of the Columbia River estuary: marine zone (stripes), estuarine mixing zone (dotted), and freshwater zone (black) (after Simenstad et al. 1990). East Sand Island is outlined with double-lined rectangle.



Tris HCl pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS) until shipment to Celera AgGen (Davis, California) for molecular sexing.

Spatial foraging patterns

Between 1 June and 26 July, we conducted 20 and 17 aerial telemetry surveys (usually twice weekly and lasting 1–5 h) in 2000 and 2001, respectively (survey area depicted in Fig. 1). During each survey, we attempted to relocate each actively nesting, radio-tagged cormorant using a fixed-wing aircraft (Cessna 206) equipped with an antenna mounted on each wing and a switch box system to isolate signal location. To reduce potential sampling biases, we randomly selected the starting point for each telemetry survey. From our starting point, we flew in the most direct flight path to cover the water bodies (river channels, bays, coastline) of the entire survey area during each flight; we did not survey areas more than once per flight (i.e., if we flew over the same region of the river twice for logistical purposes we did not search for radio-tagged birds the second time). We used a VHF receiver (R4000, ATS) to continuously scan for each radio-tagged cormorant (ca. 5 s per frequency). Once a radio frequency was detected, we tracked the individual until we were close enough to fix a position. A bird was considered relocated when the strength of its transmitter signal was continuous while we were circling and using only one antenna. A Global Positioning System receiver was used to determine coordinates (latitude and longitude) of the relocation.

The error ellipse associated with locating a radio-tagged cormorant averaged 0.50 ± 0.13 km, based on three trials of locating transmitters ($N = 7$) at fixed positions in the estuary that were unknown to the radio-trackers. Relocations were not sufficiently precise to assign a foraging habitat to each relocation but were used to determine the salinity zone used

by foraging cormorants and their distance from the colony. Radio-tagged cormorants were removed from the sample when (i) their nest failed, (ii) the radio-tag transmitted a mortality signal, (iii) the wing-tagged cormorant was observed on-colony without its radio-tag, or (iv) the signal was repeatedly relocated at the same site (repeated relocations were eliminated from the data set retroactively).

Temporal foraging patterns

In 2001, we continuously monitored the colony attendance patterns of actively nesting radio-tagged cormorants between 1 June and 26 July. Temporal attendance patterns (i.e., frequency and duration of colony absences, proportion of time spent off-colony) were assessed using two fixed receiving stations located at the edge of the colony (see Suryan et al. 2002). Fixed receiving stations consisted of a VHF receiver (R4000, ATS) connected to a data collection computer (DCC II, ATS). Each receiving station was powered by a 12-V deep-cycle marine battery connected to a solar panel. A two-element "H" antenna was connected to each receiver and oriented to provide approximately 1.0 km horizontal reception range and approximately 1.5 m vertical reception range (equivalent to the maximum range in elevation of nests). The receiver scanned for each transmitter frequency for 20 s; cycle duration to scan all programmed frequencies ranged between 13.3 and 18.5 min. Once a signal was detected, the DCC logged the radio transmitter frequency and the time. The receivers were also programmed to scan for two reference transmitters (i.e., radio-tags placed on the colony) and three nonexistent transmitter frequencies each cycle to validate detections by the receivers. For our analyses, we included only those cycles where both reference frequencies were detected and none of the nonexistent frequencies was detected (92% of cycles qualified for analyses). Only those

radio-tagged cormorants that were observed nesting for a minimum period of 7 d (mean = 40.1 ± 3.0 d, $N = 33$, range = 9–56 d) were included in subsequent analyses.

Data analysis

Spatial foraging patterns

We estimated the proportional use of the three salinity zones within the Columbia River estuary by radio-tagged cormorants actively nesting on East Sand Island during June and July of 2000 and 2001. To account for the potential lack of independence between observations made on the same individual (e.g., Kenward 1992), we randomly subsampled our data set so that each individual contributed one aerial telemetry relocation to the following analyses ($N = 45$). We tested for an association between time (year \times month) and the distribution of aerial telemetry relocations among the three salinity zones of the Columbia River estuary for both male ($N = 29$) and female ($N = 16$) radio-tagged cormorants using Fisher's exact tests (SAS Institute Inc. 1999). Subsequently, interannual, monthly, and gender differences in distribution of radio-tagged cormorants among the three salinity zones were examined using χ^2 tests (SAS Institute Inc. 1999).

To determine whether relocations for individuals that were relocated more than five times were randomly distributed throughout the estuary, we used a χ^2 test of the observed mean nearest neighbour distance and the expected value of $0.5(A/N_i)^{1/2}$, where A is the area of the estuary and N_i is the number of relocations for individual i (sensu Boots and Getis 1978). To determine whether relocations for particular individuals had a clumped rather than a regular spatial distribution throughout the estuary, we compared expected and observed values of mean nearest neighbour distance. Additionally, we used a Wilcoxon's rank-sum test to determine whether there was a difference in median foraging range (straight-line distance between the relocation and the East Sand Island colony) between the sexes.

Temporal foraging patterns

We attempted to distinguish between short absences from the colony when breeding adults collected nest material or bathed (mean duration = 16.0 ± 1.62 min, $N = 36$, range = 1 to 31 min) and longer absences that represented foraging trips, based on behavioural observations made during the 2001 nesting season. Because cormorants are believed to be exclusively diurnal foragers (Schreiber and Clapp 1987), we only considered colony absences between 0400 and 2200 as potential foraging trips. During 1 June to 26 July of 2001, sunrise occurred between 0523 and 0550 and sunset occurred between 2052 and 2111; civil twilight occurred between 0444 and 0515 and between 2128 and 2149 (United States Naval Observatory 2002). Therefore, foraging trips were defined as colony absences lasting at least two scanning cycles (>13.3 min) that occurred between 0400 and 2200 and did not exceed 1 d. Using these criteria, absences from the colony lasting as long as 37 min could potentially be classified as nonforaging trips.

