# NEST TAPHONOMY OF POPLAR ISLAND COMMON TERNS AND CARIBBEAN FLAMINGOS OF THE SMITHSONIAN NATIONAL ZOO

by

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# ABSTRACT

Theropod nesting localities suggest some dinosaurs incubated eggs in a manner similar to modern birds; however, taphonomic studies of modern nesting localities are limited. Here, I document Common Terns (*Sterna hirundo*) and Caribbean Flamingos (*Phoenicopterus ruber*) nesting sites at Poplar Island, Chesapeake Bay, MD, and Smithsonian National Zoological Park, Washington D.C., respectively. *Sterna hirundo* construct scrape nests with loose vegetation and produce 2-3 eggs; *P. ruber* build mud mounds containing one egg. Both species exhibit biparental care. Nests were surveyed on multiple occasions. Documentation included nest composition, density, and distribution, as well as eggshell concentration and orientation. Of 80 tern nests with 193 eggs, 12 nests hatched, 7 were predated, 31failed, and 30 were of unknown fates. Thirty-two flamingo nests averaged 32 x 31 cm, with mean nearest neighbor distance of 63.8 cm. Both species displayed abundant eggshell at nest centers. Concave-up eggshell characterized hatched and predated nests, whereas trampled areas favored concave-down. Wind or colony members likely transported random eggshell present on the colony. Eggs buried in nest and soil indicated adult abandonment. The results of this study may help determine nest fate for modern birds and provide paleontologists with physical characteristics to consider when excavating fossil sites.

Keywords: dinosaur; tern; flamingo; nest; taphonomy; eggshell

# CONTRIBUTION OF AUTHORS AND CO-AUTHORS

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# INTRODUCTION

Fossilized eggs from the Mesozoic Era have been discovered on every continent except Antarctica, and the diversity in egg size, shape, and eggshell microstructure suggest they include a variety of dinosaur taxa (Carpenter & Alf, 1994). Some carnivorous theropod dinosaurs such as the small manoraptorian theropod *Troodon* share several reproductive features with extant birds. These features include a rigid calcite eggshell comprised of two or more structural layers (Mikhailov 1997), large egg to body size, asymmetric egg shape, open nests with raised rims (Varricchio et al., 1997; Varricchio et al., 1999), and water vapor conductance rates that are equal to or lower than a bird egg of comparable mass (Deeming, 2006). The latter two features suggest that at least some theropod dinosaurs incubated eggs in a manner somewhat similar to birds, where eggs were partially exposed to the atmosphere, rather than completely buried in a substrate or vegetation mound like those of most extant reptiles (Jackson et al., 2010; Varricchio, 2011). Discoveries of partial adult theropod skeletons on top of unhatched egg clutches further support this inference (Clark et al., 1999; Varricchio et al., 1997; Varricchio et al., 1999). Other avian-like behaviors attributed to some dinosaurs include pre-hatching care of eggs, post-hatching parental care (Clark et al., 1999; Horner, 1982; Varricchio, 2011), site fidelity (Horner, 1982) and colonial nesting (Carpenter, 1999). Avian nesting localities, therefore, may serve as a useful model for studying dinosaur reproduction and fossilized egg assemblages. However, taphonomic studies of modern avian nesting localities are limited to only a few previously published reports (Hayward et al., 2011 and references therein). To provide context for my research, I briefly review these studies.

Horner (1994) reports bone distributions at American white pelican (*Pelecanus erythrorhynchos*), double-crested cormorant (*Phalacrocorax auritus*), and herring gull (*Larus argentatus*) colonies located on islands in Lake Bowdoin at Bowdoin National Wildlife Refuge in Montana. Horner (1994) notes that colony surfaces were littered with scattered remains of juvenile carcasses and bones throughout the nesting season. Shallow soil excavation (12 cm) revealed isolated juvenile skeletal elements as well. No adult remains occurred on the colony surfaces or in the excavated sites.

Hayward et al. (1997) used chicken (*Gallus gallus*) eggs as experimental models to identify taphonomic factors influencing egg and eggshell fossilization. Their experiments compared the distribution of simulated eggshell transport by turbidity currents to fragment orientation along transects through a glaucous-winged gull (*Larus glaucescens*) colony on Protection Island National Wildlife Refuge in Washington. Hayward et al. (1997) report a preferred 2:1 concave-up to concave-down orientation for these eggshell fragments. In contrast, fragments transported in turbidity currents did not vary significantly from an expected 50:50 ratio. Hayward et al. (1997) thus conclude that eggshell fragment orientation may provide a useful tool for recognizing fluvial transport at fossil egg localities.

Hayward et al. (2000) studied five factors influencing egg and eggshell distribution at the glaucous-winged gull (*Larus glaucescens*) colony on Protection Island in Washington: weathering, fragmentation, dispersal, orientation, and predation. In the same study they report that gull eggshell fragmentation results not only from hatching and predation, but also from trampling and breakage due to wind. They note that eggshells are difficult to find within days of hatching because parents remove the material from the nest sites to reduce predation. Hayward et al. (2000) also compare hatched eggs to relatively intact, depredated eggs at the gull colony. The large ends of hatched eggs were missing, whereas it remained relatively intact in depredated eggs. Eggshell fragments were most abundant near the nest centers, and eggshell densities were 10-30 times higher at egg-robber sites than in non-egg-robber territories. Furthermore, a 60:40 ratio between concave-up and concave-down shell fragments characterized both sites. They speculate that the 60:40 ratio may characterize relatively undisturbed avian nesting sites and result from the hatching process and subsequent trampling.

Hayward et al. (2000) examines the impact of habitat on egg predation by experimentally placing chicken eggs in a ring-billed gull (*L. delawarensis*) colony. More egg predation occurred inside than outside of the colony. The presence of tall grass vegetation, inside or outside the colony, provided the best protection from predators, compared to other habitat types (e.g., sparse vegetation, rocky beach, and low dense vegetation).

In a more recent study, Hayward et al. (2011) confirm that non-transported avian eggshells were more commonly observed concave-up (compared to concave-down) at both hatching and predation sites. Trampled and wind and water transported fragments, however, favored a concave-down orientation. Larger fragments also traveled further than small fragments when transported by wind or water (Hayward et al., 2011).

Taphonomic studies of modern nesting sites such as those described above provide paleontologists with several physical characteristics to consider when excavating fossil nesting sites: 1) eggshell surface weathering and fracture patterns, 2) density of eggshells and other biologic materials, 3) proportions of concave-up to concave-down eggshell orientations, and 4) sedimentary evidence of transport. Correlations between egg and eggshell attributes and the reproductive behaviors of extant parents and offspring may also provide insight into dinosaur reproductive biology. The objective of my study is to document modern avian ground nesting sites in order to formulate a potential model for the study of fossil egg assemblages. Data collected on nest abundance and spacing in modern avian colonies, along with the taphonomic study of post-reproductive and post-rearing nest structures (type, condition and spatial arrangement of biologic material), will help establish criteria for the interpretation of fossil nesting localities. This study may also benefit current research on the evolutionary transition of non-avian theropods and birds. The two species of colonial, ground nesting birds selected for this study were based on nesting similarities to some non-avian theropods, variability in nest complexity, and study site locality.

# REVIEW OF STUDIED SPECIES

## *Sterna hirundo* (Common Tern)

The Common Tern is the most widespread tern in North America (Figure 1). This medium-sized bird (total length of 31-35 cm) exhibits a wingspan of 75-80 cm and body mass of 110-145 g (Nisbet, 2002). They feed on small fish and invertebrates, and nest on islands, marshes, and beaches. Preferred nesting habitat consists mostly of open areas with scattered vegetation, and sand, shell, gravel and cobble substrate. Nests are primarily constructed by the males by scraping a hollow in the substrate with their feet. After the eggs are laid, parents sometimes add loose material such as dead vegetation, tide wrack (dead vegetation mats deposited by tides or storms), shell fragments and stones. Mean nest densities in colonies are 0.06-0.5 nests/m$^2$, and the range of means of nearest neighbor distance from various colonies is 87-514 cm (Nisbet & Drury, 1972; Erwin & Smith, 1985). Clutches generally consist of two to three eggs. Eggs are sub-elliptical, olive-to-buff in color with small brown spots. Egg dimensions average 42 mm x 30.5 mm, with average volume and fresh egg mass of 20 ml and 21 g, respectively. The first eggs laid in the clutch are usually the largest with thicker shells (Gochfeld, 1977).

