

NESTING ECOLOGY AND ONTOGENY OF HATCHLING NEOTROPIC
CORMORANTS (*PHALACROCORAX BRASILIANUS*)

THESIS

Presented to the Graduate Council of
Southwest Texas State University
in Partial Fulfillment of
the Requirements

For the Degree

Master of Science

By

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San Marcos, Texas
May 2004

ACKNOWLEDGEMENTS

I would like to begin by thanking my parents, Jane and David Bock, for providing both emotional and financial support during this project. I would also like to thank the members of my thesis committee for their time and help. Dr. Huffman's assistance in particular has been invaluable. Dr. Simpson answered many questions for me, and displayed a great deal of patience with me as I groped my way towards the completion of this work. Patience was also among the many virtues displayed by Dr. Baccus. I would like to thank Winnie Burkett for allowing me to have access to the rookery on a daily basis, and for providing me with housing. Finally, I would like to thank the birds at the rookery for sharing their lives with me, and for adding a little wonder and beauty to the world.

This manuscript was submitted on April 22, 2004.

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ABSTRACT

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The Neotropic Cormorant is one of the most widely ranging members of its genus. The justification of lethal control of piscivorous birds to protect fisheries requires a firm understanding of the population status and dynamics of the problem species.

The nests of 7 pairs of Neotropic Cormorants were observed to determine: parental behavior when adding material to the nest; parental behavior prior to and during hatching; brooding behavior; number and duration of feeding intervals and how the age of chicks affects these numbers; behavior of chicks during feeding and how hatch order and age affect this behavior; and interaction among chicks in the parents' absence.

Incubating adults became agitated a few hours prior to the hatching of each egg. Eggs hatched 1 to 2 days apart. Adults removed eggshells after hatching. Brooding continued without a break after hatching for several days. Parents took turns brooding

the chicks. Nest repair occurred frequently in the first 2 weeks after hatching, then ceased.

The number of feeding intervals per observation period ranged from 0 to 4. There was a general trend for feeding intervals to increase in frequency after sunrise until the peak in feeding activity at 3 to 4 hours after sunrise. The number of feeding attempts per feeding interval ranged from 1 to 11, with a mean of 2.18. The highest number of feeding intervals per day occurred 1 or 2 days after hatching, with the number of feeding intervals decreasing steadily until fledging. The mean number of feeding attempts per feeding interval also declined as the chicks aged. The latest observed feeding occurred on day 60.

Most chicks fledged 47 days after hatching. The mean number of chicks fledged per nest was 2.71. No chick or adult mortality was observed.

INTRODUCTION

The Neotropic Cormorant [*Phalacrocorax brasilianus* (Gmelin, 1789)] ranges northward from Tierra del Fuego, to the coasts of Texas and Louisiana where it reaches its northern-most and densest North American breeding concentration. It is one of the most widely ranging members of the genus, inhabiting areas near coastal waters, marshes, lakes, and mountain streams from sea level to 4,419 m.

Adult Neotropic Cormorants are black with a slight olive gloss on the back and wings. The dull yellow throat pouch is small for the cormorant family, and develops a white border in the breeding plumage. Irises are emerald green in adults. There is no sexual dimorphism (Palmer, 1962; Morrison, 1977; Tveten, 1993).

Breeding is restricted to coasts, lakes, and reservoirs. There is a prolonged breeding season in Texas, with egg-laying occurring from early February to mid-October and peaking in April (Palmer, 1962; Morrison, 1977; Morrison et al., 1979). These cormorants prefer to nest in small trees, and often share rookeries with Roseate Spoonbills [*Ajaia ajaia* (Linnaeus, 1819)] and various species of herons, egrets and ibises. When an intruder disturbs the rookery, Neotropic Cormorants form rafts on nearby water and slowly return to the rookery. The presence of spoonbills modifies this reaction by causing the cormorants to return the nest more quickly (Morrison, 1978; Telfair and Morrison, 1995).

Clutch size ranges from 1-4 eggs, with a mean of 2.87 eggs. Eggs are laid at 2-day intervals with incubation beginning after the second egg is laid. Eggs hatch asynchronously, leading to variation in sizes of nest mates. The smallest hatchling usually dies within a few days of hatching, as a result of crushing, selective starvation, or eviction from the nest (Morrison et al., 1979).

Adults leave the rookery to forage during the first half hour after dawn and usually satisfy their own caloric needs before returning to the nest to feed hatchlings. There are no reports of cormorants having been observed feeding at night (Morrison, 1977).

Although the Neotropic Cormorant is one of the most widely distributed of the cormorants, many aspects of its life history are poorly known, and Morrison's (1977) study was the first to document their breeding biology. Because few studies have been conducted, many aspects of the breeding biology of Neotropic Cormorants remain unclear. Little mention of brooding or feeding intervals occurs in the literature, and no reports on parental behavior prior to and during hatching are found.

More information is available for other cormorant species. Other cormorants do not exhibit parental assistance during hatching, and eggshells are tossed over the side of the nest (Telfair and Morrison, 1995). Dunn (1975) observed fewer feeding attempts as the chicks of Double-crested Cormorants [*Phalacrocorax auritus* (Lesson, 1831)] grew older and accepted whole fish. She also observed the behavior of Double-crested Cormorant chicks during feeding. Younger chicks stimulated feeding by peeping and

uncontrolled head waving. Older chicks had a hoarser voice and stood and waved their bill back and forth (Dunn, 1975).

Cormorants have been associated with avian predation at fish farms in the United States. The aquiculture industry has responded by a number of methods, including roost harassment and lethal control. However, a firm understanding of the population status and dynamics of the problem species is required to justify lethal control of vertebrate pests (Blackwell et al., 2000).

My study extended the research conducted by Morrison (1977). My objectives were based on his recommendations for further research, as well as suggestions offered in *The Birds of North America* (Telfair and Morrison, 1995). My study was conducted to provide information regarding:

- (1) behavior of parents when adding material to the nest;
- (2) parental behavior prior to and during hatching;
- (3) the effect of chick age on brooding behavior;
- (4) number and duration of feeding intervals;
- (5) feeding behavior of chicks and how hatch order on this behavior;
- (6) interaction among chicks in the parent's absence.

METHODS AND MATERIALS

Study Area — High Island, Chambers County, Texas, located about a kilometer from the Gulf of Mexico, rests atop a giant salt dome, which elevates it 9.75 m above the surrounding coastal prairie (Fig. 1). Soil conditions in the area favor the growth of trees, which attract birds migrating across the Gulf of Mexico. The Houston Audubon Society operates 2 bird sanctuaries in High Island; Boy Scout Woods and Smith Oaks.

The rookery used in the study area was located on Heron Island in Clay Bottom Pond, at the Smith Oaks Sanctuary (Fig. 2). The rookery was used by a large number of Neotropic Cormorants. The rookery was used for nesting by Boat-tailed Grackles [*Quiscalus major* (Vieillot, 1819)], Snowy Egrets [*Egretta thula* (Molina, 1782)], Cattle Egrets [*Bulbulcus ibis* (Linnaeus, 1758)], Great Egrets [*Ardea alba* (Linnaeus, 1758)], Little Blue Herons [*Egretta caerulea* (Linnaeus, 1758)], Tricolor Herons [*Egretta tricolor* (Müller, 1776)], Black-crowned Night-Herons [*Nycticorax nycticorax* (Linnaeus, 1758)], Roseate Spoonbills, and White-faced Ibis [*Plegadis chihi* (Vieillot, 1817)]; as well as Neotropic Cormorants. American alligators (*Alligator mississippiensis*) living in the freshwater pond protected the rookery from terrestrial predators, but also fed on any chicks which fell from the nest. The area has been popular with birders, and at least 1 group came to observe and photograph the rookery each day. The birds showed no reaction to observers.