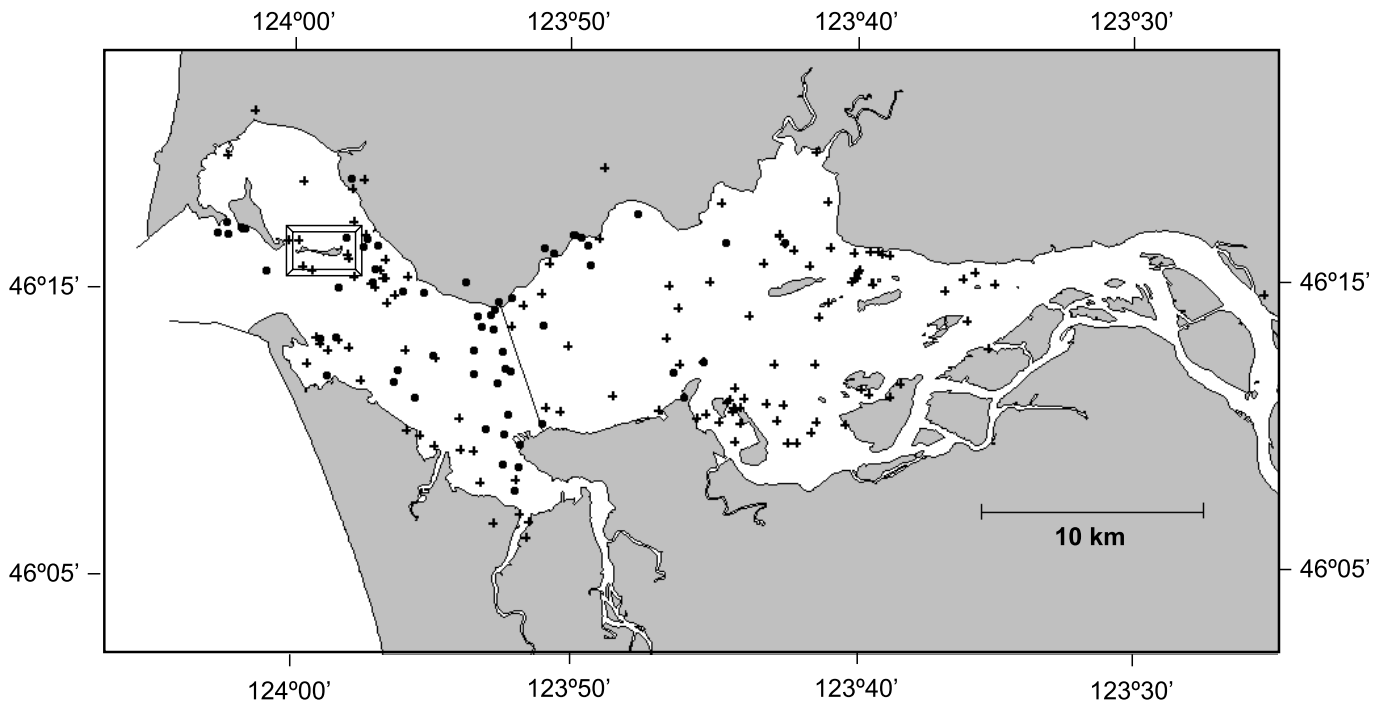
We examined temporal foraging patterns on two scales: long-term (seasonal) and short-term (diurnal and tidal). First, we considered seasonal effects on temporal foraging patterns while controlling for gender effects. We calculated means

for both months of the study period (June and July) for all response variables for each radio-tagged cormorant; 19 radio-tagged birds (8 females and 11 males) were included in the analysis ($N = 19$ birds \times 2 months = 38 observations). Because there were only two repeated measures, the Huynh-Feldt conditions were automatically satisfied, so the analysis could proceed as a split-plot-in-time model with gender as the between-bird factor and time and time \times gender as the within-bird factors (Kuehl 2000). We used two-way ANOVAs to investigate the effects of gender, month, and their interaction on the three response variables: average trip duration, total daily foraging time, and frequency of foraging trips.

Second, we considered the short-term effects of time of day and tidal cycles by exploring how the proportion of time spent foraging changed with time of day, tide stage, and tide series during the month of June while controlling for gender. Data on proportion of time spent foraging were expressed as the proportion of detection cycles in which the transmitter signal was not detected by the on-colony receiving station (see Methods) for each combination of time of day, tide stage, and tide series. We excluded short absences (one scanning cycle) from the data set prior to analyses. Additionally, we only considered data collected in June to avoid potential bias due to increased tag loss in July; nearly half of all telemetered cormorants lost their tags in July of 2001. We separated time of day into three 6-h time periods: morning (0400–1000), midday (1000–1600), and evening (1600–2200). We considered two categories of tide stage (ebb or flood) and two categories of tide series (spring or neap). Spring tides occurred on the days of the month on which the tides were the highest or lowest of the month (approximately 2 weeks per month surrounding the new and the full moon); neap tides occurred on the remaining days of the month.

For each of 32 radio-tagged cormorants (14 females and 18 males) that were actively nesting throughout June of 2001, we calculated the mean proportion of time spent foraging so that each cormorant contributed to each of the time of day and tidal cycle categories described above ($N = 12$ categories in total); the categories for each cormorant constitute a multivariate response with a three-way factorial structure ($3 \times 2 \times 2$). Gender is a between-bird factor, while the three main effects (time of day, tide stage, and tide series) and the four interaction effects in the three-way structure are within-bird factors. Each of the seven factorial effects from the three-way structure (along with its interaction with gender) had its own error term (which is equivalent to analyzing each within-bird factorial effect separately). For the within-bird factorial effects having a single df (e.g., main effect of tide series and interaction between tide series and gender), the analysis reduces to a split-plot type model with an error term representing the variation in the factorial effect across the birds within each gender (30 df, with $14 - 1 = 13$ from females and $18 - 1 = 17$ from males). For within-bird factorial effects having 2 df (e.g., main effect of time of day and interaction between gender and time of day), a more liberal split-plot type test was used (with $2 \times 30 = 60$ df for the within-bird error term), as well as a more conservative MANOVA test (does not require the Huynh-Feldt assumptions; Kuehl 2000). Because in each case both tests supported the same conclusions, only the simpler split-plot type tests were reported.