*Figure 1.* Distribution of the Common Tern in North and Central America (Nisbet 2002). Blue area designates breeding grounds and orange designates wintering grounds.

Common Tern development is approximately 22-27 days. Once pipped, the hatching process takes about one hour. Chicks enlarge the pip-hole at the large end of the egg and push the cap off.  Parents do not assist with hatching but remove eggshells from the nest within 15 minutes, flying off with each piece and dropping it 20-100 m away. The semi-precocial chicks hatch with eyes open and can stand and take food within 1-3 hours.  Chicks move away from the nest within 2-3 days to seek cover, and the chicks fledge about 22-29 days after hatching.  Egg and chick predation and colony flooding represent the primary causes of nest failure.  The most common predators of the Common Tern include the Norway Rat (*Rattus norvegicus*), the Great Horned Owl (*Bubo virginianus*), Short-Eared Owls (*Asio flammeus*), Black-Crowned Night Herons (*Nycticorax nycticorax*), Herring (*Larus argentatus*) and Great Black-Backed Gulls (*Larus marinus*), American Crows (*Corvus brachyrhynchos*), ants, red foxes (*Vulpes vulpes*), raccoon (*Procyon lotor*) and mink (*Mustela vison*) (Nisbet, 2002).

The Common Tern's International Union for Conservation of Nature (IUCN) status is *least concern*; however, in some states they are listed as endangered, threatened, or of special concern (Nisbet, 2002).  Populations declined in the late 19th century because of the millinery trade, but recovered with protection.  In the 1970s populations declined again as a result of pesticide poisoning.  More recently (since the 1990s), population decline has resulted from nesting habitat loss (shore development, beach erosion, and sea-level rise), interspecific and intraspecific competition, and nest and chick predation (Nisbet, 2002; Brinker et al., 2007; Rounds et al., 2004).

Nest spacing and presence of concealing vegetation are often important in nest-site selection and reproductive success in colonial ground nesting birds (Wittenberger & Hunt, 1985).  Barbour et al. (2000) report significantly higher egg and chick predation in Common Tern colonies with low vegetation cover.  Hernandez-Matias et al. (2003) report greater protection from aerial predators in large Common Tern colonies and aggregated territories than in smaller colonies. They also report that birds nesting asynchronously early in the season are more susceptible to egg predation than late asynchronous nesting birds; however, synchrony within the colony typically does not impact the risk of egg predation.

### *Phoenicopterus ruber* (Caribbean Flamingo)

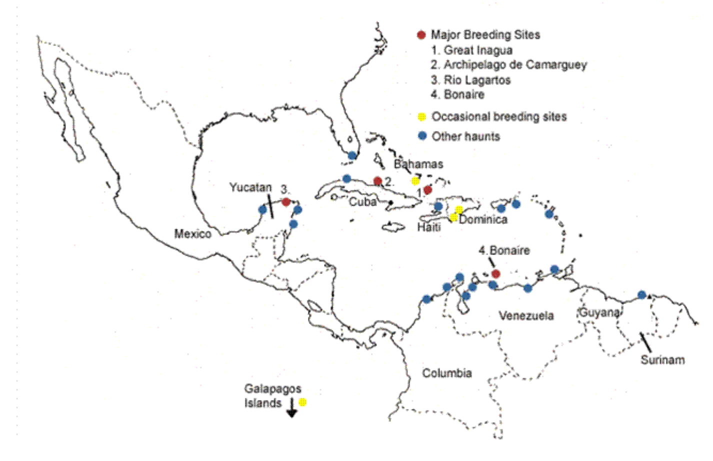

*Figure 2.* Distribution of the Caribbean Flamingo (Ogilvie & Ogilvie 1986). Red and yellow symbols designate major and occasional breeding sites, respectively. Blue designate other haunts.

The Caribbean Flamingo lives in five recognized colonies around the Caribbean Sea: Cuba, the Yucatan Peninsula of Mexico, Bahamas, Netherlands Antilles, Venezuela, and a small flock on the Galapagos Islands in the Pacific (Figure 2). Males range from 120-145 cm, weigh from 2.8-4.0 kg, and exhibit a wingspan of up to 145 cm. Females are usually 20% smaller than males. Caribbean Flamingos feed in shallow water in estuaries, lagoons, shallow inland lakes, and mudflats by filtering small crustaceans (brine shrimp, copepods, and amphipods), mollusks, insect larvae, and seeds from marsh grass in the mud (Caribbean Flamingo, 2009).

The Caribbean Flamingo is highly social and lives and breeds in colonies. Colony sizes range from a few dozen to hundreds of thousands of individuals. This species engages in synchronized, group courtship behavior which ensures that individuals in the colony are ready to mate at the same time. Breeding sites for the Caribbean Flamingo are saline lagoons in Cuba, the Yucatan Peninsula, on the coast of Venezuela, and on Bonaire Island in the Netherlands Antilles (Caribbean Flamingo, 2009).

Both parents are involved in nest construction, using the bill to bring mud toward the feet. The nest is composed of mud, small stones and feathers piled into a smooth cone of up to 30-40 cm in height. A shallow depression on the top measures no more than 2-4 cm deep (Ogilvie & Ogilvie, 1986). The mound nest raises the egg out of the water and protects the egg and hatchling from extreme heat and flooding; the shallow depression prevents the egg from rolling out of the nest. Mound building begins up to six weeks prior to egg laying and continues through the incubation process. Nests in the colony are typically spaced just beyond pecking distance to the nearest neighbor. Clutch size consists of one egg that is incubated by both parents for 27-31 days (Caribbean Flamingo, 2009). Eggs are white with a chalky texture, and average 90 mm x 55 mm in size and weigh approximately 140 g (Ogilvie & Ogilvie, 1986).

Unassisted by the parents, the hatching process takes approximately 24-36 hours. Once the chick emerges, the parents often push the eggshell over the side of the nest. In some cases, however, the chicks’ movement crushes the eggshell into the nest cup; the chick may also eat some eggshells (Ogilvie & Ogilvie, 1986). Chicks stay in the nest after hatching for approximately 6-8 days, after which they gather in large crèches that are overseen by a small number of adults in the colony, along with the parents. Fledging occurs between 9-13 weeks (Caribbean Flamingo, 2009). Chicks are most susceptible to avian predators and human interference due to egg poaching. Ecotourism to view the birds can cause significant disturbance and result in loss of eggs and young (Baldassarre & Arengo, 2000).

The Caribbean Flamingo’s IUCN status is *least concern*; however, threats include coastal development, habitat loss, and human disturbance of coastal habitat and breeding sites. The population remains relatively large (260,000-300,000) and possibly increasing (Bird Life International, 2011). Other factors that negatively impact populations include predation, colony flooding, and shifts in food abundance, water depth, and salinity due to tropical storms and hurricanes that impact wetlands (Baldassarre & Arengo, 2000).