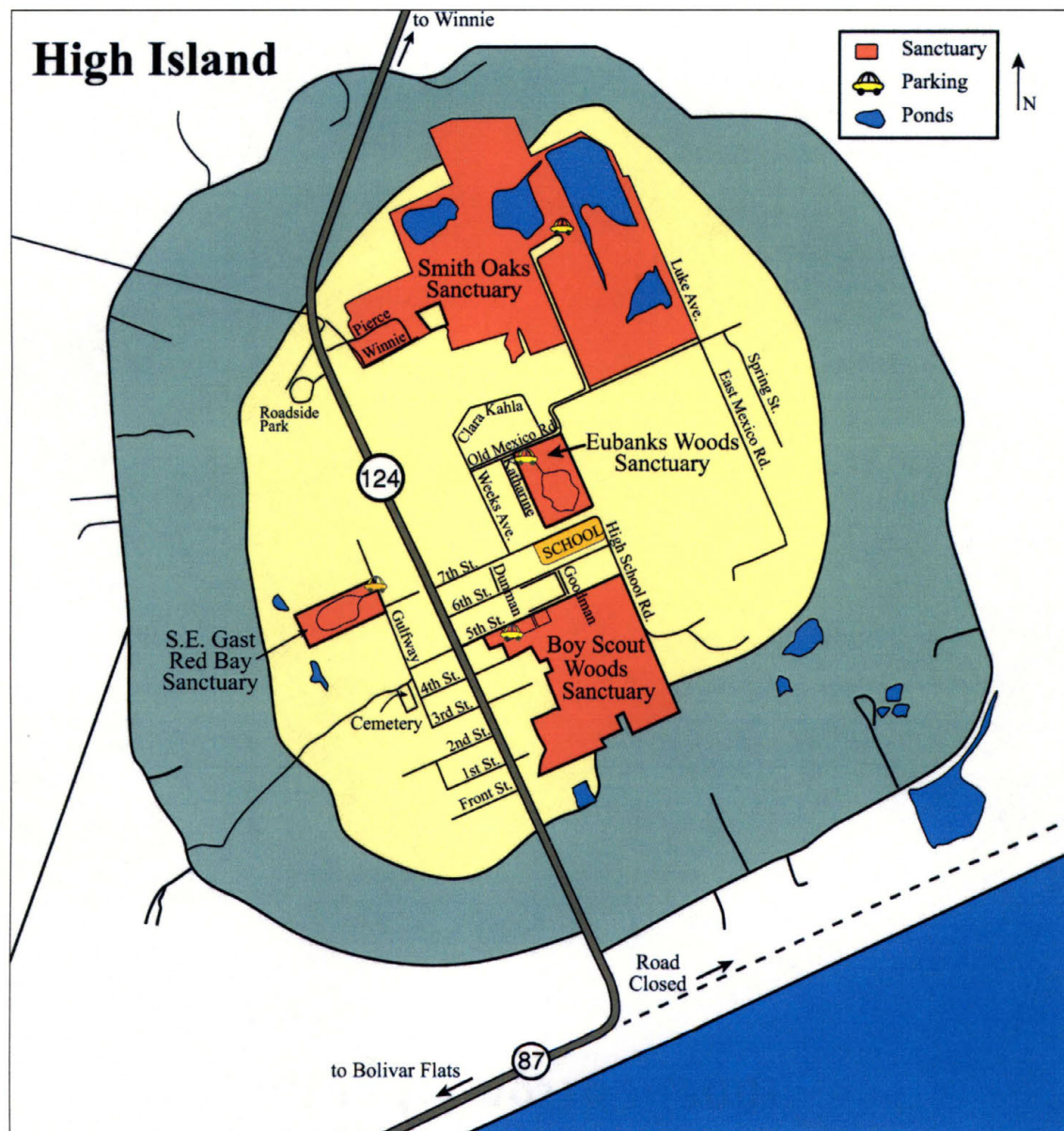


Fig. 1. Map of High Island, Chambers County, Texas 2002

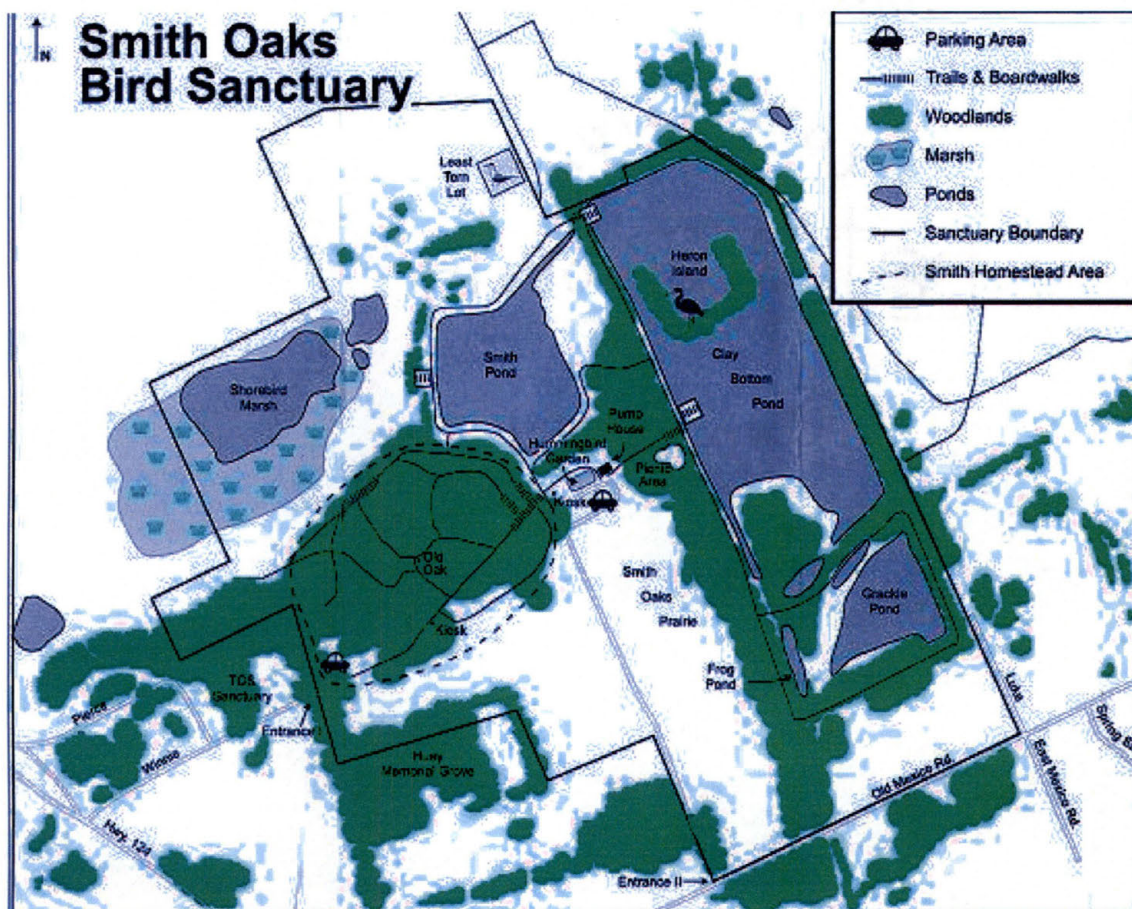


Fig. 2. Map of Smith Oaks Bird Sanctuary, 2002, showing the island upon which the rookery is located.