Fig. 3. Off-colony relocations of radio-tagged male (+; $N = 125$) and female (●; $N = 61$) Double-crested Cormorants actively nesting on East Sand Island (double-lined rectangle). Off-colony relocations were recorded throughout the Columbia River estuary between 1 June and 26 July in 2000 ($N = 138$ relocations) and 2001 ($N = 48$ relocations).



Because of unequal numbers of males and females, Type III sums of squares were used for testing main effects and interactions (SAS Institute Inc. 1999).

We accounted for potential differences among individuals of the same sex (Grémillet et al. 1998) by using a nested classification of individual cormorant within the levels of sex. All response variables yielded normal distributions and homogeneous variance. For all tests of significance we used an alpha level of 0.05 and reported two-tailed P values.

Results

Of the 85 radio-tagged individuals, 58 (68%) were males and 27 (32%) were females. This bias in sex ratio of radio-tagged individuals likely reflects more pronounced territorial behaviour by nesting male cormorants early in the nesting season (Hatch and Weseloh 1999) and (or) that males may conduct more of the nocturnal incubation shifts than females (see Jones et al. 2002). Of the radio-tagged individuals, 56 (66%) were subsequently verified to be nesting through direct observation from blinds and were radio-tracked throughout the respective study periods; 34 (61%) were males ($N = 16$ in 2000, $N = 18$ in 2001) and 22 (39%) were females ($N = 7$ in 2000, $N = 15$ in 2001).

Spatial foraging patterns

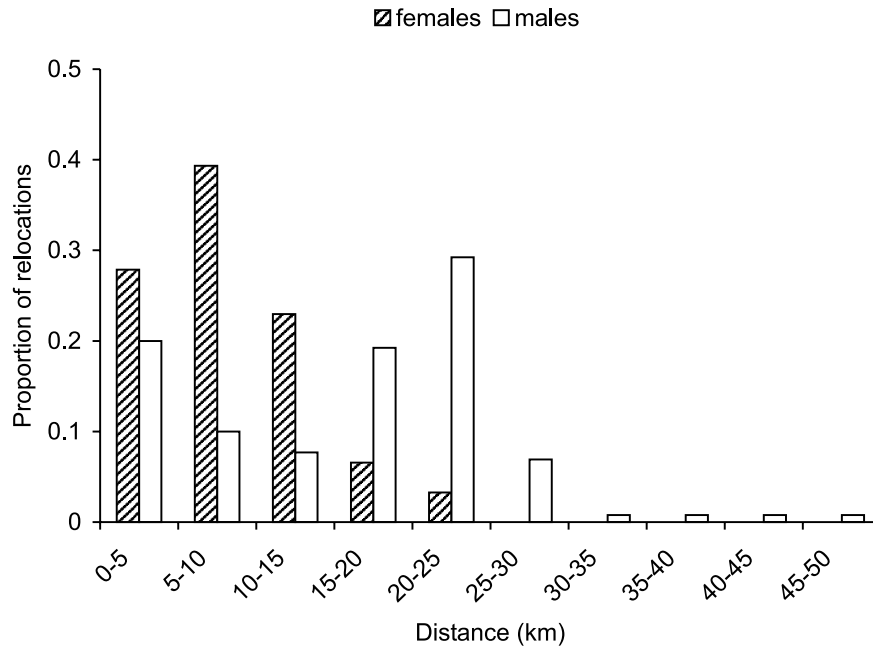
We relocated foraging radio-tagged cormorants that were nesting on East Sand Island 138 and 48 times during the 2000 and 2001 nesting seasons, respectively (Fig. 3). Males were relocated off-colony twice as often as females ($N = 125$ relocations and $N = 61$ relocations, respectively). The sex bias in number of relocations occurred primarily because

there were more than twice as many males as females radio-tracked in 2000, when the majority of relocations were made.

Forty-five (80%) radio-tagged nesters ($N = 56$) were relocated at least once while off-colony (and presumably foraging) during the season when they were radio-tagged; of those radio-tagged nesters, the average number of relocations was 4.04 (SE = 0.47, $N = 45$, range = 1 to 12). No radio-tagged cormorants that were known to be nesting were relocated outside of the Columbia River estuary (i.e., in Willapa Bay or along the coast) in either 2000 or 2001 (Fig. 1). All off-colony relocations occurred >0.50 km from the nesting colony in 2001 (when nest attendance was monitored) and, therefore, outside the average error ellipse associated with transmitters on the cormorant colony. In 2000 (when nest attendance was not monitored), we considered all relocations that occurred >0.5 km from the nesting colony to be off-colony.

After accounting for potential autocorrelation between foraging relocations for each individual, we found no association between month, year, or their interaction (year \times month) and the distribution of the subsample of aerial telemetry relocations ($N = 45$) among the three salinity zones of the Columbia River estuary either for males ($N = 29$; Fisher's exact test, $P = 0.66$) or for females ($N = 16$; Fisher's exact test, $P = 0.89$). The distribution of the subsample of foraging locations among the three salinity zones was similar between the 2000 and 2001 breeding seasons ($\chi^2_2 = 1.68$, $P = 0.43$); therefore, we combined the data from the two years for further analyses. For all the relocations ($N = 186$), the distribution among the salinity zones was as follows: 51 (27%) in the marine zone, 66 (35%) in the estuarine zone, and 69 (37%) in the freshwater zone (Fig. 3). There was no

Fig. 4. Proportion of total off-colony relocations for female ($N = 61$) and male ($N = 125$) radio-tagged Double-crested Cormorants in each 5-km interval (straight-line distance) from the nesting colony on East Sand Island in the Columbia River estuary. All relocations were determined from aerial telemetry surveys conducted during the 2000 and 2001 nesting seasons.