# MATERIALS AND METHODS

## Common Tern Study Site

The Common Tern study was conducted on June 2, 22, 28, and July 6 (to document asynchronous hatching), and August 17, 2011 (to survey the colony post-fledging) on Poplar Island in the Chesapeake Bay, Talbot County, Maryland (Figure 3). Historically, Poplar Island was a long, narrow island, exceeding 440 ha. Erosion and sea-level rise during the 19th and 20th centuries reduced the island to less than two hectares by the early 1990s (Erwin, Miller & Reese 2007). Restoration of the island began in 1998, with scheduled completion in 2027 (Poplar Island, 2011). The purpose of the restoration focuses on

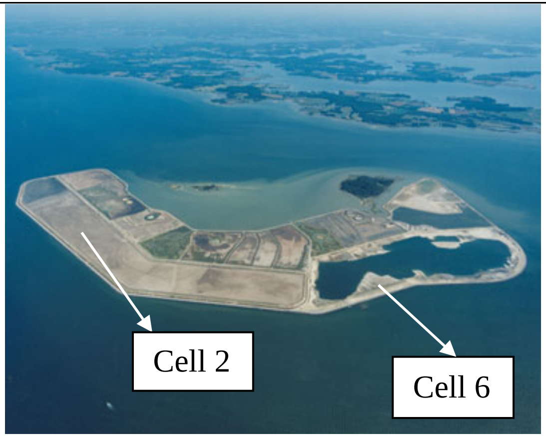

*Figure 3*. Poplar Island 2008. Cells 2 and 6 contain Common Tern nesting colonies.

creation of 1715 acres of wetland, upland, and open water habitat. An armored dike constructed of large quarry stones surrounds the restored island. The interior construction consists of cells of uncontaminated dredged material and sand cross-dikes. Sand-shell islands constructed within some of the cells provide shorebird nesting habitat (Erwin et al., 2007). Within a year of the restoration project, Common Terns and other shorebirds began to colonize the island during breeding season (Erwin et al., 2011). In 2011, Common Terns established nesting colonies in Cell 2 and Cell 6 (Figure 3).

## Predator Control

Personnel of the United States Fish and Wildlife Service (USFWS) at the Chesapeake Bay Field Office actively control predation on Poplar Island. Predators include Great Horned Owls (*Bubo virginianus*), Herring Gulls (*Larus argentatus*), and Great Black-Backed Gulls (*Larus marinus*). Two Great Horned Owls from adjacent Coaches Island were recognized as major predators of nesting birds and therefore USFWS personnel eliminated these birds in February 2011. In addition, newly hatched Common Terns represent a food source for developing gull chicks; therefore, lethal control measures include applying oil to gull eggs in order to terminate chick development (McGowan, 2011, personal communication). Other means of lethal control of gulls includes the use of firearms on Poplar Island from May through July 2011.

## Common Tern Survey

The Common Tern survey included colonies in Cell 2 (101 m x 8 m; 38°46’N, 76°22W), Cell 6 (93 m x 9.6 m; 38°44’N, 76°23W) and Cell 6 Peninsula (Cell 6P) (38°45’N, 76°23W). Small, shallow bodies of fresh water (< 2 m deep) lie adjacent to each colony and function as sediment control structures; in addition, the Chesapeake Bay lies approximately 35 m west of Cell 6. These water sources provide food for nesting birds. Cell 6P was included three weeks after the beginning of the study (i.e., June 22, 2011) because of its potential for flooding and the opportunity to assess the impact on the nesting grounds.

Table 1
*Nest Fate Criteria*

| Fate | Description |
|---|---|
| Hatched | Live or dead chicks present<br>Hatched eggs |
| Failed | Evidence of flooding<br>Erosion of nest substrate<br>Abandoned eggs (i.e. eggs present after 30 days or embedded in substrate) |
| Predated | Dead chicks or adult<br>Broken or pecked egg<br>Presence of blood<br>Physical disturbance of substrate |
| Unknown | Loss of eggs with no evidence of disturbance, predation or hatching |

Due to nesting and brooding activities, survey time at each colony was limited to 30 minutes. On June 2, 2011, a team of 6 people, separated by 1 - 2 m, walked in a line from south to north, surveying all nests. Nests were counted in Cells 2 and 6 and marked with wooden sticks in consecutive order. Latitude and longitude of each nest was recorded with a Global Positioning System (GPS). The clutch size and distance to its nearest neighbor nest (as measured from the south-to-south edge of the nests) were also recorded. Each nest was photographed to document egg arrangement. A map of each site was constructed using Generic Mapping Tools Version 3 (GMT3), provided by Woods Hole Science Center. Nest density and mean nearest neighbor spacing were calculated for each colony. Because Cell 6P was included later in the study, nest density and spacing were not recorded for this colony due to time constraints.

Cell 2 and 6 were re-visited on June 22 and 28, July 6, and August 17; Cell 6P was revisited only on August 17. Marked nests were examined and evidence of hatching, predation, and flooding were documented and photographed. These infrequent visits contribute to the difficulty in assessing egg predation and hatching. Nest fate, therefore, was determined using taphonomic criteria in Table 1, established by United States Geologic Survey (USGS) biologists. An “unknown” designation indicates young may have moved away from the nest, or eggs may have been predated by other birds. Calculations include the percent of hatched, failed, predated, and unknown nest fates. The percent of each of these attributes for Cell 2 and Cell 6 was compared using a student *t*-test to evaluate the relative impact of abundant and sparse vegetation on hatching success. An additional *t-test* was used to compare the possible outcomes from both vegetated colonies combined (Cell 2 and Cell 6P) relative to Cell 6 with sparse vegetation.

The final visit on August 17 occurred after all birds had left the three colonies. A 30 cm x 30 cm grid, divided into nine 10 cm x 10 cm squares, was placed over nests containing biologic material such as eggshell, skeletal remains and invertebrate shells. Data collected included location, orientation (concave-up and concave-down), size of eggshell fragments (<1 cm or ≥ 1 cm), bite marks, and eggshell fracture patterns. Bite marks on eggshells, as described by Kandel (2004), could include single and multiple openings along the sides of the eggs. In largely intact eggshells, hatched and depredated eggs could be distinguished by the fracture pattern along the large end of the shell; in hatched eggs the large end is missing, and in predated eggs the large end is intact (Hayward et al., 2000). The x, y, and z coordinates for each element were recorded. Eggshell fragments buried or pushed into the nest vegetation and/or sand substrate were considered evidence of nest trampling. Eggshell orientation data from all three colonies were combined with nest fate (Table 1). Chi-square analysis was performed on the combined nest fate data to compare concave-up and concave-down eggshell fragment orientation. An unpaired *t*-test was also performed to compare the difference in concave-up and concave-down eggshell orientation between hatched and predated nests.

Because I was unable to participate (due to course work completion in Montana) data collected on June 28 and July 6 from Cells 2 and 6 were obtained by USGS staff from the Patuxent Wildlife Research Center who led the Common Tern population study on Poplar Island (Erwin 2011, personal communication).

Caribbean Flamingo Study Site

The Caribbean Flamingo study was conducted at the Smithsonian National Zoological Park (NPZ) in Washington, D.C. A small moat surrounds the 8.55 m x 5.30 m mud island within the 10,000 ft$^2$ flamingo enclosure. The NPZ flock consists of 64 birds, with 25 pairs nesting in 2011. Once nesting behaviors began, nest construction was completed by the adults in less than a week. Nests consist of a mixture of mud, topsoil, and peat provided by NPZ staff (Figure 4 A). While the birds

*Figure 4.* (A) Flamingo nest. (B) Artificial flamingo egg.

are incubating eggs and tending young in the nest, the adult pairs perform constant nest maintenance. However, natural erosion of the nests begins about 3-5 days after the chicks fledge.

In 2011, each nesting pair produced one egg. All eggs were removed from nests by NPZ staff and replaced with artificial eggs (composed of plaster) to simulate nesting behavior within the flock (Figure 4 B). Twelve fertile eggs were sent to another zoo, whereas two eggs were artificially incubated at 37.5C and 50-60% relative humidity for 27-29 days or until pipping occurred. The remaining eggs were terminated because of the limited physical capacity of the enclosure. Two pipped eggs were returned to nests where the natural hatching process was completed, unassisted by the parents. Hatching occurred on July 17, 2011 and the flock remained on the nesting colony until late July. Access to the flamingo enclosure for this study began on July 26, after the flock left the nesting colony. Time on the island was limited to 1.5 hours per visit in order to minimize stress to birds since the flock remains in the enclosure.

### Caribbean Flamingo Survey

On July 26 the nests in the colony were counted and the nest cone length and width recorded. However, measurement of nest height (from the base of the nest to the cone rim) was somewhat questionable because of the unevenness of the ground and nest cone shape. Distance to the nearest neighbor nest was measured from nest cup to nest cup (Figure 4A). A map of the nesting colony was constructed using AutoCAD 2002.