Data Collection — I spent 4 hours a day observing 7 nests in the rookery at Smith Oaks, High Island from May 9 2002 to July 17 2002. All 7 nests were observed continuously and simultaneously during each 4-hour observation period from the same location. Observations were conducted from a bench situated on a dike slightly higher than the nests and about 9 m east of the island using 8x42 Bausch and Lomb binoculars. I staggered the hours of observation to include morning, noon and evening. Observation began at 0600 h on the first day and ended at 1000 h. I delayed the beginning of each observation period by 1 hour each day until the observation period began at 1600 h and ended at 2000 h. Observations then began at 0600 h again. I collected data on the number of adults and chicks present and the duration of all recorded behaviors. Behavioral information included feeding intervals and feeding attempts, nest repair, incubation and brooding, and aggression and begging among the chicks. Brooding sessions were defined as the time one adult began brooding until the time it was relieved by its partner. I defined a feeding interval as the time during which the adult engaged in frequent (near continuous) feeding attempts. Each time a chick's head was inserted in the adult's mouth was counted as a feeding attempt. I also recorded changes in the chicks' behavior and appearance with age. I spent an additional 3 hours observing the early stages of nest construction on 12 March 2003. I observed brooding, feeding, and standing adults as well as chicks in nests. Any adult observed brooding or feeding at a nest was considered to be a parent of that nest. Chicks were considered fledged at their first observed flight away from the rookery.

Nests I observed during the study were of various ages. Three of the 7 nests were still in incubation at the start of the study. Nests 3 and 7 hatched on the second day of the study, and Nest 2 hatched 5 days after the study started. Nest 8 was not located until a few days after hatching. The other three nests contained chicks about 2 weeks old at the start of the study. Because of this variation in the ages of the chicks, I analyzed data by days from fledging rather than by days of age. Nest 4 was unusual, because an adult or former fledgling sometimes sat among the chicks and was occasionally fed, and so Nest 4 was excluded from analysis of feeding.

Simple linear regression was used to describe the pattern of change in number of feedings and number of feeding attempts per trip as the chicks aged.

RESULTS AND DISCUSSION

Nest Structure and Placement — Nest structure and location, as well as behavior of adult birds, determine the risks of predation and predation is the primary cause of nest failure (Gill, 1989). Vermeer (1969) found all colonies of Double-crested Cormorants were located on islands. The High Island rookery offered cormorants protection due to inaccessibility, safety in the numbers of a large colony, and protection from terrestrial predators provided by the alligators in the waters around Heron Island. The only avian predators nesting in the rookery at High Island were Grackles and Black-crowned Night-Herons. The latter were observed taking an occasional chick from other species in the colony, but not from cormorant nests.

Cormorant nests in the High Island rookery were placed in Chinese tallow and yaupon trees. Morrison (1977) saw Neotropic Cormorants nesting in Chinese tallow, but I am unaware of records of them nesting in yaupon. Nests were located in the forks of tree limbs, mostly in the upper one-third of trees. Nests were often placed near other cormorant nests of a similar age. Vermeer (1969) found nests of Double-crested Cormorants were in contact with each other. This may have allowed adults to share the duties of nest protection, or it may simply have been the result of concurrent onset of breeding times and limited space in the rookery.

Nests were constructed of large twigs. The nest design, a simple platform with raised rims (Fig. 3), seemed adequate to prevent chicks from falling from the nest. The observed nests under construction in the early spring of 2003 were lined with pine needles.

Adults occasionally were observed adding green vegetation to their nests. Some ornithologists think this may combat disease and ectoparasite infection (Gill, 1989). All materials used for nest repair were carried in the beak; presumably materials for nest construction also were carried in this manner.

The rookery was used for nesting by many species, including Roseate Spoonbills. Morrison (1978) observed Neotropic Cormorants nesting near Roseate Spoonbills and other species of herons, egrets and ibises.

Brood Size — Broods which had hatched prior to 9 May contained 2 chicks when my study began. Subsequent broods had 3 chicks each. Kalmbach et al. (2001) reported a mean brood size of 3.1 and 3.0 respectively for Neotropic Cormorants nesting at the same site in Chile for 2 consecutive years (Kalmbach et al., 2001). Morrison (1977) reported a mean brood size of 1.65 for Neotropic Cormorants nesting on Sydney Island, Texas. It is possible that the difference in brood sizes between my study and Morrison's (1977) were due to a difference in food availability. High water may have contributed to poor hunting success during Morrison's (1977) study, and deterioration of the food supply can be compensated for by a decrease in clutch size, or by reduction of the brood size by selective starvation (Morrison, 1979; Ricklefs, 1968).



Fig. 3. Photograph of a Neotropic Cormorant nest in the High Island rookery.

However, Kalmbach et al. (2001) found that clutch and brood size were not reduced in Neotropic Cormorants because of poor feeding conditions (Kalmbach et al., 2001). If the difference in brood size between Morrison's study on the one hand, and my study and Kalmbach's on the other hand was not due to differences in food availability, then it may have been due to weather-related factors. However, it is noteworthy that Morrison (1977) repeatedly disturbed the nesting birds in his study by climbing the trees. This most likely had some detrimental effect on nesting success in his study, and could have been responsible for the observed difference.

Hatching — Vocalizations from within the egg probably alerted the adults to the imminence of hatching, as the incubating adult became agitated a few hours prior to the hatching of each egg. Behaviors observed during this time included preening, moving around on the nest, pecking at the nest bottom, turning, looking under itself, and frequent flapping of wings. Near the time of hatching, both parents sometimes stood on the edge of the nest, and peered into the nest, and often put their heads into the nest. My study was the first to document that, as in other cormorant species, there was no parental assistance during hatching, and eggshells were tossed over the side of the nest (Telfair and Morrison, 1995).

Eggs hatched 1-2 days apart, as reported by Morrison (1977). Asynchronous hatching may be an adaptation to breeding under uncertain feeding conditions. In asynchronously hatching species, the normal clutch size is likely to be larger than that which the adults can raise in an average year, with the extra eggs only resulting in

fledglings when feeding conditions are good (Lack, 1954). Morrison (1977) reported nests with more than 2 eggs produced 2 chicks of similar size, while the remaining chicks were substantially smaller. This difference in size is important, as the smallest chick in the brood usually dies within a few days of hatching due to starvation or crushing by nest mates (Morrison, 1977). Although the oldest chick in each nest was distinguishable for a brief period after hatching because of size differences, nest mates in my study rapidly became indistinguishable. Amundsen and Stokland (1988) found that the size difference in asynchronously hatched Shags [*Phalacrocorax aristotelis* (Linnaeus, 1761)] decreased as the chicks aged, and concluded that their study had taken place during a year when feeding conditions were good (Amundsen and Stokland, 1988). Differences in food availability during Morrison's (1977) study and this study likely accounted for the differences in the sizes of chicks between the 2 studies.

