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BEHAVIORAL VARIATIONS OF
BRANDT'S CORMORANTS (Phalacrocorax penicillatus)

A Thesis
Presented to
The Faculty of the Department of Marine Science
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
James Walter Scholten
May, 1999

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ABSTRACT

BEHAVIORAL VARIATIONS OF BRANDT'S CORMORANTS (Phalacrocorax penicillatus)

by James Walter Scholten

This thesis addresses the topic of behavioral and abundance variations within a colony of Brandt's Cormorants (Phalacrocorax penicillatus) at Point Lobos State Reserve, California. It focuses on a three year period following an El Niño Southern Oscillation (ENSO), which affected the breeding success of these seabirds, and charts the recovery of this colony from 1994 to 1996. A number of variables were observed to determine variations within the colony including abundance of Brandt's Cormorants, behavioral variations over time, foraging frequency, and nesting activity.

Results from this thesis suggested the population of cormorants at Point Lobos was decreased early in the colony's recovery from the ENSO event and, during the three year study, increased in numbers to historical norms. Breeding and nesting activity increased similarly. In addition, results indicated a lack of substantial behavioral variations among the three recovery years.

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INTRODUCTION

The timing and duration of certain behaviors of seabirds may vary within and among years. Some avian species spend different amounts of time foraging or in intraspecific interactions during breeding than during the non-breeding season. There also are species that exhibit behavioral shifts such as within single breeding seasons (Payne 1965, Weeden 1966, Preston 1968, Wolf and Hainsworth 1971, Dunn 1975, Withers 1977, Austin 1978, Howe 1978, Walsberg 1978, Burley 1980, Ettinger and King 1980, Briggs et al. 1987, Weathers and Sullivan 1989). Variations in seabird activity have also been observed within non-breeding seasons. Ainley and Boekelheide (1990) noted a general northerly dispersion of cormorants away from breeding sites during the non-breeding season. However, Palmer (1962) indicated a southerly dispersion of these seabirds. The onset of nest-building also has been noted as variable in cormorants and other seabirds. Nest building by Brandt's Cormorants (Phalacrocorax penicillatus) can begin from February to July and fledging can be as late as October (Hatler et al. 1978, Speich and Wahl 1989, Ainley and Boekelheide 1990, pers.obs.).

Expected environmental changes or singular environmental events may cause behavioral variations. During El Niño

Southern Oscillation (ENSO) years certain breeding and foraging activities are known to decrease in some species (Ainley and Lewis 1974, Howe 1978, Ainley and Boekelheide 1990). ENSO events are responsible for decreased survival of seabirds (Hodder and Graybill 1985). The breeding success of many species also is decreased during these warm water events (Hatch 1987, Ainley and Boekelheide 1990, Wilson 1993).

Behavioral studies that assess and predict large scale behavioral variations of avian populations are required in order to evaluate population condition. Sheer abundances of seabirds provide data for one time period and this may be useful in determining the effects of a present or past environmental or biological event, whereas a study of behavioral shifts could predict and explain these events. This could be beneficial to both protection and management of seabird species.

To better understand the response of seabirds to seasonal and interannual changes in their environment, long-term (>1 year) studies are needed that address behavioral shifts in a quantitative manner. Behavioral studies are frequently dismissed as subjective or biased. They can be highly descriptive and detailed but biased due to the observer's lack of awareness of what is affecting the species. Behaviors may be identified or classified inconsistently by different observers. Distinct seasons or natural rhythms of the species in question may be unknown.

Observer decisions cannot enter into the assessment. It is easy to assess the behaviors of a group of animals from one's own perspective but it is useless unless all things are equal through time and among studies. Many different researchers may compound these difficulties. Spurious conclusions may be made if a researcher is unaware of forces natural or otherwise affecting a site.

Strict definitions of behaviors are required so observers are not confusing more than one activity for a single behavior. Collecting quantitative data using scientific methods should reduce the possibility of subjectivity.

Reported here are results of a long-term study of behavioral variations within a large colony of Brandt's cormorants. These birds are gregarious, heavy-bodied aquatic seabirds found along the Pacific West Coast from Cabo San Lucas to southeast Alaska, as well as in the Gulf of California. Unlike many seabirds, all cormorants have wettable feathers that allow them to dive in search of prey and nesting material unhampered by natural buoyant oils (Owre 1967, Rijke 1967, Curry-Lindahl 1970, Elowson 1984). They are foot-propelled divers and highly maneuverable underwater. Although cormorants are able to fly necessary distances for foraging purposes, they return nightly to their roosting sites (Ainley and Boekelheide 1990). Because of this fact,

cormorants are available nearshore in large numbers for observation.