difference between months (June versus July) in the distribution of subsampled relocations among zones ($\chi^2_2 = 0.751$, $P = 0.69$). There was a considerable difference, however, between the sexes in the spatial distribution of the subsample of relocations among the three salinity zones in the Columbia River estuary ($\chi^2_2 = 18.49$, $P < 0.0001$). Overall, most of the relocations of radio-tagged females were within the estuarine mixing zone (66%, $N = 40$, 0.34 relocations·km⁻²), followed by the marine zone (28%, $N = 17$, 0.19 relocations·km⁻²) and the freshwater zone (7%, $N = 4$, 0.02 relocations·km⁻²). In contrast, most relocations of radio-tagged males were within the freshwater zone (52%, $N = 65$, 0.35 relocations·km⁻²), followed by the marine zone (27%, $N = 34$, 0.29 relocations·km⁻²) and the estuarine mixing zone (21%, $N = 26$, 0.29 relocations·km⁻²).

Nesting males commuted significantly greater distances (mean = 15.98 ± 0.72 km) from East Sand Island to forage than nesting females (mean = 8.93 ± 0.55 km; $Z_{228} = 5.94$, $P < 0.0001$). The majority of off-colony relocations for females were <10 km from the nesting colony, whereas the majority of off-colony relocations for males were >15 km from the nesting colony (Fig. 4). Two off-colony relocations of actively nesting males were >40 km from the colony (41.9 and 47.2 km). To our knowledge, these distances exceed previously published records of the maximum foraging range for nesting Double-crested Cormorants (cf. 40 km; Custer and Bunck 1992).

There was strong evidence that the relocations for individual radio-tagged cormorants were not randomly distributed throughout the study area ($\chi^2_{15} = 6747.67$, $P < 0.0001$). Fourteen of the 16 individuals that were relocated off-colony more than five times (88%) had observed values of mean nearest neighbour distance that were less than expected values, indicating that individual relocations had a clumped rather

than a regular spatial distribution throughout the estuary. Figure 5 depicts the off-colony detections for two radio-tagged nesting adults, a female and a male, that were repeatedly detected in the same foraging areas.

Temporal foraging patterns

Average foraging trip duration was significantly greater for females than for males ($F_{[1,17]} = 6.73$, $P = 0.02$; Table 1), although there was no difference between the sexes in total time spent foraging after controlling for differences due to month ($F_{[1,17]} = 0.82$, $P = 0.38$; Table 1). Furthermore, males went on more foraging trips than females ($F_{[1,17]} = 10.06$, $P = 0.006$; Table 1). This suggests that females compensated for fewer foraging trips by taking trips of greater duration compared with those of males.

There was no statistical difference in average trip duration ($F_{[1,17]} = 0.03$, $P = 0.86$) or total time spent foraging ($F_{[1,17]} = 3.22$, $P = 0.09$) between June and July after controlling for gender differences; however, there was a tendency for cormorants to spend more total time foraging in June than in July (Table 1). There was no evidence of an interaction effect of sex \times month on average trip duration or total time spent foraging ($F_{[1,17]} = 1.01$, $P = 0.33$ and $F_{[1,17]} = 2.65$, $P = 0.12$, respectively). There was convincing evidence, however, of an interaction effect of sex \times month on frequency of foraging trips ($F_{[1,17]} = 6.66$, $P = 0.02$); females went on more foraging trips in June than in July, whereas males went on more foraging trips in July than in June.

There was a significant short-term effect of time of day ($F_{[2,60]} = 27.19$, $P < 0.0001$) and of tide stage ($F_{[1,30]} = 34.77$, $P < 0.0001$) on proportion of time spent foraging, regardless of sex (Table 2). There was also a significant three-way interaction effect of daytime \times tide stage \times tide

Fig. 5. Distribution of aerial telemetry relocations for two individual radio-tagged Double-crested Cormorants (six relocations for one female (●) and five relocations for one male (+)) actively nesting at East Sand Island (double-lined rectangle) in the Columbia River estuary.