On July 29 and August 8, eggshell and other biologic material were documented and photographed in and around the nests using a grid as previously described in Materials and Methods. However, an additional eggshell orientation was included in order to more accurately describe eggshell that occurs vertically with the concave surface facing into the nest. This orientation is referred to as “vertical concave-in (VCI)”. Eggshell size and orientation were documented, and a Fisher’s exact test was used to compare concave-up and concave-down fragment orientation.

On August 8 and 12 cross sectional views of four nests were exposed using a saw or trowel. These cross sections were excavated and documented at 2-5 cm increments, beginning at the upper nest surface and extending in a downward direction. The four cross sections included two nests that received pipped eggs (nests 23 and 29) and two that contained artificial eggs (nests 5 and 22). On August 12, nest cone length and width was re-measured in order to document the amount of nest erosion during a three week period.

# RESULTS AND DISCUSSION

## Common Tern Survey– June to July, 2011

The nesting substrates in Cells 2, 6 and 6P consist of well-rounded, medium-grained quartz sand (0.25-0.5 mm) and small (0.5-3.0 cm) mollusk shell fragments. Most nests in Cells 2 and 6P were shallow scrapes filled primarily with dead vegetation. In Cell 6, however, most scrape nests contained only occasional pieces of dead vegetation and mollusk shell fragments. Abundant and sparse vegetation characterize Cells 2 and 6, respectively, whereas Cell 6P contained even greater vegetation density and nests tend to cluster within tall grasses.

Vegetation in all 3 colonies consists of white sweet clover (*Melilotus albus*), crab grass (*Digitaria sanguinalis*), lambs quarter (*Chenopodium berlandieri*), ragweed (*Ambrosia artemisiifolia*), and other plants.

## Cell 2 Colony

Cell 2 contained 29 nests, 16 of which were studied. The 16 nests were distributed along an almost straight line in a southwest-to-northeast direction (Figure 5 A). The distance to the nearest neighbor nest ranged from 167 cm to 603 cm, with a mean distance of 334 cm (s.d. 133). The Cell 2 colony exhibited a nest density of 0.02/$m^2$ (Table 2).

Table 2
*Common Tern Characteristics for Three Colonies*

| Colony | Total Nests Studied | Nearest Neighbor Distance (cm) | Mean Distance Nearest Neighbor (cm) | Nest Density ($m^2$) |
|---|---|---|---|---|
| Cell 2 | 16 (29) | 167 - 603 | 334 | 0.02 |
| Cell 6 | 25 (48) | 187 - 874 | 432 | 0.03 |
| Cell 6P | 39 (39) | NA | NA | NA |

*Note.* Nest density and distance between nests was not determined for Cell 6P. Values in parenthesis = total nests/colony.

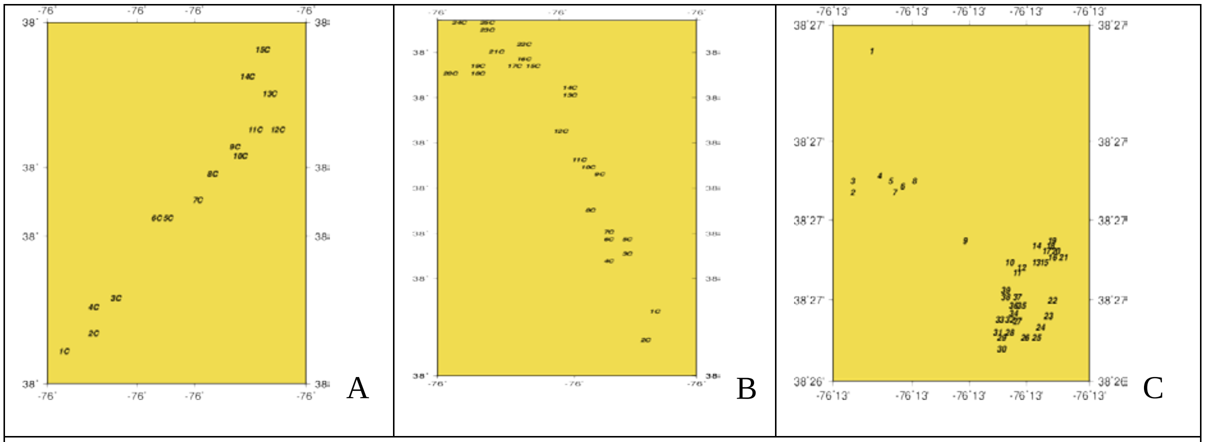

*Figure 5*. Distribution of Common Tern Nests in (A) Cell 2 , (B) Cell 6, and (C) Cell 6P.

The 16 nests in Cell 2 contained a total of 33 eggs (Table 3), with a mean clutch size of 2.2 eggs. Twenty-five percent of nests hatched at least one chick, 13% were predated, 31% failed, whereas the status of 31% remains unknown. As indicated by the presence of eggs embedded in the substrate, parents sometimes abandoned nests (Figure 6 A). Abandonment also may have occurred because eggs rolled out of nests. In 2 of the 16 nests in this colony, whole eggs were observed 30 – 50 cm from the nests. Cell 2 nests included 1 dead chick, 4 hatched and 2 predated clutches (Figure 6 B). No dead adults were observed in the Cell 2 colony.

Table 3

*Common Tern Nest for Three Colonies*

| Colony | Number Nests | Number of Eggs | Mean Clutch Size | % Nests Hatched (N) | % Nests Predated (N) | % Nests Failed (N) | % Nests Unknown (N) |
|---|---|---|---|---|---|---|---|
| Cell 2 | 16 | 33 | 2.2 | 25 (4) | 13 (2) | 31 (5) | 31 (5) |
| Cell 6 | 25 | 64 | 2.6 | 24 (6) | 4 (1) | 44 (11) | 28 (7) |
| Cell 6P | 39 | 96 | 2.5 | 8 (3) | 10 (4) | 38 (15) | 44 (17) |
| Total | 80 | 193 | | (13) | (7) | (31) | (29) |

*Note.* Values in parenthesis are numbers of nests designated for each fate.

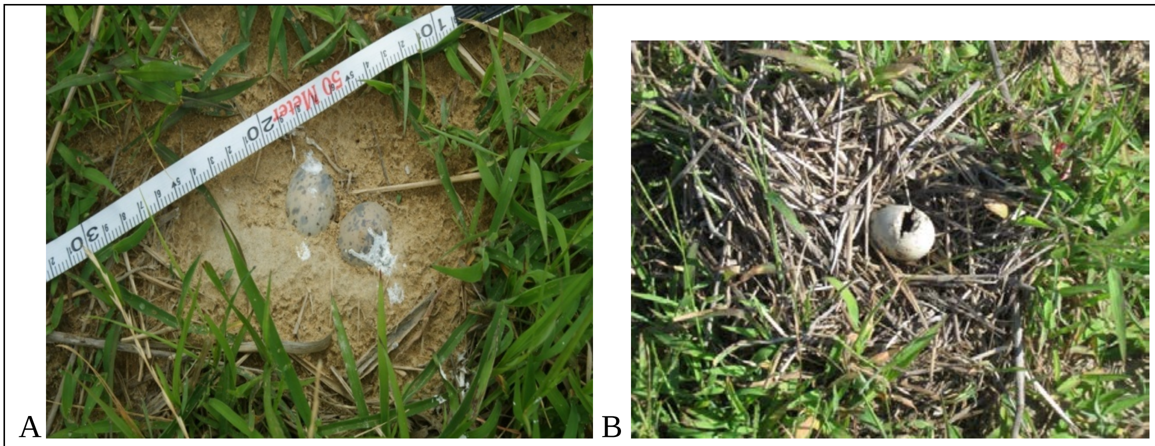

*Figure 6.* Cell 2. (A) Abandoned scrape nest. (B) Predated egg. Nest constructed of dead plant material.

Five nests in Cell 2 (nests 7, 11, 12, 13, 16) contained eggshell fragments indicating evidence of hatching or predation (as observed at the final survey in August). Nest 7 clearly contained eggshells from hatched eggs. Two of the fragments at the surface were quite large (2 – 3 cm), with three smaller fragments adjacent to them, all oriented concave-up. Directly underneath these fragments were 24 tiny eggshells (< 1 cm), 15 of which were concave-down (Table 6). All fragments occurred in the nest cup center. The presence of a dead chick on July 6 further supported the interpretation of a hatched nest.