In 1980, approximately 59,000 Brandt's Cormorants occurred in California (Sowls et al. 1980). They are most abundant along the coast of the central portion of the California Current. The largest colony in the world is on the Farallon Islands, near San Francisco. Another major breeding site is at Point Lobos State Reserve (PLSR), near Monterey Bay (Briggs et al. 1987)

Brandt's Cormorants choose nesting sites that are protected from predators. These sites are commonly offshore islands, where nests are built on the flat or sloping leeward side (Hatler et al. 1978). Nests are evenly spaced and as far apart as neighboring birds can peck (Ainley and Boekelheide 1990). Although the beginning of the breeding season is generally predictable for individual breeding sites, the onset of cormorant breeding on the Channel Islands, in southern California, has fluctuated from February to May among years (Sowls et al. 1980).

The researcher examined behavioral, abundance, and nesting variations of Brandt's Cormorants at PLSR from 1994 through 1996. This was a good long-term study site and period for two reasons. First, from 1992 to 1994 an ENSO event occurred, affecting the timing and numbers of breeding cormorants at this site. Behavioral variations were expected during this three year period. Second, Brandt's Cormorants

generally dispersed from the breeding site during the non-breeding season, but a percentage remained at PLSR through winter. This allowed a year-round assessment of behavioral variations.

Decreased parental responsibilities and breeding failure of seabirds have been noted during ENSO events. In the year following such an event, when the abundances of Brandt's Cormorants at PLSR were less than historical norms, it was expected that competition and subsequent aggression would occur less frequently than years without the effects of an ENSO event. With decreased competition for food, space, and nesting material during the first ENSO recovery year (1994), I expected an increase in resting and preening and a decrease in foraging and alertness. I expected the opposite to occur as the population (and competition) recovered and increased through the three years of the study. An increase in the numbers of Brandt's Cormorants present at Point Lobos was also expected through the years following the ENSO.

During the non-breeding season (October to February) when few cormorants used the roosting site at PLSR, the demands on individual birds were expected to be less than during the breeding season. There were no juveniles, no nests, and less competition for space. The researcher expected Brandt's Cormorants to spend a greater amount of time preening and resting and a decrease in foraging and

alertness during the non-breeding season compared to the breeding season.

Materials and Methods

All observations of Brandt's Cormorants were conducted from a cliff overlooking the offshore roosting site, Bird Rock (Fig.1). The observation site was at the end of a small peninsula, and was the closest mainland point to Bird Rock. The island was approximately 50 meters offshore, devoid of unnatural disturbance (e.g. boat traffic, divers, swimmers, construction). There was no access to the public. A large flat area in the middle of the island served as the primary roosting site and was protected from wind and spray by a ridge on the western edge of the island. This layout is typical of Brandt's Cormorants nesting and roosting requirements (Hatler et al. 1978).

From July 1994 until December 1996, data were collected at PLSR from four to six times per month excluding a two month period in the spring of 1995. This hiatus was due to flood destruction of a highway bridge restricting access to the observation site. Observations were conducted from mid-morning (0900h) to early afternoon (1300h) so the time interval was consistent in avoiding potential confounding factors within days (e.g. consistently different activity

patterns at different times of day) and glare from the afternoon sun.

At the beginning and end of each day of observations, (1) the number of Brandt's Cormorants on the main colony, (2) total number of visible cormorants on the island, (3) number of nests and (4) number of juveniles were determined. Mean abundances were calculated for each day.

During a period of fifteen minutes, the frequency of departures from the island was assessed. Every Brandt's Cormorant that flew off the island within that period was counted and this number was multiplied by four to determine the number of departures per hour. These frequencies of departure were divided by the total number of birds to achieve a relative departure rate, then transformed using a natural log transformation.