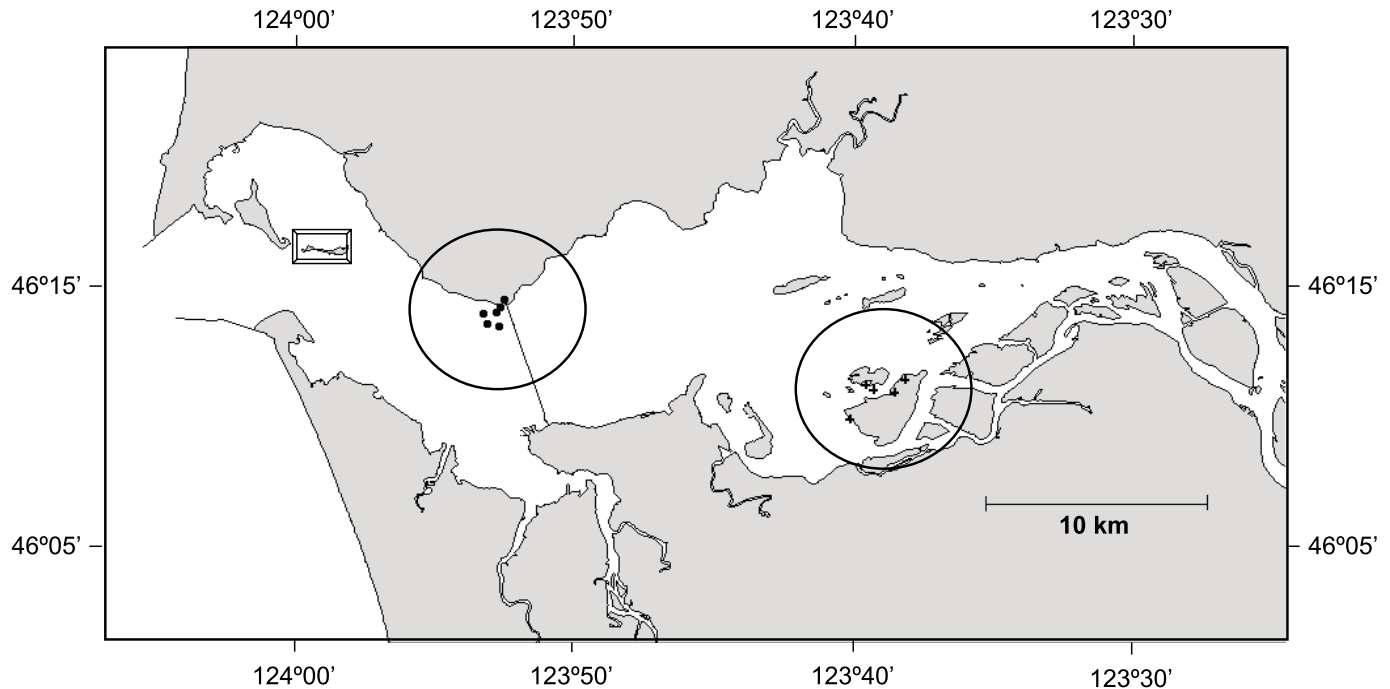


Table 1. Average foraging trip duration (h) (A), time spent foraging ($\text{h}\cdot\text{d}^{-1}$) (B), and frequency of trips ($\text{trips}\cdot\text{d}^{-1}$) (C) for male and female Double-crested Cormorants (*Phalacrocorax auritus*) nesting on East Sand Island during June and July of 2001.

(A) Trip duration.			
	Females ($N = 8$)	Males ($N = 11$)	Mean
June	2.56±0.28	1.94±0.24	2.25±0.18
July	2.72±0.28	1.71±0.24	2.21±0.18
Mean	2.64±0.24	* 1.82±0.20	ns
(B) Time spent foraging.			
	Females ($N = 8$)	Males ($N = 11$)	Mean
June	3.39±0.42	3.01±0.36	3.20±0.28
July	1.93±0.42	2.94±0.36	2.43±0.28
Mean	2.66±0.26	ns 2.97±0.22	ns
(C) Trip frequency.			
	Females ($N = 8$)	Males ($N = 11$)	Mean
June	1.46±0.20	1.61±0.17	1.53±0.13
July	0.65±0.20	1.74±0.17	1.20±0.13
Mean	1.06±0.15	** 1.67±0.13	ns

Note: Results of two-way repeated measures ANOVAs are expressed as means ± SE. Day refers to the 18-h daytime period (0400–2200) considered for these analyses. ns, not significant; *, $0.05 > P > 0.01$; **, $P < 0.01$.

series on proportion of time spent foraging ($F_{[2,60]} = 59.69$, $P < 0.0001$; Table 2). Nesting cormorants spent a greater proportion of time foraging during morning ebb tides in spring tide series, but during evening ebb tides in neap tide series (Fig. 6).

Discussion

Spatial patterns

Radio-tagged Double-crested Cormorants nesting on East Sand Island usually commuted at least 5 km to forage in the shallow bays, tidal flats, and nearshore areas of the estuarine mixing and freshwater zones rather than the marine zone that surrounds the nesting colony (Fig. 3). These findings were consistent with a study of Double-crested Cormorant foraging locations in Lake Erie, where cormorants were predominantly located within 2.5 km from shore and in relatively shallow water (~10 m; Stapanian et al. 2002). Of the three salinity zones, the estuarine mixing zone is reported to have the greatest average densities of forage fishes, especially in shallow bays and nearshore environments (Bottom and Jones 1990; Jones et al. 1990). The observed distribution of foraging cormorants is also consistent with potential localized depletion of forage fishes (Furness and Birkhead 1984) and (or) disturbance to fishes through inter- and intra-specific competition (Lewis et al. 2001) by the large numbers of piscivorous waterbirds nesting and roosting on East Sand Island.

Although most of the off-colony relocations of radio-tagged females were in the estuarine mixing zone, most off-colony relocations of males were in the freshwater zone. This finding was unexpected because the freshwater zone of the Columbia River estuary is the farthest from the nesting colony on East Sand Island and is reported to have lower densities of forage fish than the other two zones (Bottom and Jones 1990, but see Stapanian et al. 2002). Many of the predominant species in the assemblage of schooling forage fishes in the estuary, such as Pacific herring (*Clupea pallasii* Valenciennes, 1847), northern anchovy (*Engraulis mordax* Girard, 1854), Pacific

Table 2. Separate split-plot-in-time ANOVAs for each factorial effect of time of day, tide stage, and tide series on the proportion of time actively nesting Double-crested Cormorants spent off-colony during June of 2001.

Effect	df	Mean square	Sum of squares	F	P
Sex	1	0.3433	0.3433	4.11	0.0517
	30	<i>0.0836</i>	<i>2.5087</i>		
Daytime	2	1.1583	2.3165	27.19	<0.0001
Sex × daytime	2	0.0372	0.0743	0.87	0.4235
	60	<i>0.0426</i>	<i>2.5581</i>		
Tide stage	1	0.3921	0.3921	34.77	<0.0001
Sex × tide stage	1	0.0006	0.0006	0.05	0.8224
	30	<i>0.0113</i>	<i>0.3381</i>		
Tide series	1	0.0645	0.0645	2.78	0.1058
Sex × tide series	1	0.0205	0.0205	0.88	0.3553
	30	<i>0.0233</i>	<i>0.6982</i>		
Daytime × tide stage	2	0.2289	0.4579	13.65	<0.0001
Sex × daytime × tide stage	2	0.0083	0.0166	0.49	0.6121
	60	<i>0.0168</i>	<i>1.0071</i>		
Daytime × tide series	2	0.0411	0.0821	2.54	0.0876
Sex × daytime × tide series	2	0.0008	0.0016	0.05	0.9525
	60	<i>0.0162</i>	<i>0.9715</i>		
Tide stage × tide series	1	0.0060	0.0060	0.45	0.5058
Sex × tide stage × tide series	1	0.0053	0.0053	0.40	0.5300
	30	<i>0.0131</i>	<i>0.3917</i>		
Daytime × stage × tide series	2	1.1806	2.3611	56.69	<0.0001
Sex × daytime × tide stage × tide series	2	0.0182	0.0364	0.92	0.4042
Residual	60	<i>0.0198</i>	<i>1.1867</i>		

Note: Error terms are shown in italics below each set of factorial effects.

tomcod (*Microgadus proximus* (Girard, 1854)), and Pacific sardine (*Sardinops sagax* (Jenyns, 1842)) (Bottom and Jones 1990), are restricted to the marine and estuarine mixing zones. Nesting male cormorants presumably commuted significantly greater distances to forage in areas of the estuary that are generally less productive to exploit prey resources or foraging opportunities that are less available in the other two zones.