Nest Repair — Nest repair occurred frequently in the first 2 ½ weeks after hatching, then ceased about 6 to 8 days before chicks began to leave the nest for nearby branches. Nest repair probably reduced the risk of chicks falling from the nest, and became unnecessary when chicks left the nest. The 24 observed instances of nest repair occurred either when the mate brought twigs to the brooding parent, or when the brooding parent rearranged the placement of twigs in the nest. At no time did a brooding adult leave the nest to find materials for nest repair. During the day, adults frequently returned to their nests to bring the brooding mate twigs for nest repair. When the partner brought a large stick to the nest, both adults attempted to place the stick in the nest at the

same time. Although no ceremony was observed at these times, it is possible that some of this behavior was a displacement activity.

Many species of birds exhibit nest building behavior as a part of nest relief. In Herring Gulls [*Larus argentatus* (Pontoppidan, 1763)] the relieving bird may bring nesting materials, especially when the partner is not willing to leave. The relieved bird may also bring nest material, sometimes even collecting it a considerable distance from the nest and bringing a load to the nest more than once (Tinbergen, 1952).

The frequency of nest repair varied greatly among nests, with 13 of the observed occurrences at Nest 2, 8 at Nest 7, 2 at Nest 4, 1 at Nest 3, and none at Nest 8. All observed nests were totally destroyed about the time chicks began to fly away from the rookery. Although observations did not reveal the fate of nests, it is likely that other birds in the rookery may have robbed twigs from the abandoned nest to repair their own nests.

Brooding — A lack of sexual dimorphism in adults of the species prevented a determination of brooding time by sex. However, each parent spent some time incubating eggs prior to hatching, and both parents alternated brooding the chicks. Double-crested Cormorant males and females also share incubation duties (Morrison et al., 1979). The shortest observed brooding session lasted 19 minutes. I observed 13 brooding sessions that lasted longer than the 4-hour observation period.

The Neotropical Cormorants in my study appeared to exhibit a nest relief ceremony. During typical incubation and brooding switches, the incoming adult perched next to the nest. Both birds then stretched their necks towards each other and waved their

heads; often bumping their bills together, before switching places. The departing partner then left the nest and the incoming partner, perched on the edge of the nest, then scooted forward into the nest. This ceremony may have allowed brooders to recognize their partners or to maintain the pair bond. Many species, including Brown Pelicans [*Pelicanus occidentalis* (Linnaeus, 1766), terns, herons and cranes exhibit nest-relief rituals (Welty and Baptista, 1988).

Of 31 observed brood changes, most took less than a minute from the arrival of the returning parent to the departure of the relieved parent (Fig. 4). In sessions lasting more than a minute, the additional time was spent by the outgoing adult perched on a branch near the nest for periods ranging from a few minutes to about an hour.

Brooding ceased when chicks were between 4 and 10 days of age. Nest 8 was brooded continuously for 4 days; Nest 3 was brooded continuously for 4 days with a final brooding session on day 10, Nest 2 was brooded continuously for 10 days and Nest 7 was brooded continuously until day 6, with a final session on day 7 after 1630 h. The mean duration of continuous brooding was 6 days after hatching.

During the first week or so chicks are unable to regulate their body temperatures and need near constant brooding or shading from parents. After this time, the chicks can thermoregulate. Temperature regulation improves during development because of increased mass relative to surface area, improved insulation, increased metabolic heat production, and the development of nervous and endocrine system control (Gill, 1989).

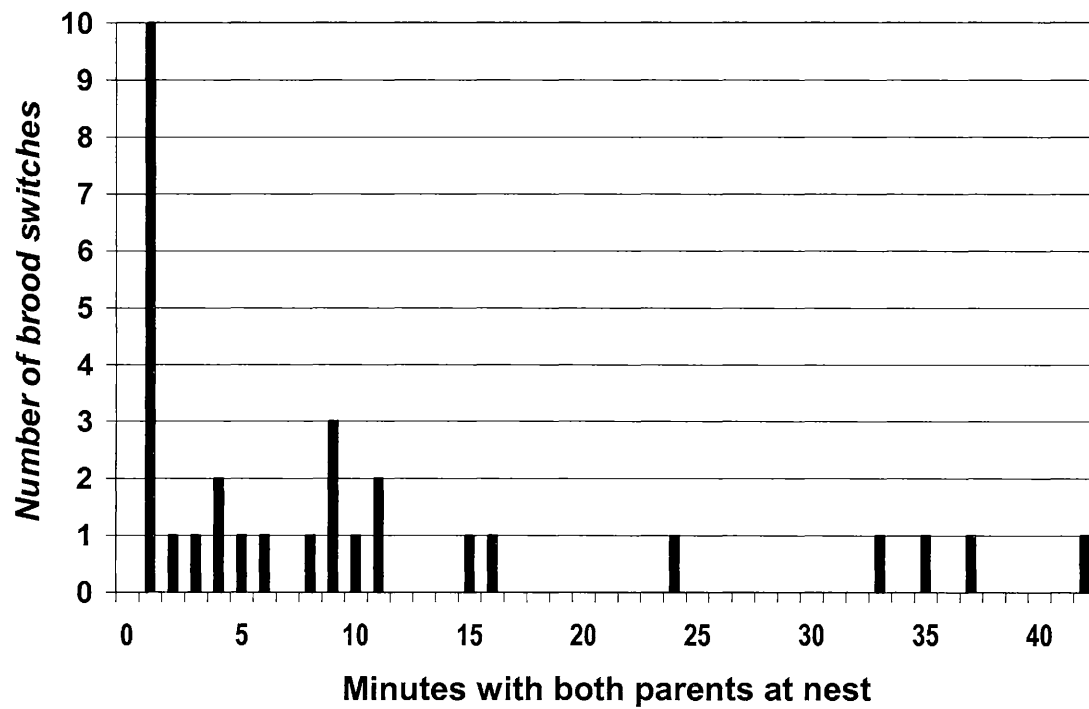


Fig. 4. Amount of time during which both parents were present at the nest during brood switches.

Nest 2 was brooded 10 days; perhaps the chicks were slow to develop thermoregulatory abilities because of a lack of food, genetic causes, or some other reason. Adults tended to stay near the nest or perched on the rim of the nest for several days after brooding ceased, with nest attendance lasting a mean of 12 days after hatching. Nest attendance likely discouraged avian predators using the rookery from feeding on chicks. Both partners took turns in this nest guarding. Changes in the brooding or guarding adult were commonly followed by a feeding of chicks. The returning adult fed the chicks within 10 minutes of arriving at the nest in 23 of 31 observed changes.

Plumage and Development of Chicks — My study contributed substantial information on the growth of Neotropic Cormorants. Prior to my study there was no information on the colors and development of bill, iris, gular pouch, legs and feet of hatchlings (Telfair and Morrison, 1995). Little was known about the development of the juvenal plumage. I could find no information about changes in the beak, feet, and legs of Neotropic Cormorants. As the chicks aged they exhibited behaviors requiring an escalating amount of muscular development and control. I could find no literature regarding these stages of development in the Neotropic Cormorant, however some information is available for other cormorant species. All descriptions of development were based on the most advanced chick in each nest and were based only on nests for which the exact age was known. A summary of these developments are listed in Table 1.

Chicks hatched naked, with grayish-pink skin. The first natal down was gray and became apparent during the first day after hatching.

Table 1. Days of age at which certain developmental milestones occurred in Neotropic Cormorant chicks.