Nest 11 displayed two large concave-up eggshells at the surface, and six very small fragments directly underneath; the latter occurred in a concave-down orientation (Table 6). All fragments were in the nest cup center. This nest was documented as predated on June 28, based on remnants of a partially consumed egg.

Eighty centimeters east of nest 12, 6 eggshells occurred, primarily concave-up, with two additional fragments oriented vertically in the mud. This nest was documented as hatched on June 28, based on egg remnants. However, the eggshell data at the end of the study suggests predation also occurred at this site. The clutch size at this nest was two; it is likely that one egg hatched and the other was depredated.

Eggshells were also present at the surface and nest cup center of nests 13 and 16; both were documented as unknown fates (Table 6). Fragments in nest 13 occurred only at the surface, mostly in a concave-down orientation. It remains unclear from these data whether this nest was hatched or predated. However, nest 16 revealed 23 fragments directly beneath the surface fragments, embedded in the vegetation of the nest. Most were concave-down. Based on the taphonomy of nest 7 in Cell 2 (Table 6) and nest 39 in Cell 6P (Table 7), it is likely that this nest contained hatched eggs. Both nests 7 and 39 were documented as hatched and numerous eggshell fragments were buried deep in the vegetation of the nests, primarily in the concave-down orientation.

### Cell 6 Colony

The 25 nests in Cell 6 showed a similar distribution as Cell 2 except the nests occurred in a southeast-to-northwest direction, with more visible clustering (Figure 5 B). The nearest neighbor nest distances in this colony varied from 187 cm to 874 cm, with a mean distance of 432 cm (s.d. 226). The Cell 6 colony showed a nest density of 0.03 nest/m$^2$ (Table 2). Mean nest density for both Cell 2 and Cell 6 was slightly less than reported by Nisbet and Drury (1972); however, the mean distance to the nearest neighbor nest for both colonies fell within expected ranges (Nisbet & Drury, 1972; Erwin & Smith, 1985). The mean nearest neighbor distance in both Cell's 2 and 6 was approximately five times the adult wingspan.

The 25 nests in Cell 6 contained a total of 64 eggs (Table 3), with a mean clutch size of 2.6 eggs. Twenty-four percent of nests hatched at least 1 chick, 4% were predated, 44% failed, and 28% were of unknown status. Of 25 nests observed in Cell 6, 6 contained hatched eggs and one contained a dead chick, likely predated. Many dead chicks were observed by USGS biologists in the area around the colony during the July 6 survey (Erwin 2011, personal communication). Adult remains, scattered throughout Cell 6, included 2 heads, 4 femora, and 2 piles of feathers.

An unpaired *t*-test allowed evaluation of the relative impact of abundant vs. sparse vegetation on nest fate in Cells 2 and 6. The two-tailed *p* value of 0.3407 indicates no statistical difference between nest fates in Cell 2 and 6. The confidence interval was 95%, and the standard error of difference was 2.175; therefore, it is likely that the mean outcome for nest fate is the same between Cell 2 and Cell 6, regardless of vegetation abundance. This may be due to the small sample size, especially for Cell 2 (16 nests) compared to Cell 6 (25 nests), and the fact that both samples were dominated by unknown nest fates.

### Cell 6P Colony

On June 22, 3 weeks after the initial visit to Cell 2 and 6, Cell 6P contained 39 nests. Nest distribution, however, differed from the linear pattern characteristic of Cells 2 and 6 (Figure 4 C); instead, the nests clustered in two groups within the tall grass near the tip of the peninsula. The 39 nests in Cell 6P contained a total of 96 eggs (Table 3), with a mean clutch size of 2.5 eggs. The late inclusion of this locality in the study prevented assessment of nest density and distance to the nearest neighbor.

Seven nests in Cell 6P (nests 4, 11, 12, 23, 27, 37, 39) contained eggshell fragments indicating evidence of hatching or predation (as observed at the final survey in August). Nest 4 contained remnants of two hatched eggs. Two clusters of large eggshell fragments occurred near the center of the nest, separated by ~3.5 cm. Each eggshell cluster extended over ~5 cm area, with smaller fragments dispersed around each set. A large piece of eggshell membrane (~3 cm in diameter) covered one eggshell cluster. Only four eggshells were buried in the sand substrate beneath the surface fragments. Most of the fragments in this nest were concave-up and 1 cm in size (Table 7).


*Figure 7.* Evidence of predated egg in nest 23, Cell 6P.

No evidence was found of nests 11 and 12; however, 3 eggshells formed a straight line extending 3.2 m, 3.4 m, and 3.56 m east of the nest area, with the smallest fragment occurring the furthest away (Table 7). These two nests were designated predated, based on the close proximity (1.3 m) of a partial adult skeleton and nest fate criteria (Table 1). These nests were located very close together as indicated by the map (Figure 5 C).

Nest 23 contained a large portion of an egg that appeared to be depredated (Table 7), with the side of the egg cut in half longitudinally. The larger egg fragment was positioned concave-up within the nest, with the smaller portion oriented concave-up inside this partial egg (Figure 7). When the two halves lie adjacent to one another, they comprise almost an entire egg. This depredated egg was located at the nest edge.

Nest 27 showed evidence consistent with hatching and subsequent trampling. Eight small eggshell fragments were clustered in two small groups, ~10 cm apart, and embedded in the nest vegetation. All fragments were concave-up. No eggshells were found at the surface in this nest.

Nest 37 was of unknown nest fate. One eggshell occurred concave-down, 10 cm south of the nest edge. No adult or chick predation was evident.

Nest 39 also showed evidence of hatching and trampling. This nest contained two clusters of eggshell fragments at the surface, ~8 cm apart, with one cluster near the center of the nest cup. These fragments were mostly small and concave-down. The other cluster of eggshells included two large fragments at the surface and five large fragments layered underneath; most of these fragments were concave-up. This nest also contained two clusters of fragments buried in the sand substrate near the nest cup center. The clusters were buried 3 cm and 4 cm below the base of the vegetation nest, on the left and right side of the center surface fragments, respectively. All buried eggshells were concave-down.

Only 8% of nests in Cell P6 showed evidence of hatching, 10% predated, and 38% failed, whereas the status of 44% of nests remains unknown (Table 3). Evidence of adult predation or natural death with scavenging included 1 sternum and 3 femora associated with nests 2 and 4, respectively. In addition, one partial skeleton occurred adjacent to nest 12 that included a full wing with some feathers attached, 1 sternum, 2 femora, 1 humerus, and 4 ribs.

Nest fate outcomes from Cell 2 and Cell 6P were combined to perform an additional unpaired *t*-test to evaluate the relative impact of abundant vegetation in these colonies vs. the sparse vegetation in Cell 6 on nest fate. The two-tailed *p* value of 0.1825 indicates no statistical difference between nest fates in Cell's 2 and 6P, and Cell 6. The confidence interval was 95%, and the standard error of difference was 4.811. It is likely, therefore, that the mean outcome (hatched, predated, unknown, or failed) in Cell 2 and Cell 6P approximates that of Cell 6, despite vegetation abundance. These data differ from Hayward et al.'s (2000) experimental data with chicken eggs inside and outside a ring-billed gull colony, where the presence of tall grass vegetation provided the best protection from predators. The small sample size of this study, along with the high percentage of unknown nest fates, may have adversely impacted the statistical outcome.