To determine if intraspecific interactions may be important in regulating bird density, Backward Stepwise Multiple Regressions were computed using departure rate (log transformed) as the dependent variable and various measures of abundance as independent variables. Abundance measures included: total number of all birds, number of birds in the main colony, number of juveniles and number of nests. Preliminary tests were conducted to insure that the independent variables used in the analysis were not correlated. Because all independent variables were not assessed or appropriate during different seasons, three

separate analyses were conducted. During the non-breeding season, juveniles or nests were not present, and therefore not appropriate in an analysis of that season. Because number of juveniles and nests were correlated, they could not be used in the same analysis; therefore they were addressed separately. The three models were as follows:

<u>Season</u>	<u>Dependent Variable</u>	<u>Independent Variable</u>
Non-breeding	Departures	Main, Total Abund.
Breeding	Departures	Main, Total, Nest Abund.
Breeding	Departures	Main, Total, Juv. Abund.

To assess whether or not behavior changed with respect to breeding season or sampling year three points within the main colony were selected randomly within a gridwork consisting of several permanent or semi-permanent transect points (boulders, discolorations, crevices, carcasses) along the length and width of the colony. A spotting scope was trained upon each of the three points (one at a time) for no more than six minutes (data period). First, the total abundance of cormorants within the view was assessed. During the remainder of the data period, the behavior (preening, resting, alert) of each bird was recorded. Preening was assigned to birds adjusting feathers, scratching, or otherwise grooming themselves. Birds lying on the ground or in nests with their heads turned and tucked under their wings were considered resting. Alert behavior was assigned to

birds standing still on the ground or on the edge of a nest making only small head movements. To determine the percentage of birds engaged in the three behaviors, during each data period, the number of birds engaged in each of these behaviors was recorded and this number was divided by the total abundance of cormorants in the scopes view. Each data period was followed by a four-minute period of data recording. This process was repeated three times in 30 minutes, and this 30 minute period was repeated three times during a data collection day (total of nine data periods per day) and alternated with the three observations of departures.

A Log Linear analysis of these data was performed to determine the relationships between behaviors, seasons, and years. In order to compare behavioral variations between and among years, the following two models were generated:

1. Behaviors (preening, resting, alert) X Year (1994, 1995, 1996)
2. Behaviors (preening, resting, alert) X Season (non-breeding, breeding) (years combined)

RESULTS

Abundances of Brandt's Cormorants increased during the three years (Fig. 2). Based on maximum counts, there was an increase of 395 individuals from 1994 to 1995 and an increase

of 840 individuals from 1995 to 1996. Abundances of cormorants within the main nesting area increased similarly (Fig. 2). Seasonal and annual fluctuations occurred throughout the study. The fewest (9) Brandt's Cormorants occurred in January of 1995 and the most (1750) were observed in June of 1996. The most cormorants were observed in the breeding season.

The number of nests increased during the three breeding seasons (Fig. 3). Forty-eight nests were observed in 1994. In the second year, a maximum of 222 nests were seen, and a maximum of 580 nests were observed in 1996. There was a 362.5% increase in the number of nests from 1994 to 1995 and a 161.3% increase from 1995 to 1996.

Juvenile Brandt's Cormorants were observed at all nesting sites. In 1994, a maximum of 56 juveniles were observed on 21 July at the main colony. One hundred twenty were observed at the same colony on 16 July, 1995, and 240 were observed on 28 June, 1996. There was a 114.3% increase in the number of juveniles from 1994 to 1995 and a 100% increase from 1995 to 1996 (Fig. 3).

Three additional nesting areas, spatially and temporally separated from the main colony, were observed in the second and third years after the ENSO event (Fig. 4). Colony A consisted of nine nests, and began approximately one month after the onset of the 1995 breeding season at the main breeding colony. Colonies B and C also began later than the

main colony in 1996. Colony B, comprising of 73 nests and located on a small island adjacent to Bird Island, began breeding one month after the main colony began. Colony C, comprising of 48 nests, was located on the eastern edge of Bird Island. It began six weeks after the first nests appeared in the main colony.

Chicks hatched approximately one month following the onset of nesting in each colony. Chicks were guarded closely by their parents, and huddled near the nest in the first few weeks even when they were old enough to walk. Chicks that wandered away from their nests were attacked and sometimes killed by other protective nesting pairs. After four to six weeks, chicks ceased huddling together but were still dependent upon adults for food. At this point, before they fledged, chicks successfully begged food from their parental pair as well as from other adults.

The Stepwise Multiple Regression analyses indicated that, during the breeding season, the frequency of departures was most closely related to the abundance of nests ($r^2=0.317$, $p<0.001$) and juveniles ($r^2=0.237$, $p=0.003$). In the non-breeding season, the frequency of departures was most closely related to total abundance of cormorants ($r^2=0.078$, $p=0.025$).