Behavior	N2	N3	N7
Can insert head into adult's beak	2	2	2
Body covered in down	2	2	2
Able to orient on parents	3	3	2
Able to walk in nest	8	6	6
Back to edge of nest to defecate	9	12	unknown
Last nest repair	18	1	14
Last day of continuous brooding	10	4	6
First wing flapping	21	20	26
On rim of nest	11	7	21
Out of nest	28	33	23
First practice flight	33	32	31
First chick fledged	50	42	49
Second chick fledged	52	42	53
Third chick fledged	53	43	55

Chicks hatched with a triangular bill, which was yellow with a black smudge on the tip. The gular pouch was straw yellow, but appeared pinkish because of blood vessels under the skin. The eyes of chicks were closed on hatching.

The eyes opened the second day after hatching and had black or dark-brown irises, which remained this color through fledging, as in other cormorants (Telfair and Morrison, 1995). The age at which iris changes color to the emerald green of adults remains unknown.

During the day of hatching, chicks were unable to orient to their parents, only waved their heads feebly and could not raise their heads very far above their bodies. Similarly, newly hatched Shag chicks are only capable of raising and waving their heads (Snow, 1960). At this point, begging consisted solely of the chick waving its head back and forth. Chicks were fed a liquid dripped down from the parent's beak during the day they hatched.

By the first day after hatching, or day 2, wooly, dark-gray natal down covered the entire body except for the gular pouch and the capital pterylae of the head. This down developed sooner than Double-crested Cormorants, which develop a full covering of down after 2 weeks (Palmer, 1962). The skin of the capital pterylae remained bare and pinkish, gradually diminishing in size until it disappeared around the eighth day after hatching, leaving a gray patch of bare skin on the forehead. The pharyngeal pouch was straw yellow as in other ages, but appeared pinkish in light because of blood vessels under the skin. By the second or third day after hatching, head waving was more

energetic, and chicks could insert their heads into the parent's mouth, orient on parents, and inflate the pharyngeal pouch. These developments may have occurred rapidly to allow the chicks to more effectively stimulate the adults to feed.

Chicks pecked at each other occasionally and had developed a long, hooked bill, similar to adults by day 3.

By day 5, the gular pouch was still bare and the culmen had become black. Chicks could stretch their necks to full length and hold their heads high above the nest for considerable lengths of time when begging.

On days 6 to 8, the chicks could move their wings and walk in the nest, although they appeared clumsy. The down on the head was gray; the down on the body was nearly black.

Between days 7 and 21 the chicks perched on the side of the nest and moved around the nest more easily, even climbing over siblings. The oldest chick could walk over the others when begging.

By day 8, the bald spot had vanished, leaving a gray area of bare skin above the beak. This skin remained bare until about the fortieth day after hatching, although the bare area shrank steadily. The upper mandible was entirely black, while the lower mandible was yellow.

Chicks backed to the rim of the nest to defecate over the rim by days 9 to 12. This behavior had not been reported before, and must have contributed to keeping the nest clean.

Their down was completely black, and the bare area on the forehead was large and gray.

Between days 10 and 12, 1 row of remiges developed along the trailing edge of each wing and stubby rectrices appeared. The rectrices gradually lengthened, until they achieved the adult length at around day 31 or 32 after hatching. Chicks began sitting on the rim, and spent considerable time on the rim of the nest from this point, returning to the interior of the nest only to sleep and feed. The chicks could flap their wings feebly, but could not hold them out straight (Fig. 5).

By day 13 or 14, rectrices were about 2.5 cm long. There was still only 1 row of remiges on the trailing edge of wings, but the feathers were longer and more visible. The chick's ventral feather tracts were downy. The lower mandible was yellow with a black tip and legs and feet were gray. By this time, the chicks had grown quite large, although they were still much smaller than adults.

Bare patches began to appear on the chick's ventral feather tracts by day 16, although they were still mostly downy. The ventral feather tracts became progressively more bare until the nineteenth or twentieth day of age, when they were almost totally bare. The skin on the belly was pink. The upper mandible was black; the lower was yellow with a black tip.

At 17 days after hatching, the chicks could move their tails and hold their wings straight. A row of feathers was barely showing along the humeral pterylae. Chicks were about 2/3 adult size.



Fig. 5. Early wing flapping behavior in a Neotropic Cormorant chick, demonstrating that the wings are not held straight.

By day 18 to 19, a second row of remiges had developed along the alar feather tract, although the feathers looked ragged. The rectrices were 1/5 of the adult length.

On day 19 or 20, two rows of feathers existed on the leading and trailing edges of the wing with a downy strip between, the bare area under the throat was white, and the feet were chalky gray.

Between days 20 and 28, the chicks began flapping their wings vigorously. The first of these exercises in Nests 2 and 7 occurred during a strong gust of wind, which seemed to cause chicks in the rookery to do the same. Wing flapping may have allowed chicks to develop muscles necessary for flight. It might also have helped them to balance during high winds.

By day 21, the first 2 rows of remiges on the alar feather tract were well defined, with a third row just starting to show. The 3 rows of remiges on the alar feather tract became better defined by day 22.

There were three 3 rows of ragged looking remiges on the bottom of the wing by day 23. The bare area on the forehead was still large. The chicks had down on their dorsal pterylae between the wings. Chicks moved out onto branches near the nest by day 23-33. Double Crested Cormorant chicks began venturing beyond the rim of the nest after the third week (Drent et al., 1964).

On days 25 and 26, the bare area on the forehead was still present but receding in size, the wing feathers looked ragged, and the tail was 1/4 adult length. The dorsal pterylae were still downy.

By day 27, the belly was partially feathered and rectrices were 2/3 of adult length.

By day 28, although the chick's dorsal tracts were downy, their wings were fully feathered, the ventral feather tracts were fully feathered although still sparse, and the tails were 1/3 adult length. The chicks still appeared clumsy as they moved about on the branches. Their feet were light gray.

By day 31, the tail had nearly reached adult length, the dorsal tract was feathered, and the chicks still had a gray bare area on the foreheads. Chicks began making practice flights around the rookery by day 31-33. Double Crested Cormorant chicks on Mandarte Island began to make short flights around the colony at 5-6 weeks of age (Drent et al., 1964).

By day 32, the chicks had attained adult characteristics except for a small bare area on the forehead and gray feet and legs.

On days 33 through 40, the skin began peeling on the bare area on the forehead, beak and feet. At the end of this period, the bare area on the foreheads had vanished and the feet were dark gray, although not as dark as those of adults.

By days 42-50, chicks began flying away from the nest, although still fed by the parents at the nest site. Similar lengths of time from hatching to fledging have been reported for many other cormorant species. White-breasted Cormorants [*Phalacrocorax carbo* (Linnaeus, 1758)] were capable of flight and began feeding on live fish at 45-48 days of age (Du Plessis, 1957; Junor, 1972). The juvenile plumage of Double-crested

Cormorants disappeared and chicks begin to leave the colony after the sixth to seventh week of life (Drent et al., 1964). Shags fledged at 48-58 days (Snow, 1960).