## Impact of Flooding in Cell 6 and 6P

Cell 6 experienced loss of nine nests due to high rainwater runoff, cliff erosion, and collapse. In each case, the nests were located near the edge of the cliff that separated Cell 6 and Cell 6P; no evidence remained of the nests (Figure 8). In addition, waters from an adjacent sediment control pond flooded and/or eroded 12 of 39 nests in the Cell 6P colony. These nests were located near the edge of the peninsula and were either lost to rising water or erosion (Figure 5 C; Table 4). Cell 6P retained no obvious evidence of the nests or their contents in the adjacent standing water of the sediment control pond. Two additional nests within the

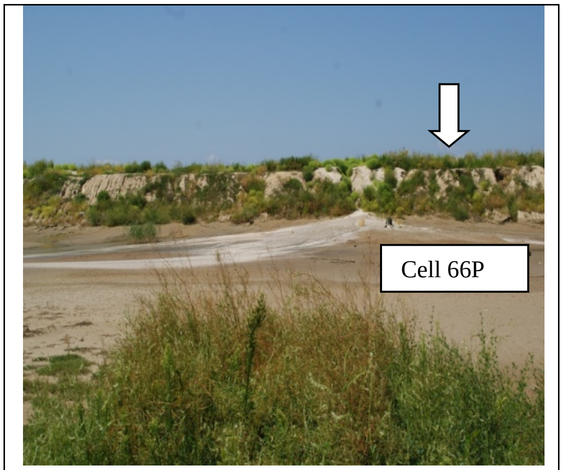

*Figure 8.* Arrow shows steep slope that separates Cell 6 from Cell 6P in the foreground. Photograph taken after water receded.

colony exhibited evidence of a washout (Table 4). The rippled flow pattern preserved in the sand indicated a west-to-east direction, and originated from the steep slope that separated Cells 6 and 6P (Figure 8). All of the nests in Cells 6 and 6P lost to erosion, flooding or washout were identified as failed nests (Table 5).

Table 4
*Summary of Common Tern Nests Lost to Flooding*

| Colony | Total Nests Lost (of total) | Percent Nests Lost | Nests Lost to Washed-Out |
|---|---|---|---|
| Cell 6 | 9 (25) | 36 | |
| Cell 6P | 12 (39) | 31 | 9,11 |
| Total | 21 (64) | 33 | 2 |

<u>Final Survey – August, 2011</u>

A final survey was conducted on August 17th after adults and chicks had abandoned the colonies. The only biologic material remaining in nests was eggshell fragments or whole eggs embedded in the sand substrate (Table 5). Eggshell fragments were found in hatched, predated, and nests of unknown fate in Cells 2 and 6P. Fifteen percent of total nests contained eggshell fragments and 46% lacked these remains. Failed nests were either abandoned, as indicated by eggs embedded in the substrate, or were lost to erosion, flooding, or washout. Ten percent of total nests contained embedded eggs and 29% of total nests were lost to erosion and/or flooding.

Table 5

*Summary of Nest Fate and Presence of Eggshell or Egg*

| Colony | Nest Total | Hatched Eggshell Present | Hatched Eggshell Absent | Predated Eggshell Present | Predated Eggshell Absent | Unknown Eggshell Present | Unknown Eggshell Absent | Failed Eggs Embedded | Failed Eggs Lost |
|---|---|---|---|---|---|---|---|---|---|
| Cell 2 | 16 | 2 | 2 | 1 | 1 | 2 | 3 | 5 | 0 |
| Cell 6 | 25 | 0 | 6 | 0 | 1 | 0 | 7 | 2 | 9 |
| Cell 6P | 39 | 3 | 0 | 3 | 1 | 1 | 16 | 1 | 14 |
| Total | 80 | 5 (6) | 8 (10) | 4 (5) | 3 (4) | 3 (4) | 26 (32) | 8 (10) | 23 (29) |

*Note.* Numbers in parentheses are percent of total.

Lack of eggshell in nests may be related to parental removal during the hatching process or may have been transported out of nests by wind or water.

## Cell 2 Colony

Eighty eggshells in Cell 2 represented the only biologic material remaining in 5 of 16 nests (Tables 6 and 8). Forty-one percent of the fragments were concave-up (N = 33), 56% concave-down (N = 45), and 3% vertical (N = 2) (Table 8). Seventy-six percent (N = 61) of the eggshells measured less < 1 cm in size (Table 6). Eggshells only occurred in hatched, predated or nests of unknown fate; no eggshells were found in failed nests. None of the eggshells contained bite marks. Eggshells primarily occurred in nests composed of vegetation and in the nest cup center, either stacked on top of one another or pressed deep into the nest substrate. The latter suggests trampling by chicks and/or adults.

## Cell 6 Colony

Of the 25 nests documented in Cell 6, only one identifiable nest remained at the end of the survey. The adults abandoned this nest, as evidenced by a partially buried egg 1.8 cm below the sand substrate. Most of the remaining nests, which consist of sand scrapes, were likely covered by wind-blown sand. No eggshells occurred in the areas surrounding any of the nests. However, nine nests occur in areas of the colony subject to erosion and were presumably lost for this reason.

Table 6
*Summary of Cell 2 Eggshell Orientation*

| Nest Number | Fate | Location in Nest | Surface | | | | | | Buried | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *< 1 cm* | | | *≥ 1 cm* | | | *< 1 cm* | | | *≥ 1 cm* | | |
| | | | CU | CD | V | CU | CD | V | CU | CD | V | CU | CD | V |
| 7 | Hatched | Center | 3 | - | - | 2 | - | - | 9 | 15 | - | - | - | - |
| 11 | (1DC) | Center | 1 | - | - | 2 | - | - | - | 6 | - | - | - | - |
| 12 | Predated | East* | - | - | 2 | 5 | 1 | - | - | - | - | - | - | - |
| 13 | Hatched | Center | - | - | | 1 | 7 | - | - | - | - | - | - | - |
| 16 | Unknown | Center | 1 | 1 | | 1 | | - | 8 | 15 | - | - | - | - |
| | Unknown | | | | | | | | | | | | | |
| Total | -- | -- | 5 | 1 | 2 | 11 | 8 | 0 | 17 | 36 | 0 | 0 | 0 | 0 |

Abbreviations: DC, dead chick; CU, concave-up; CD, concave-down; V, vertical.
* Eggshell fragments were 80 cm east of the nest.

## Cell 6P Colony

Seven of the 39 nests contained eggshells and one nest contained a fragment of eggshell membrane (Table 7). Sixty-seven percent of the fragments were concave-up (N = 49) and 33% (N = 24) concave-down (Table 8). Sixty-seven percent (N = 49) of the fragments measured ≥1cm (Table 7). As in Cell 2, eggshells occurred only in hatched, predated, or nests of unknown fates; none of the eggshells contained bite marks; and eggshells primarily occurred in nests composed of vegetation, with most fragments located in the nest cup center and, in some cases, pressed deep into the nest vegetation.

Table 7

*Summary of Cell 6P Eggshell Orientation*

| Nest Number | Fate | Location in Nest | Surface | | | | | | Buried | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *< 1 cm* | | | *≥ 1 cm* | | | *< 1 cm* | | | *≥ 1 cm* | | |
| | | | CU | CD | V | CU | CD | V | CU | CD | V | CU | CD | V |
| 4 | Hatched | Center | - | - | - | 2 | 4 | - | - | - | - | 4 | - | - |
| 11/12 | Predated (wash-out) | 3.2-3.56 m east of nest | - | 1 | - | 4<br>1 | 1 | - | - | - | - | - | - | - |
| 23 | | Nest edge | - | - | - | | - | - | - | - | - | - | - | - |
| 27 | Predated | Center | - | - | - | 2 | - | - | 8 | - | - | - | - | - |
| 37 | Hatched | 10 cm south of | - | - | - | -<br>- | 1 | - | - | - | - | - | - | - |
| 39 | Unknown<br>Hatched | nest<br>Center | 3 | 7 | - | 3 | - | - | - | 5 | - | 4 | 5 | - |
| Total | -- | -- | 3 | 8 | 0 | 30 | 6 | 0 | 8 | 5 | 0 | 8 | 5 | 0 |

Abbreviations: CU, concave-up; CD, concave-down; V, vertical.

Total numbers of concave-up and concave-down fragments from Cells 2 and 6P were combined to perform a chi-square analysis of fragments buried in nest vegetation and/or the sand substrate. This chi-square test compared my CD:CU (N = 46:33) fragments in buried nests to that of the trampled fragment ratio (60:40 CD:CU) reported by Hayward (2011). The chi-square was equal to 0.103 with 1 degree of freedom. The two-tailed *p* value was equal to 0.7478, demonstrating that this difference is not statistically significant. These data indicate that eggshells buried in the nest or ground substrate subject to trampling are more likely to be oriented concave-down than concave-up, thereby supporting Hayward's (2011) findings.