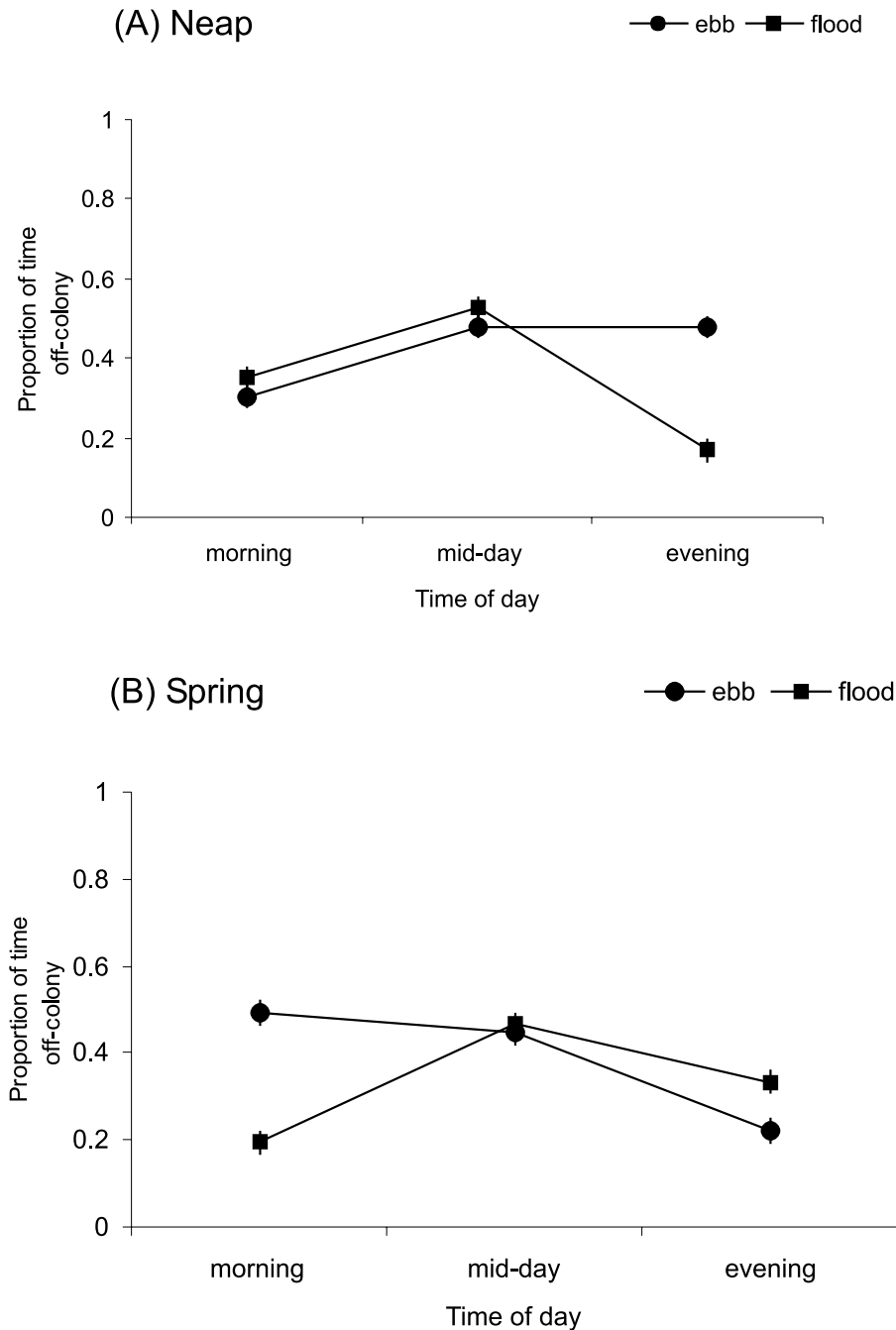
Male cormorants are reported to use a wider array of foraging techniques than females, which may allow them to exploit a wider variety of prey (Grémillet et al. 1998). Males may commute greater distances to use foraging sites where they are able to forage individually on larger demersal prey (Voslamber et al. 1995; Ishikawa and Watanuki 2002). Solitary foraging has been reported as an efficient foraging strategy for cormorants to pursue concealed prey (e.g., demersal fishes that hide in bottom sediments, such as mud or rocks (Voslamber et al. 1995; Hebshi 1998)). Double-crested Cormorants are believed to probe bottom sediments to locate and capture hidden prey (Voslamber et al. 1995; Hatch and Weseloh 1999) and have been reported to shift to solitary foraging behaviour when the water is turbid (Custer and Bunck 1992; Van Eerden and Voslamber 1995).