Most chicks fledged around 47 days after hatching; however chicks at Nest 3 began fledging earlier at 42 days. Within a brood, there tended to be a 1 to 2 days difference between the dates at which chicks began to fly from the rookery. This was probably due to the 1 to 2 days delay between hatching. Some nests had unfledged chicks for up to 6 days after the first chick fledged. A fledging time of 47 days was a much faster average development time than the 77 days reported by Morrison (1977) for *P. brasiliensis*. Individuals within a species can exhibit markedly different growth rates as a result of variations in quality and quantity of food, temporal pattern of feeding and temperature (Gill, 1989). Morrison (1977) conducted his study near High Island and at a similar time of year, so seasonality and location cannot account for the observed differences in rate development. High water levels may have decreased the cormorant's hunting abilities during Morrison's (1977) study and this difference in food availability may have delayed the chicks' fledging. The maturation rate of some species can be greatly influenced by the availability of food. The maturation of Common Swifts [*Apus apus* (Linnaeus, 1758)], for example, varies from 35 to 56 days based on feeding conditions (Gill, 1989).

Neotropic Cormorants developed full Juvenal plumage faster than Double-crested Cormorants, which require 58 days (Palmer, 1962). This quicker development may have been due in part to the Neotropic Cormorant's smaller size. The fledgling plumage

resembles that of the adult, except that the feet and legs were not as dark as the adults. I was unable to determine anything about plumage characteristics beyond this point.

By day 58, the nests had either been reduced in size or destroyed.

The last observed feeding of a chick by an adult in the rookery occurred at 60 days, at least 8 days after it fledged. This was a fairly lengthy period of reliance on adults. Although the young of large species usually require more time to reach adult size than smaller species, young fed by their parents tend to develop faster than those that feed themselves (Ricklefs, 1968). The relatively long growth periods of some species, especially those nesting on oceanic islands or in protected areas, can be attributed to the relative freedom from predation (Ricklefs, 1968).

Thermoregulation — Although other species using the rookery shaded their eggs or chicks during the hottest part of the day by standing with their wings spread over the nest in such a way as to cast a shadow onto the nest, and Telfair and Morrison (1995) observed shading in Neotropic Cormorants, I never observed cormorants shading their nests.

During hot periods of the day, chicks thermoregulated using gular fluttering, the rapid vibration of the hyoid muscles and bones in the throat, which increased the rate of evaporative heat loss from the lining of the mouth and throat. Similar behavior has been reported in White-breasted Cormorant chicks (Du Plessis, 1957; Gill, 1989). This form of temperature regulation may have been especially important to Neotropic Cormorant chicks because of the absence of parental shading.

Watering behavior, the transfer of water from the adult to the chick, occurs in Double-crested Cormorants and in Southern Cormorants, but is fairly uncommon and tends to occur in only a few members of the colony (Madsen and Sparch, 1950; Kuiken, 2001). Watering behavior had not been reported in Neotropic Cormorants prior to my study.

Most observed episodes of watering occurred during the hottest part of the day from 1200 h until around 1430 h, when many cormorant chicks in the colony were engaging in gular fluttering. I observed 1 episode at 900 h. Watering may have helped to replace water lost to evaporative cooling during gular fluttering. The parents of Nest 2 brought water to the nest on 8 occasions from 25 May to 14 June. Watering sometimes occurred in response to begging by the chicks. Double-crested Cormorant chicks beg for water by waving their heads with the bill open and tilted upwards. This differed from begging for food where the bill was closed when begging for food (Kuiken, 2001). Southern Cormorants [*Phalacrocorax carbo sinensis* (Linnaeus, 1756)] spray water over the nest until the chicks open their mouths to receive the water directly while Double-crested Cormorants insert their heads into the chick's mouths in response to begging (Madsen and Sparch, 1950; Kuiken, 2001). Neotropic Cormorants appeared to incorporate both of these behaviors. Although adults sometimes simply spit a stream of water onto the nest and chicks, at other times water was directly transferred into the chick's mouth. At these times the adult gently placed its beak inside the chick's beak and dripped water into its mouth. This differs from feeding behavior, during which the chick

had its entire head down the adult's throat. The differences between feeding, and watering behavior may explain the differences between chick behaviors prior to watering versus feeding. I saw Neotropic Cormorant chicks accepting water in a different way from that of food acceptance, but did not note a difference in begging behaviors.

Nest 2 was the only nest in which watering behavior was observed. The reason why Nest 2 was the only nest in which watering occurred is unclear. Several other nests had equal exposure to sunlight. Watering behavior occurred while chicks were between 10-30 days old and began around the time when brooding ceased. In the last observation of watering, the chicks returned to the nest from nearby branches to receive the water (Table 2). Kuiken (2001) observed Double-crested Cormorants watering their chicks from 14 to 28 days of age. It is not clear why watering began and ceased at these ages. Perhaps shade from the brooding adult protected chicks younger than 10 days of age from the sun.

Behavior of Chicks — During the parents' absence, chicks slept or remained still in the nest. Similar behavior occurred in young White-breasted Cormorants (Du Plessis, 1957). Occasionally, younger chicks briefly pecked at each. I observed 2 instances during which one chick appeared to swallow a sibling's head.

Chicks begged by swaying their heads and bodies to and fro and extending the pharyngeal pouch. They also pecked at the area around the adult's beak. Following the day of hatching, chicks fed by inserting their head into the adult's mouth, often a considerable distance into the adult's throat.

Table 2. Incidence of chick watering by adult Neotropic Cormorant in Nest 2 during May and June of 2002, with notes on age and incidental behaviors.

Date	Time(h)	Days		# of Adults	Notes
		of Age	till Fledging		
25 May	1231	10	44	2	Non-brooding parent returned; spit water on nest and chicks.
6 June	1434-1438	22	32	2	Both parents present, one watering
7 June	1327-1330	23	31	1	Parent w/ beak in chick's mouth; watered 3 times for 12s
8 June	1247-1249	24	30	1	Parent placed its beak in the chick's mouth, and also dripped water all over nest
10 June	0856-0858	26	28	1	Parent placed its beak in the chick's mouth, and also dripped water all over nest
10 June	0900-0902	26	28	1	Parent back and spitting water on nest, nest very wet
13 June	1320-1321	29	25	1	
14 June	1207-1207	30	24	1	Water spitting, chicks returned to the nest

Play is a form of practice of essential skills (Gill, 1989). Older chicks were occasionally seen pulling on twigs in the nest or on nearby branches, and tossing Chinese tallow leaves into the air and catching them. This may have been a form of play intended to prepare the chicks to build nests or to pursue prey. I observed this behavior in chicks as young from 18 to 49 days of age (Table 3). Southern Cormorant nestlings have been reported to make catching movements and later to ‘mock-hunt’ objects found in the nest such as twigs and small stones. These behaviors were observed in chicks as young as 18 days old, and continued until less than a week before fledging (Madsen and Sparch, 1950).

Sibling rivalry, or aggressive behavior between nest mates, is observed in several species. It is common for the largest sibling to prevent younger siblings from receiving food (Ricklefs, 1968). Although I observed chicks engaged in aggressive behavior on several occasions, sibling rivalry did not seem extreme to me. Most incidents of aggressive behavior among nest mates occurred during feedings, when the chicks competed for the adult’s attention and feedings. Chicks fought by pecking at each other’s heads and necks. I twice observed chicks apparently attempting to swallow a sibling’s head.

Differences in weights of siblings often result from competition for food (Ricklefs, 1968). Approximately three days after all the eggs had hatched, older chicks got closer to the feeding parent and begged more energetically than their younger siblings; thus, they received more feedings.