## Combined Data for Cell 2 and 6P Colonies

A total of 153 eggshell fragments remained in 12 nests in Cells 2 and 6P, with more fragments generally found in hatched nests (Table 8). There seemed to be no relationship between clutch size and number of remaining eggshell fragments. Fifty-four percent of the total fragments for both cells were concave-up and 45% were concave-down. Fifty-two percent of the total fragments were buried in the nest or soil substrate.

Table 8
*Summary of Nest Fate and Eggshell Orientation for Cells 2 and 6P*

| Cell 2 | | | | Surface | | | Buried | |
|---|---|---|---|---|---|---|---|---|
| Nest Number | Clutch Size | Fate | Total Fragments | CU (%) | CD (%) | V (%) | CU (%) | CD (%) |
| 7 | 3 | Hatched | 29 | 5 | -- | -- | 9 | 15 |
| 11 | 3 | Predated | 9 | 3 | -- | -- | -- | 6 |
| 12 | 2 | Hatched | 8 | 5 | 1 | 2 | -- | -- |
| 13 | 3 | Unknown | 8 | 1 | 7 | -- | -- | -- |
| 16 | 1 | Unknown | 26 | 2 | 1 | | 8 | 15 |
| Total | 12 | | 80 | 16 (20) | 9 (11) | 2 (3) | 17 (21) | 36 (45) |
| Cell 6P | | | | | | | | |
| 4 | 2 | Hatched | 32 | 24 | 4 | -- | 4 | -- |
| 11/12 | 2/1 | Predated | 3 | 1 | 2 | -- | -- | -- |
| 23 | 3 | Predated | 2 | 2 | -- | -- | -- | -- |
| 27 | 3 | Hatched | 8 | -- | -- | -- | 8 | -- |
| 37 | 2 | Unknown | 1 | -- | 1 | -- | -- | -- |
| 39 | 2 | Hatched | 27 | 6 | 7 | -- | 4 | 10 |
| Total | 15 | | 73 | 33 (45) | 14 (19) | -- | 16 (22) | 10 (14) |
| Grand Total | 27 | | 153 | 49 (32) | 23 (15) | 2 (1) | 33 (22) | 46 (30) |

Table 9 shows the total number of eggshells for each colony by nest fate. Hatched nests contained 64% and 36% concave-up and concave-down fragments, whereas predated nests contained 43% concave-up and 57% concave-down eggshells.

The nests with unknown fates contained 31% concave-up and 69% concave-down fragments. Chi-square was used to compare concave-up (CU; N = 71) vs. concave-down (CD; N = 45) fragments to an expected 50:50 distribution. The Chi-square test equaled 5.828 with 1 degree of freedom. The two-tailed *p* value was 0.0158, demonstrating a statistically significant difference. These data indicate that the orientation of CU:CD does not represent a random distribution.

Two additional chi-square tests were performed; the first compares hatched and predated concave-up (CU; N = 71) and concave-down (CD; N = 45) values to the 60:40 ratio reported by Hayward (2000) in hatched and predated nests. The chi-square equaled 0.036 with 1 degree of freedom, and the two-tailed *p* value was 0.8495. This *p* value demonstrates that the difference between the data presented here and Hayward's (2000) data was not statistically significant. This study, therefore, supports the earlier findings: eggshell fragments from hatched and predated nests are more likely to be oriented concave-up than concave-down at a ratio of approximately 60:40.

Table 9
*Eggshell orientation according to nest fate for Cells 2 and 6P*

| Nest Fate | CU eggshell (%) | CD eggshell (%) |
|---|---|---|
| Hatched | 65 (64) | 37 (36) |
| Predated | 6 (43) | 8 (57) |
| Total Hatched & Predated | 71 (61) | 45 (39) |
| Unknown | 11 (31) | 24 (69) |
| Total | 82 (54) | 69 (46) |

CU, concave-up; CD, concave-down.

The later chi-square compares the combined CU:CD (N = 82:69) from hatched, predated and unknown nest fates to the expected 60:40 CU:CD distribution of Hayward

(2000). The chi-square was equal to 2.240 with 1 degree of freedom. The two-tailed *p* value was 0.1345, indicating that this difference is not statistically significant. This *p* value also suggests that in hatched, predated and nests of unknown fate, eggshell fragments are more likely to be oriented concave-up than concave-down, thereby supporting Hayward's findings (2000).

An unpaired *t*-test was performed to evaluate the difference in CU:CD orientation in hatched (64% CU, 36% CD) and predated (43% CU, 57% CD) nests. The two-tailed *p* value was 0.0885; not quite statistically significant. The confidence interval was 95%, and the standard error of difference was 14.036. These data suggest that there is no significant difference between the concave-up vs. concave-down orientation in hatched and predated nests. The small sample size of eggshells in predated nests (14) compared to those in hatched nests (102), along with the high percentage of unknown nest fates, may have adversely impacted the statistical outcome.

## Caribbean Flamingo Survey

The Caribbean flamingo nesting colony contained 32 nests constructed by 25 breeding pairs. The nest cones averaged 32.4 cm in length (s.d. 5.4) by 30.9 cm in width (s.d. 6) (Table 10), whereas the mean weathered cone was 29.3 cm by 28.2 cm. This represents an erosional loss of 3.1 cm and 2.7 cm over a two week period.

Table 10
*Caribbean Flamingo Nest Measurements*

| Mean Distance to Nearest Neighbor (cm) | Mean Nest Cone Length (cm) | Mean Nest Cone Width (cm) | Weathered Nest Mean Cone Length (cm) | Weathered Nest Mean Cone Length (cm) |
|---|---|---|---|---|
| 63.8 | 32.4 | 30.9 | 29.3 | 28.2 |

The mean nearest neighbor nest distance within the colony measured 63.8 cm (Figure 9), representing less than half of the average wing span of the Caribbean flamingo (Table 10). Only six nests (2, 5, 22, 23, 29, and 32) contained biologic material at the surface (Table 11). Three of the nests (5, 23, and 29) included feathers embedded in the nest material near the surface and three nests (2, 5, and 22) exhibited eggshell fragments at the surface. Nest 32 contained an entire egg, partially buried in the side of the nest (Figure 10). Unfortunately, this egg was removed and destroyed by NZP volunteer staff prior to a physical assessment.

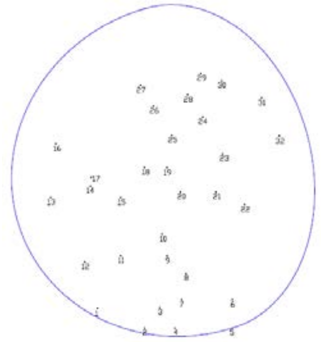

*Figure 9.* Flamingo colony map showing nests and measured distances between nests. Scale: 1:57 cm. Blue circle indicates boundary of nesting island.

Six eggshells occurred on nest surfaces, near the upper edge or embedded in the side of the nest (Table 11). Four were oriented concave-down (CD), and two occurred vertically, with the concave surface extending into the nest (VCI). All fragments measured < 1 cm in diameter.

Table 11
*Caribbean Flamingo Nest Surface Biologic Material*

| Nest Number | 2 | 5 | 22 | 23 | 29 |
|---|---|---|---|---|---|
| Embedded Feathers | | 5 | | 1 | 2 |
| Eggshell / Orientation | 1/VCI | 1/CD | 1/VCI ,<br>3/CD | | |

VCI, vertical concave-in; CD, concave-down. All eggshells < 1 cm.

*Figure 10.* Nest 32 exhibits recent erosion that exposed a partially buried flamingo egg.

Ten eggshells were present between nests in the colony; with the exception of one fragment that was oriented concave-up, all occurred concave-down and mostly measured < 1cm (Table 12). The Fisher's exact test compared the number of concave-down vs. concave-up eggshell fragments in the trampled areas of the colony to the expected 50:50 distribution if the orientation was random. The two-tailed *p* value was 0.1409, demonstrating that this difference is not statistically significant. These data indicate that the orientation of concave-down (N = 9) to concave-up (N = 1) may be random and/or is likely due to the small sample size. If the eggshell fragments in the colony between nests are considered trampled and/or transported, the observed concave-down orientation may support Hayward's (2011) findings, but this correlation requires more data.