Findings from a concurrent study of diet composition (percent identifiable fish biomass in stomach contents) in Double-crested Cormorants nesting on East Sand Island support the hypothesis that males use a wider array of foraging tactics than females and have a greater tendency to pursue benthic prey. During 2000 and 2001, the diet of males consisted of a significantly greater proportion of demersal prey

(i.e., flounder) compared with the diet of females ($\chi^2_1 = 5.42$, $P = 0.02$; D. Roby, unpublished data). Starry flounder (*Platichthys stellatus* (Pallas, 1788)) were more than twice as prevalent in the diet of males (25%) than in that of females (Fig. 7), although the difference was not statistically significant (exact Wilcoxon's rank-sum test, $P = 0.19$). Starry flounder are reported to travel up into the tidal-fluvial regions of rivers (Morrow 1980), perhaps because of higher standing stocks of benthic infauna compared with the estuarine mixing zone (Jones et al. 1990). This species avoids predators by hiding in the sand on the bottom and assuming cryptic colouration (Orcutt 1950). Pacific sand lance (*Ammodytes hexapterus* Pallas, 1814) were significantly more prevalent in the diet of males than in that of females (exact Wilcoxon's rank-sum test, $P = 0.03$; Fig. 7). Pacific sand lance are also known to bury themselves in sediment during the day to avoid predators (Emmett et al. 1991). Our findings are consistent with a recent study of Japanese Cormorants (*Phalacrocorax capillatus* (Temminck and Schlegel, 1850)), which showed that males foraged more on demersal fishes than did females (Ishikawa and Watanuki 2002).

Females took foraging trips of longer duration than did males, suggesting that the more restricted foraging range of females was not a reflection of time constraints. Females may have been energetically constrained, however, owing to the higher investment by females in egg production (3–6 eggs/clutch; Hatch and Weseloh 1999) and incubation (Carey 1996), which may have precluded longer distance foraging trips that were energetically expensive. Consistent with results from this study, activity budgets of South Georgian

Fig. 6. Proportion of time spent off-colony (and presumably foraging) in June 2001 for radio-tagged Double-crested Cormorants actively nesting on East Sand Island during neap (A) and spring (B) tide series by time of day and tide stage. Proportion of time off-colony is expressed as the proportion of detection cycles during which a transmitter was not detected for at least two consecutive scanning cycles by on-colony receiving stations for each combination of time of day, tide stage, and tidal series.

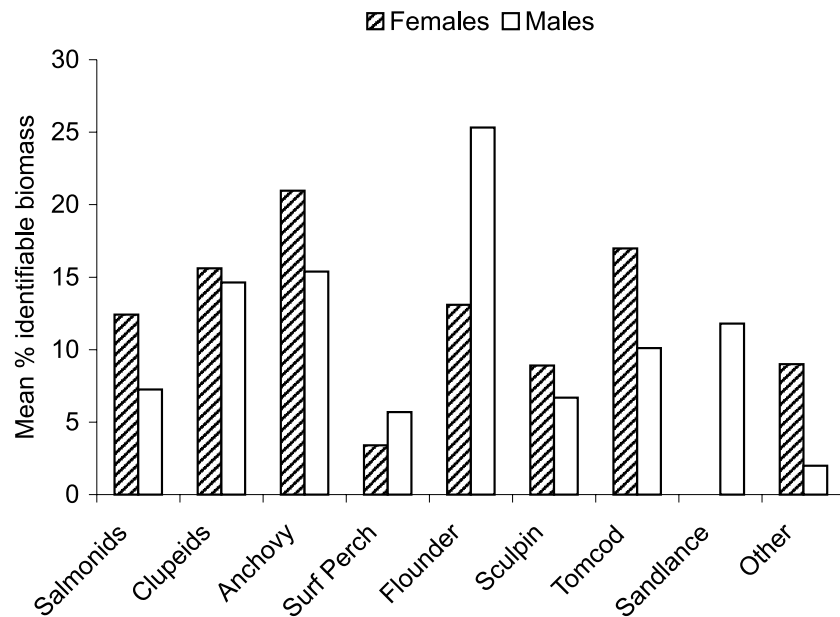


Shags (*Phalacrocorax georgianus* Lonnberg, 1906) revealed that males spent more time flying than females (Wanless et al. 1995). Flight is an energetically expensive activity in species with high wing loading, such as cormorants (Pennycuick 1975).

Optimal foraging theory predicts that because male cormorants flew significantly farther to forage and took more foraging trips than females, males should somehow compensate for this additional energy expenditure (Krebs 1978).

Avoiding competition with females for food or gaining access to more easily captured or higher energy prey (Mauer 1996) are potential benefits explaining the observed patterns of male foraging. Furthermore, these sexual differences in foraging behaviour may be influenced by other factors not investigated in this study. Male and female cormorants may have different foraging capabilities related to the sexual dimorphism in this subspecies. Differences in diving capacity, bill size, and pharyngeal opening may allow the sexes to

Fig. 7. Diet composition (mean percent identifiable fish biomass) of collected female ($N = 25$) and male ($N = 40$) Double-crested Cormorants nesting at East Sand Island in June 2000 and 2001 (D. Roby, unpublished data).



efficiently exploit different habitats and (or) prey types (Selander 1966; Mauer 1996; Watanuki et al. 1996).

Distinct individual foraging patterns, such as those depicted in Figure 5, indicate that individual cormorants return to foraging sites where they were previously successful in capturing prey and that individuals may be employing specific foraging strategies that are particularly suited for the environment where they are foraging. Further investigation into the foraging strategies of individual cormorants may elucidate what specific foraging techniques are used (i.e., group versus solitary foraging) to capture certain prey types (i.e., schooling or benthic fishes) and under what specific environmental conditions (i.e., tide stage, water depth, substrate type, etc.) they are used.

Temporal patterns

Double-crested Cormorants nesting at East Sand Island also exhibited sexual differences in foraging patterns that changed as the nesting season progressed. The higher foraging intensity of males in July suggests that males may bear a greater proportion of chick provisioning duties late in chick rearing compared with females. Gender differences in foraging intensity may also help ensure that the nest site is defended more by the larger male than by the female at times when nest contents are most vulnerable to predators, such as during the incubation or chick brooding periods (Hatch and Weseloh 1999).