Table 3. Incidences of behaviors suggestive of play in Neotropic Cormorant chicks during May and June of 2002.

Date	Nest	Days		Activity
		of Age	till Fledging	
27 May	3	18	26	Chicks plucking at twig in nest
1 June	3	23	21	Chicks playing with stick in nest
3 June	3	25	19	Chicks tossing leaf
3 June	3	25	19	Chicks tossing leaf
6 June	1	unknown	6	Chicks tossing piece of Chinese tallow
10 June	1	unknown	2	Chicks pulling on twigs
28 June	7	49	7	1 chick tugging on Chinese tallow leaves

However, shortly after that, there was no noticeable size difference in the chicks. After chicks could walk, they often crawled over each other to be fed. Because of the adults' habit of landing some distance away from the nest before feeding, the first chick to leave the nest often reached the parent and begged from it before the parent reached the nest, and therefore got fed first. However, it appeared that once a chick had received a few feedings, it stopped begging and the other chicks were fed.

Behavior of Adults — Adults began leaving the rookery in groups or singly within the first hour after sunrise, and began returning to the rookery for the night within 1 hour before sunset. Morrison et al. (1977) observed similar behavior. No adults were observed feeding in the lake surrounding the island on which the rookery was located.

The adults returned to the nests to feed chicks at varying intervals throughout each day. I observed 301 feeding intervals. The first feedings of the day sometimes occurred as early as 1 hour after sunrise. The number of feeding intervals increased dramatically after sunrise until a peak at 3-4 hours after sunrise, and then declined steadily until 14 hours after sunrise, at which time adults began returning to the rookery for the evening (Fig. 6).

Morrison et al. (1977) also observed cormorants returning to the rookery within 1 hour of sunrise, although most did not return until at least 2.5 hours after sunrise. They concluded that adults satisfy their own nutritional needs before beginning daily parental activities.

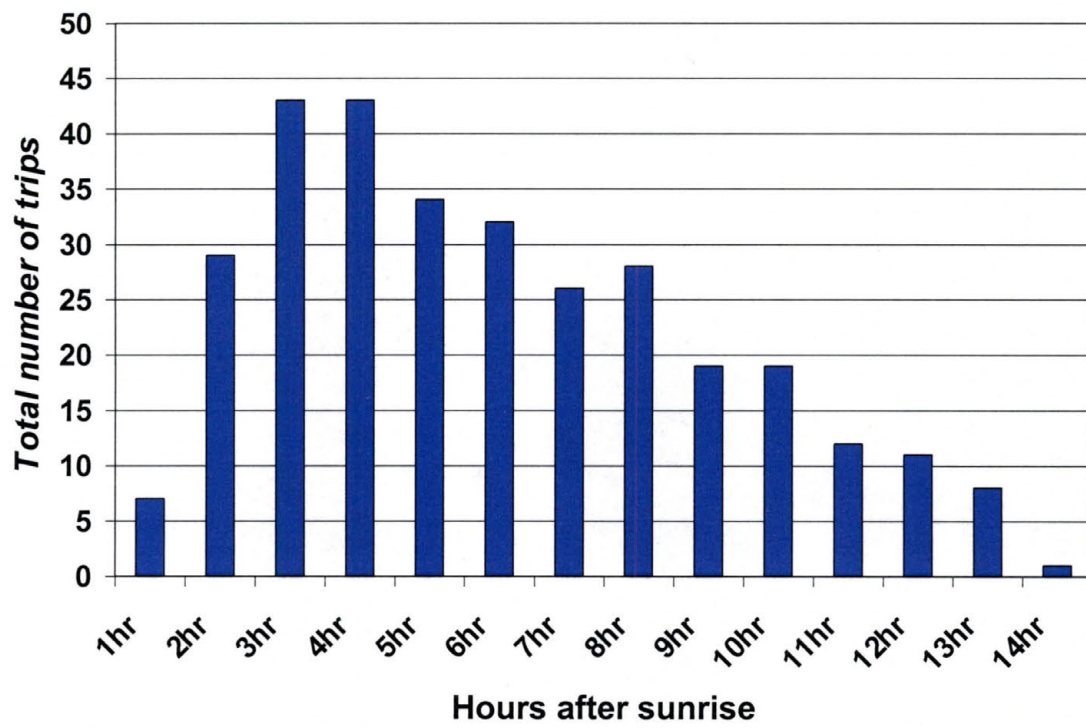


Fig. 6. Number of feeding intervals by adults by hours after sunrise.

The adults reduced energy expenditures by foraging for themselves, digested this food at the foraging area, and then foraged for the young on that same trip rather than separate trips, to the foraging area (Morrison et al., 1977).

Adults often fed chicks almost immediately after returning to the nest to take a turn at brooding or guarding the nest. Of the 31 observed changes of this kind, 21 were followed by a feeding from the returning adult within 10 minutes of its arrival at the nest.

During the day of hatching, the adult fed chicks a regurgitated liquid that dripped down from the parent's beak. Morrison et al. (1977) found that chicks are fed partially digested food for the first week, as noted in Double-crested Cormorants by Mcleod and Bondar (1953). By the second day, chicks inserted their heads into the parent's beak. Very young chicks stimulated feeding by uncoordinated head waving, and probably peeping. Older chicks begged by standing and swaying their heads and bodies to and fro and extending the pharyngeal pouch (Fig. 7). They also pecked at the adult's gular pouch. Sometimes they flapped their wings. Older chicks shoved their heads far into the parent's throat to feed. Begging behavior similar to that of Neotropic Cormorants is seen in many pelecaniform birds and in several species of cormorants. Younger Double-crested Cormorants in particular exhibit similar begging (Du Plessis, 1957; Dunn, 1975).



Fig. 7. Older Neotropic Cormorant chicks begging.

The number of feeding intervals during each 4-hour observation period ranged from 0 to 4. During each feeding interval, the adults fed chicks a varying number of times. I observed 547 feeding attempts during 243 feeding intervals, 19 of which I could not count feeding attempts for one reason or another. The number of feeding attempts per interval ranged from 1 to 11 with a mean of 2.26 ($s_{\bar{x}} = 0.1$). There was a significant decline in the trend [$p(F_{1,232} \geq 92.5) = 1.21 \times 10^{-18}$] for the mean number of feeding attempts per feeding interval as the chicks aged and drew nearer to fledging (Fig. 8). The mean number of feeding attempts per trip probably declined as chicks grew closer to fledging because older chicks can accept larger fish from their parents. Larger fish would provide more food per feeding than smaller fish. Dunn (1975) observed that fewer feeding attempts were necessary as Double-crested Cormorant chicks grew older and better able to accept whole fish, and that digestive efficiency increases with age; the same likely holds true for Neotropic Cormorants.

Chicks were fed most frequently when young. There was a significant decline in total feedings as chicks aged [$p(F_{1,246} \geq 88.52) = 3.73 \times 10^{-18}$] (Fig. 9). Chicks often went several days without a feeding just prior to the time of leaving the rookery for the first time. Food delivery rates commonly drop just before the young of many species fledge (Gill, 1989). The parents may have been instinctively giving the chicks a hunger incentive to force them to fly away from the familiarity of the rookery for the first time. Once the chicks could fly, they often followed the adults away from the rookery after feedings. This may have been a way for the chicks to find their first feeding area.