The significant Year $\times$ Behavior interaction ($p<0.001$) from the log linear analysis indicated that the time allocated by Brandt's Cormorants to the three behaviors

varied among years. Alert was the predominant behavior through three years and became more important through time relative to preening. In 1994, Brandt's Cormorants were alert 45.3% of the time (preening=33.6%, resting=21.1%). In 1995, Brandt's Cormorants were alert 42.4% of the time (preening=32.7%, resting=24.9%). In 1996, Brandt's Cormorants were alert 48.6% of the time (preening=27.2%, resting=24.2%).

The proportion of Brandt's Cormorants performing individual behaviors increased through the three years. Of the 1545 resting cormorants observed, 20.3% occurred in 1994, 36.6% occurred in 1995, and 43.1% occurred in 1996. Of the 1986 preening cormorants observed, 25.1% occurred in 1994, 37.3% occurred in 1995, and 37.6% occurred in 1996. Of the 2970 alert cormorants observed, 22.7% occurred in 1994, 32.3% occurred in 1995, and 44.9% occurred in 1996.

The mean proportions of behaviors in relation to each other between non-breeding and breeding seasons varied. During the non-breeding seasons, Brandt's Cormorants rested 31.3% of the time, preened 36.4% of the time, and were alert 32.2% of the time. During the breeding seasons, this species rested 19.2% of the time, preened 27.0% of the time, and were alert 53.8% of the time.

DISCUSSION

Gaston and Nettleship (1982) suggested the number of seabirds in attendance at a colony during the breeding season is determined primarily by the availability of food in surrounding waters. Before this project began it was assumed that the colony at PLSR had been severely affected by food depletion as a result of factors associated with the 1992/93 ENSO event. Fewer than 10 individuals were observed on several occasions during the 1993 breeding season. Seabirds responded rapidly to the 1982/83 ENSO event, with reduced productivity in some species in 1982, almost all species in 1983, and marginal success and reduced numbers in 1984 along the coast of Peru and California (Barber and Chavez 1983, Schreiber and Schreiber 1984, Ainley and Boekelheide 1990). An apparent recovery of the PLSR colony began as environmental conditions returned to a satisfactory state for cormorant breeding. By 1996, the abundance of cormorants on Bird Island had more than tripled. The dispersal of Brandt's Cormorants during the non-breeding season of this species was evident during the fall and winter months because of their greatly decreased numbers during these months. Although there were fewer cormorants during the three non-breeding seasons compared to the breeding seasons, as the post-ENSO recovery proceeded, non-breeding abundances increased substantially.

Although Bird Island appears to have adequate space for increased numbers of breeding cormorants, a strict boundary was observed for the main colony. During 1994, nests were only within the bi-lobed (main) nesting area. Nests were evenly spaced but the majority were not within pecking distance of neighbors. This also was true for 1995, but in that second year of recovery a small, separate group (A) began breeding later than the main colony. By 1996, breeding numbers at PLSR had recovered to near maximum totals (Alan Baldrige, pers. comm.).

The main nesting area remained similar in size and shape to previous years as the density of individuals increased. Birkhead (1978) demonstrated that aggression increases with density and competition among guillemots (Uria spp.) and suggested selection will favor those individuals who return early and maintain nests throughout the breeding season. It appeared there was a point during the nesting period after which other potential nesters would not join the main group in deference to a smaller and similarly timed group. Also, a temporally and spatially similar formation can inhibit avian predators and scavengers from easily penetrating the colony (Siegel-Causey and Hunt 1986, Hill et al. 1997).

In the present study, breeding cormorants that arrived late at PLSR may have been faced with extreme aggression resulting in their expulsion from the main colony. Groups A

(1995), B (1996), and C (1996) were not restricted by lack of space but nested in small groups distinctly separate from the main colony. Locations of these outlying subcolonies differed in the two years. This fact may indicate the three groups were composed of different birds. Otherwise, one would expect the same birds to nest in similar areas at similar times from year to year (Leger and McNeil 1987). Siegel-Causey and Hunt (1986) indicated that different occupants of a colony may have enhanced reproductive success at certain regions within a nesting site. Boekelheide and Ainley (1989) showed Brandt's Cormorants have low site fidelity and poor synchrony. This may lead to random or varied sites for late nesters. The different nesting locations also may indicate that the first individual to initiate a later nesting pulse sets the timing and specific nesting site for the remaining late nesters.