Our findings suggest that foraging is more productive for nesting Double-crested Cormorants during ebb tides. Similarly, Dunn (1975) reported that Double-crested Cormorants in New Hampshire fed their young more during ebb tides and van Tets (1959) reported that Double-crested Cormorants foraged in channels during ebb tides in British Columbia. There are likely two reasons for this foraging pattern. First, receding water during ebb tides can concentrate benthic fishes, such as flounder, in shallow bays, shoals, and

nearshore environments and make them more conspicuous (Wirjoatmodjo and Pitcher 1984; Raffaelli et al. 1990). Richner (1995) reported that Great Cormorants (*Phalacrocorax carbo* (Linnaeus, 1758)) foraged most actively during ebb tides, when foraging was predominately on flounder. Flounder have been shown to follow ebb tides as they forage, perhaps to avoid increased risks of stranding and depredation by piscivorous birds (Wirjoatmodjo and Pitcher 1984).

Second, in the Columbia River estuary, tidal currents are markedly stronger during ebb tide owing to the combination of tidal flow and river discharge (Center for Operational Oceanographic Products and Services 2002), and plankton distribution in estuaries is known to be strongly associated with tidal currents (Trinast 1975). Because a large proportion of cormorant prey comprises planktivorous fishes (e.g., clupeids, anchovies; Collis et al. 2002), it is likely that cormorants are foraging during ebb tide to follow the tide-influenced movements of their planktivorous prey. Alldredge and Hamner (1980) reported that plankton biomass and density were greatest in nearshore and shallow areas located in the lee of points of land that created eddies. Off-colony relocations of cormorants in the estuary were often either in close proximity to the shoreline or associated with structures that create eddies, such as points of land (Fig. 3), pile dikes, and jetties.

To our knowledge, no other studies of cormorant foraging patterns have found an effect of tide series (Richner 1995; Dorfman and Kingsford 2001), although tide series is known to influence the foraging patterns of other piscivorous seabirds (Irons 1998). The reason for the relationship between foraging patterns and tide series is not clear. Foraging patterns may be influenced by the extent of salt water intrusion within the estuary, which is known to influence the distribution of marine forage fishes (Bottom and Jones 1990). Salinity intrusion is greater during neap tide series compared with spring tide series in the Columbia River estuary, despite smaller tidal incursion on neap tides (Jay and Smith 1990).

The reduced vertical mixing during neap tides reduces friction between salt- and freshwater layers and permits greater salt water intrusion (Jay and Smith 1990); hence, greater incursion into the upper estuary by marine forage fishes may occur during neap tides. Furthermore, the increased turbidity associated with spring tides (Jay and Smith 1990) may alter the distribution of forage fishes in the estuary and the behaviour of foraging cormorants.

Prey availability and diet

Marine forage fishes were notably more abundant in the Columbia River estuary in 2001 than in previous years (Brodeur et al. 2003). Data on cormorant diets in 2001 indicated that the large breeding colony on East Sand Island relied mostly on schooling marine forage fishes for food. The higher availability of marine forage fishes suggests that nesting adult cormorants should have taken fewer foraging trips of shorter duration and spent less total time foraging and more time attending the nest. Our findings support these hypotheses; cormorants nesting at East Sand Island spent, on average, only 16% of daylight hours foraging during the 2001 nesting season. This is a much lower proportion of time spent foraging than that reported for Double-crested Cormorants nesting on Lake Champlain, Vermont (44%; Fowle 1997). Our findings suggest that prey depletion and (or) competition for food resources were not major factors during this year of high marine forage fish availability.

A recent study of the diet composition of Double-crested Cormorants nesting in the Columbia River estuary showed that the diet of cormorants nesting on Rice Island, located in the freshwater zone, included a substantially higher proportion of salmonids (three times more by mass) compared with the diet of cormorants nesting on East Sand Island, located in the marine zone (Collis et al. 2002). These findings suggest that cormorants foraging in the freshwater zone consume more salmonids than cormorants foraging in the marine or estuarine mixing zones. Furthermore, there was a pronounced seasonal decline in the proportion of salmonids in the diet of cormorants nesting at Rice Island; most salmonids were consumed during the peak out-migration of salmonid smolts that occurred early in the nesting season (April and May) and fewer were consumed late in the nesting season (June and July; Collis et al. 2002).

Results from our study revealed that, during June, male cormorants foraged predominately in the freshwater zone, near Rice Island. This suggests that males, compared with females, should consume more juvenile salmonids. Contrary to expectation, however, males did not have a higher proportion of salmonids in their diet during June than females (Fig. 7; exact Wilcoxon's rank-sum test, $P = 0.86$; SAS Institute Inc. 1999). An important caveat is that the data presented here on diet composition of cormorants nesting on East Sand Island were from June only and thus were collected after the peak out-migration by salmonid smolts (Fish Passage Center 2002).

Seabird diets are known to vary in response to changing oceanic conditions (Montevecchi and Myers 1996; Montevecchi and Cairns 2002). We predict that in years when stocks of marine forage fish within the estuary are depressed compared with our study period (owing to El Niño perturbations or poor ocean conditions; Bayer 1986; Emmett and

Brodeur 2000), Double-crested Cormorants may become more reliant on the more predictable fish resources of the estuary, such as the 150–200 million hatchery-reared salmonid smolts that are released annually into the Columbia River basin (Fish Passage Center 2002). Because male cormorants were frequently relocated foraging in the upper estuary, despite the high availability of marine forage fishes in the estuarine mixing zone, males may forage in the freshwater zone of the estuary more during years of low availability of marine forage fish; the freshwater zone is recognized as an important transition area for juvenile salmonids during smoltification (Emmett et al. 1991).

A wide variety of prey in the diet, the ability to commute considerable distances to forage in areas of high prey availability, and gender differences in foraging distribution are all important attributes for a colonial nesting species that forages on highly variable food resources (Birt et al. 1987). The foraging patterns of Double-crested Cormorants demonstrated in this study may be critical for this large and growing colony to remain productive when forage fish stocks become more limited and competition with many thousands of other nesting and roosting piscivorous waterbirds becomes more stringent.

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