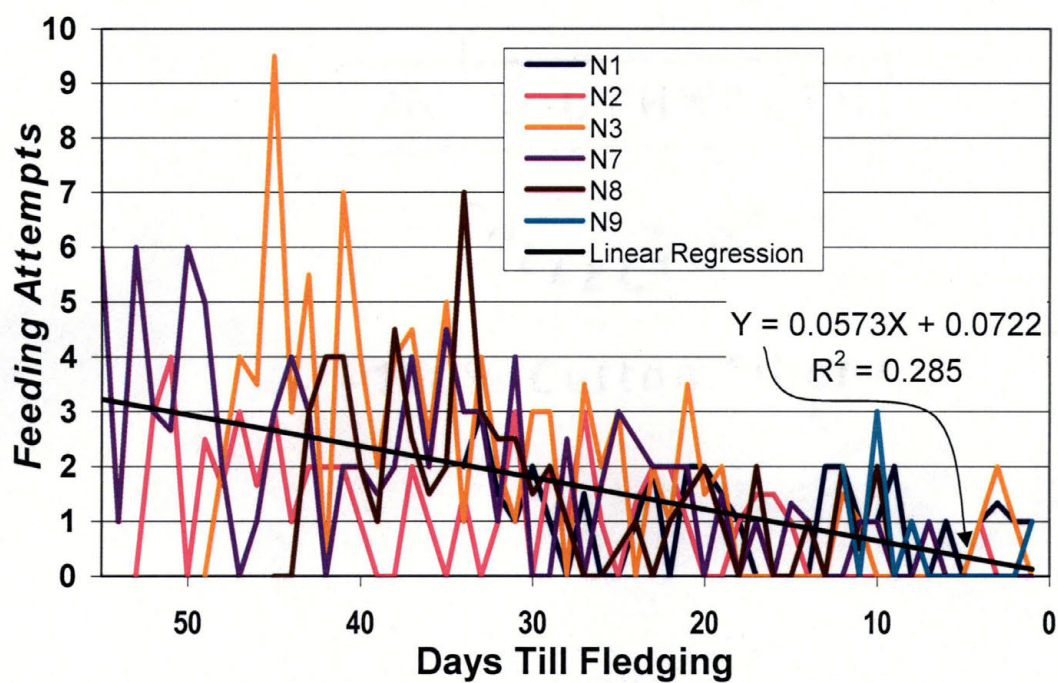


Fig. 8. Mean number of feeding attempts by adults per feeding interval as nestlings approach fledging.

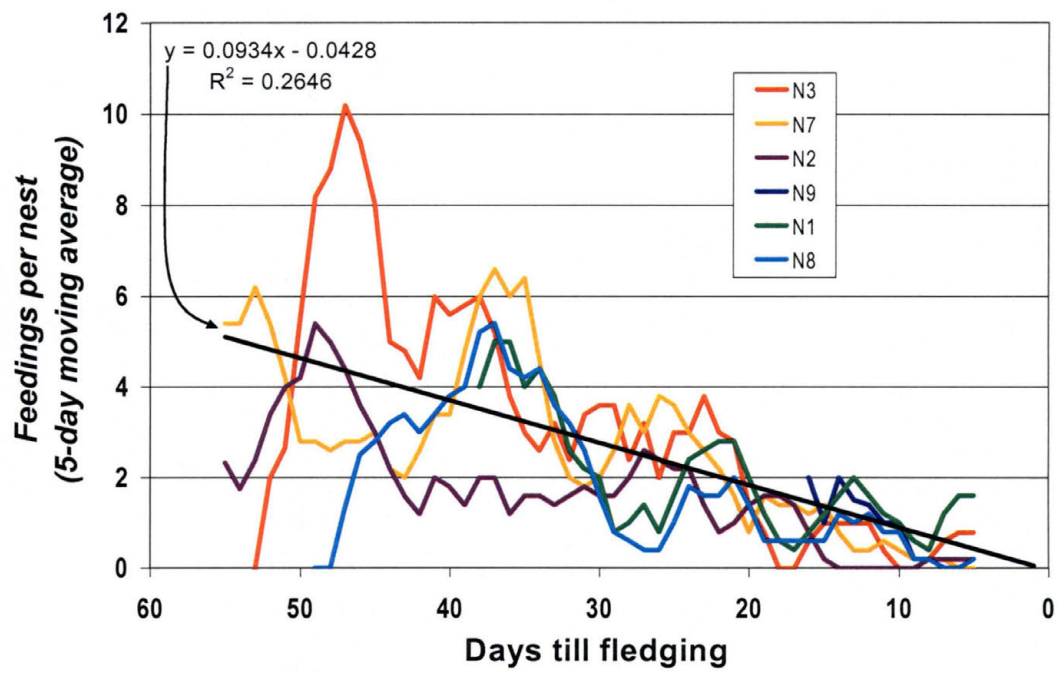


Fig. 9. Five-day moving average of the mean number of total feedings per chick as the chicks approach fledging.

Reproductive Success — The mean number of chicks fledged per nest during the study was 2.71 ($s_{\bar{x}} = 0.184$, range 2-3) (Table 4). This was higher than the 2.36 found by Kalmbach and her team in Chile (2001), and higher still than the 2.0 of Morrison's (1977) study. The high water levels and poor hunting conditions which prevailed during Morrison's study likely account for the lower fledging success he reported.

No chick mortality was observed in any of the nests used for this study. Drent et al. (1964) found that chick loss from hatching to nest departure was low among the Double-crested Cormorants on Mandarte Island. The primary causes of chick mortality in other species breeding at the rookery were falling from the nest and predation by Black-crowned Night-Herons. Displacement from the nest because of storms or sibling rivalry is another cause of mortality among cormorant chicks (Telfair and Morrison, 1995). There were no major storms in the study area until the chicks were already quite large and capable of short flights. Eggs hatched asynchronously, leading to variation in sizes of nest mates.

In Morrison's 1977 study the smallest of the hatchlings usually died within a few days of hatching, either through crushing, selective starvation, or eviction from the nest. No nest eviction was observed in any other species in the rookery during this study. Perhaps nest eviction occurs during poor feeding years, or perhaps the chicks found on the ground below the nests in Morrison's study fell for some other reason.

Table 4. Numbers of chicks fledged from each nest observed in the High Island rookery, with notes on the number of chicks in each nest at beginning of study.

Nest	# of Chicks Fledged	Notes
1	2	Found with 2 older chicks
2	3	Three chicks hatched
3	3	Three chicks hatched
4	2	Found with older 2 chicks
7	3	Three chicks hatched
8	3	Found with 3 very young chicks
9	3	Found with 3 older chicks

Several chicks came close to falling from the nest as they pursued adults during feeding sessions. High winds could also have blown chicks from the nest during Morrison's study. Chicks did sometimes scramble over each other during feedings, which could lead to death by crushing if one of the chicks were noticeably smaller than its siblings.

No adult mortality was observed. Snow (1960) observed low adult mortality rates during the breeding season among the Shag of the Isle of Lundy.

Future Research — This study adds substantially to the body of information available on the Neotropic Cormorant. This new knowledge should be useful in the management of colonial waterbirds, and may aid in the formulation of plans to control piscivorous birds. However, there are still several questions awaiting answers in regards to the breeding habits and development of the Neotropic Cormorant. The early breeding behavior of these birds needs further study. Additional work remains to be done on determining how seasonal differences affect clutch size and the development of chicks. Similar questions remain about the effects of food availability and weather on clutch size and development.

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