Due to a mimicking behavior seen in immature Brandt's Cormorants, it was difficult to assess accurately the number of successful breeding birds. At the peak of the breeding season (i.e. most nests present) in July 1996, nest abundances varied between data collection days by as many as 140. Immature and unsuccessful mature adults created nest-like indentations in the substrate and gathered or stole nearby nesting material only to abandon the project within hours of beginning. This was observed several times during the study period. From the researcher's vantage point,

therefore, it was impossible to distinguish true nests from false nests during nest or behavioral assessment.

The total number of seabirds at any given time may have an effect upon the frequency of foraging flights (Evers 1994). The number of departures of Brandt's Cormorants from Bird Island was used as a measure of foraging behavior (Bernstein and Maxson 1985). Throughout the study, foraging frequency increased and decreased as birds gathered and dispersed according to season. This, like the synchronization of group nesting mentioned above, is indicative of group behaviors apparently due at least in part to the density of animals present. The total abundance of cormorants present on Bird Island helped explain 31.7% (with nests present) or 23.7% (with juveniles present) of the variability of departures during the breeding season. All other variables tested (number of nests, number of juveniles, and abundance of cormorants in main breeding area), regardless of season, were not significant factors.

Adult seabirds must travel increasing distances for food as colony size increases (Furness and Birkhead 1984). Direct observations of cormorants foraging from PLSR were difficult because foraging flights were varied and lengthy. The waters immediately surrounding the roosting site were rarely used for foraging by this species. The researcher suspected the waters near Carmel and west of the Monterey Peninsula, a few kilometers north, were where these birds foraged during the

summer. Greater than 90% of the time they returned to the island from that direction during the breeding season. Recent bird surveys of Monterey Bay indicate rare occurrences of foraging Brandt's Cormorants (Scott Benson, pers. comm.). Less than 10% of the time were cormorants observed returning to Bird Island from the south or west.

There was little relationship between departures and number of birds in the non-breeding season. Only 7.8% of the departure behavior could be attributed to the number of birds present on Bird Island. Obviously, other environmental or biological factors (e.g. weather, temperature, age or health of remaining birds, prey supplies) were important to the frequency of departures during the non-breeding season.

Seasonal variations in the activities of cormorants among the three years of study indicated distinct patterns. Regardless of the state of this colony's recovery from ENSO with respect to abundances of adults, nests and juveniles, the proportions of behaviors in relation to each other remained relatively constant. With the exception of the preening behavior in 1996, the three behaviors differed proportionally in the same order by approximately eight to twelve percent. Typically, more birds were alert than were preening and more were preening than were resting. This may suggest that a behavioral time budget is not influenced by environmental factors. Each behavior (alert, preening, resting) may be necessary to Brandt's Cormorants for a

certain amount of time per day. Evers (1994) suggested that by quantifying and establishing behavioral standards, subtle abnormalities can be detected to better manage populations.

As the recovery of the colony progressed, a density effect was evident in the form of an increase in behavioral activity (based on the total number of observations per behavior) during the three years. More birds resulting in more behaviors seems obvious, but, because the proportional data do not take number of birds observed into account, it was necessary to reveal the recovery of the colony in concert with behavioral patterns. Again, the preening behavior was the exception to the general trend. It may be that a certain density of individuals during the breeding season inhibited an increase in preening. This may be due to the necessity of incubation and rearing and the associated increased alertness. Preening may detract from these parental responsibilities and its frequency may not increase at the same rate as other behaviors. Roberts (1995) found that an increase in flock size resulted in a decrease in vigilance among terns because individuals benefit from the vigilance of others. The researcher, however, observed that throughout the breeding season, eggs, chicks, and nesting material are fiercely guarded by adult Brandt's Cormorants and that their vigilance was an important component. Alonso and Alonso (1993) found that Common Crane (Grus grus) parents also spent

less time resting and more time alert than non-breeding individuals.

During the non-breeding seasons, the frequency of the three behaviors was approximately equal. At this time of year competition is decreased due to a dispersed population and there is decreased demands of breeding. Such conditions may have lead to the equalization of individual behaviors. Maintenance behaviors (resting and preening) were observed more frequently, thus, allowing less time for other activities. Squires and Anderson (1997) reported that the Trumpeter Swan (Cygnus buccinator) slept 42% of the time during the winter as compared to 17% in spring. Similar results were found by Eberhardt et al. (1989) who discovered time spent resting and preening increased among Canada Geese (Branta canadensis moffitti) after juveniles fledged. Alertness may not be as important in the non-breeding season. With an increase in chicks and juveniles in the breeding season it seems likely that numbers of predators would also increase at that time as would the incidence of neighboring birds stealing nesting material, so vigilance may decrease naturally when the opposite is true.

Breeding responsibilities and increased densities appeared to have affected the daily activities of Brandt's Cormorants, such that birds were more alert and spent less time resting and preening than they did during the non-

breeding season. As the species gathered in the spring to begin nesting the same behavioral shifts seen in the recovery process became apparent.

Biases

The researcher tried to assess behavioral variations of Brandt's Cormorants in a quantitative manner. Biases are present to a certain degree in all behavioral studies, however, with strict definitions of behaviors these were greatly decreased.

Defined and specific behaviors were chosen for this project. The mobile lifestyle of Brandt's Cormorants and the researcher's inability to access their roosting site at Point Lobos required that the study be limited to highly observable behaviors.

Other notable biases are as follows.

1) Although most of the Brandt's Cormorants were visible at Bird Island the entire island was not. This may have skewed results if unseen birds were behaving differently than those in the visible portion of the island. The researcher expected this limitation to be minimal as the obscured portions of the island consisted of terrain generally unsuitable for this species.

2) The hours of observation on each of the data collection days was limited for reasons stated above. Long-term changes in behaviors was the focus of the study, but,

because a broad analysis of daily behavioral patterns was limited, a complete assessment was not achieved. It is likely, however, that the length of this study compensated for any variability within days.

3) The focus of the spotting scope was not able to be trained exactly according to the random numbers generated. The distance from the roosting site made approximations necessary. When approximations are made, biases are more likely to occur. This difficulty was minimized by the fact that the researcher was the only one to position the scope.

4) Although a quick quantification of roosting site behaviors was attempted, some birds did alter their behavior before all birds within the spotting scope view could be assessed. This occurred infrequently and was assumed to be insignificant.

5) Overlap of randomized spotting scope views also occurred infrequently. Less than ten percent of these views included the same individuals in the same 30 minute roosting site survey. Even if overlap did occur, results would not be greatly affected due to the natural variability of behaviors in seabirds.

Conclusion

Populations of animals, marine or otherwise, are often altered or devastated due to environmental extremes.

Abundance patterns are important in assessing the effect of these extremes. In addition to abundance patterns, activity patterns may also be important in the prediction and explanation of behavioral variations due to catastrophic events.

This study revealed a strong response by Brandt's Cormorants to the ENSO event of 1992-94. Abundances were decreased throughout the breeding and non-breeding seasons and remained less than historical norms until the third year of recovery. Similar numerical responses were observed in numbers of nests and juvenile cormorants. Acceptable climatic conditions and the subsequent return of adequate food resources were assumed to be responsible for the colony's recovery.

No significant behavioral variations resulting from the ENSO event were detected among Brandt's Cormorants. This suggested there was little or no link between environmental factors and the behavioral time budgets of Brandt's Cormorants.

There were differences detected in the amount of time cormorants performed certain behaviors between the breeding and non-breeding seasons. These did not appear to be the result of environmental changes but rather were likely associated with natural and predictable breeding patterns.

Figure 1. Point Lobos State Reserve including Observation Site and Bird Rock

Figure 2. Number of Brandt's Cormorants present (Total Island) and main Nesting site (Main Colony) on Bird Rock at Point Lobos State Reserve for Duration of study (July, 1994 to December, 1996).

Figure 3. Number of Brandt's Cormorants nests and juveniles on Bird Rock at Point Lobos State Reserve for duration of study (July, 1994 to December, 1996).

Figure 4. Location of main colony of Brandt's Cormorants and three peripheral colonies (A, B, & C) for three years, 1994-1996, at Bird Rock Island.

Figure 5. Proportions of Roosting Site Behaviors: (A) proportions of behaviors (B) proportions of behaviors per number of observations (C) proportions of behaviors per season

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IMAGE EVALUATION TEST TARGET (QA-3)

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