Table 12

*Surface Biologic Material Between Flamingo Nests*

| Nest Numbers | 1 & 2 | 2 & 3 | 5 & 6 | 5 & 7 | 17 & 26 | 18 & 26 | 31 & EC |
|---|---|---|---|---|---|---|---|
| Eggshells/ Orientation | 1/CD | 1/CD | 1/CD, 1/CU | 1/CD | 2/CD | 2/CD | 1/CD |

CD, concave-down; CU, concave-up. All eggshells measured < 1 cm except fragments in nests 18 and 26, which were > 1cm.

## Excavation of Nests

After surface examination, excavation of 4 nests included 2 nests that received pipped eggs (23 and 29) and 2 that received artificial eggs (5 and 22). Most fragments occurred in the nest cup center at depths ranging from 0.4 cm to 6 cm (Table 13). Nest 5 included 2 eggshells at 1 cm depth and nest 22 contained one eggshell at a depth of 3 cm. These eggshells may have been deposited by adult inhabitants or other colony members, or they may have been remnants from previous years' nests. Nests with hatched eggs (nests 23 and 29) included eggshell membrane, as well as eggshell embedded within the nest substrate. Nest 23 contained two eggshells (both < 1 cm) and one small (1.5 cm x 1.5 cm) fragment of shell membrane. Both eggshells were concave-down at 0.4 cm and 1.2 cm depths, stratigraphically below the top of the nest. Eggshell membrane was directly beneath these fragments at a depth of 3 cm. All material occurred 6 cm from the edge of the nest cone. In nest 29, biologic material was directly centered in the nest cup. The first concave-up eggshell fragment was excavated at a depth of 2 cm. At a depth of 3 cm, two relatively large pieces of eggshell membrane (4 cm x 3.5 cm and 4.5 cm x 2 cm) were folded together, with five eggshells pressed against one another, standing vertically and concave into the nest (VCI). Three of these fragments exceeded 1 cm in diameter. Two additional fragments of membrane occurred at 5 cm and 6 cm depths; these measured 1.5 cm x 1.5 cm and 2.5 cm x 1.5 cm, respectively.

Table 13
*Biologic Material from Excavated Nests*

| Nest Number | 5 | 22 | 23 | 29 | 29 |
|---|---|---|---|---|---|
| Eggshell Fragment Orientation | 2 CD | 1 CU | 2 CD | 1 CU | 5 VCI |
| Depth from Cup Surface | 1 cm | 3 cm | 0.4 cm,<br>1.2 cm | 2 cm | 3 cm |

Abbreviations same as above. All eggshells < 1 cm except 1 in nest 5 and 3 in nest 29.

Table 14 summarizes the orientation of eggshell fragments in nests and on the colony surface. Forty-seven percent of nest eggshells occurred concave-down, 41% were vertical and concave into the nest, and 12% were concave-up. The Fisher’s exact test compared the number of concave-down (N = 8) and concave-up (N = 2) eggshell fragments in nests to an expected 50:50 distribution if the orientation was random. The two-tailed *p* value was 0.3498; this difference is not statistically significant. These data indicate that the orientation of concave-down to concave-up may be random and again, are likely influenced by the small sample size. If the eggshell fragments in the nests are subject to trampling, the observed concave-down orientation may support Hayward’s (2011) findings, but this correlation requires further study.

Table 14
*Summary of Combined Eggshell Fragment Orientation from Nest and Colony Surfaces and Nest Excavation*

| Nest Fragments | Number | Percent | Colony Fragments | Number | Percent |
|---|---|---|---|---|---|
| CD | 8 | 47 | CD | 9 | 90 |
| CU | 2 | 12 | CU | 1 | 10 |
| VCI | 7 | 41 | | | |

After the flamingo chicks fledge, members of the colony remain on the island, walking on and over the nests, trampling the ground surface between nests, as well as the nests themselves. Hayward’s (2011) experimental study of eggshell orientation resulting from domestic chick trampling indicated a 60:40 concave-down to concave-up orientation. In contrast, hatched and predated nests showed a preferred orientation of concave-up eggshells (Hayward, 2000). The flamingo nest and colony surface data may support Hayward's (2011) trampling hypothesis.

## SUMMARY

### Common Tern (Sterna hirundo)

Three Common Tern colonies on Poplar Island were studied, each with a characteristic habitat. Cell 2 occurred at a higher elevation (7 m compared to 3.9 m at Cell 6) and contained visibly more ground vegetation than Cell 6, and Cell 6 Peninsula (Cell 6P) was at a lower elevation (-2.7 m), prone to flooding, and contained the tallest and most dense vegetation of all three colonies. (Poplar Island Construction Datum 0.00 m)

Two different nest distribution patterns (linear and clustered) and nest types (sand scrapes and vegetated nests) were observed in the study areas (Figure 5A, B). Cell 6P (Figure 5 C) in particular exhibited nest clustering within the tall grass near the tip of the peninsula. In Cells 2 and 6P, most nests were constructed of dead plant material, and in Cell 6 most nests were scrapes in the sand substrate. The vegetated nests contain greater abundance of eggshell fragments after the chicks fledge and thus more evidence of hatching and predation. Eggshell fragments are more likely to adhere to the vegetation mat in these nests; in contrast, sand scrape nests show greater potential for transport of fragments from the sand depression by wind and water.

In all three colonies more nests were documented as failed (31-44%) or unknown status (28-44%) than as hatched (8-25%) or predated (4-13%) (Table 3). Nest predation likely resulted from Great Horned owls, which were the only predators photographed with camera traps (McGowan 2011, personal communication). During two visits to Poplar Island, however, bald eagles were observed within the three study areas, although they were not photographed depredating chicks or adults in any of the colonies.

The presence of sparse and abundant vegetation in Cell 6 and Cells 2 and 6P, respectively, and its potential influence on nest fate was compared using an unpaired *t* test. The *p* value indicated that the difference between nest fates in the colonies was not statistically significant. It is likely, therefore, that the mean outcome (hatched, predated, unknown, or failed) in Cell 2 and Cell 6P approximates that of Cell 6, despite vegetation abundance. These data differ from experimental data (Hayward et al. 2000) that indicates the presence of tall grass vegetation provides the best protection from predators. The small sample size of the current study, along with the high percentage of unknown nest fates, may have adversely impacted the statistical outcome.

Over one third of nests in Cell 6 (36%) and Cell 6P (31%) were lost to erosion and flooding (Table 4). In all cases these failed nests were located near the edge of the colony, either near the embankment (in Cell 6), or near the edge of the peninsula (Cell 6P). No evidence remained of the lost nests in either colony. There was, however, evidence in Cell 6P of nest washout. Eggshell fragments occurred in a linear arrangement, following the water flow pattern; two fragments occurred concave-down (CD) and one concave-up (CU).

Identifiable nest surfaces in all three colonies were examined for eggshell fragments and other biologic material after the chicks fledged. Forty-six percent of hatched, predated, and nests of unknown fate lacked remains; 15% of total nests contained eggshell fragments (Table 5). All of these fragments were found in Cells 2 and 6P. In Cell 6, only one abandoned nest, with one partially buried egg, was present. There was no evidence of the other nests or eggshell fragments in this colony. Most nests in this colony were comprised of sand scrapes; eggshell fragments may have been covered by wind-blown sand or may have washed away during rain events.

In Cell 2, eggshell fragments were found in 31% (*N* = 5) of nests (Table 6). Forty-one percent (*N* = 33) of the fragments were concave-up and 56% (*N* = 45) were concave-down (Table 8); most fragments (76%, *N* = 61) were less than 1 cm in diameter (Table 6).

In Cell 6P, 18% (*N* = 7) of nests contained eggshell fragments, and one nest contained a piece of eggshell membrane (Table 7). Sixty-seven percent (*N* = 49) of the fragments were concave-up and 33% (*N* = 24) were concave-down (Table 8). In this colony most fragments were 1 cm or greater (61%, *N* = 49) (Table 7). As in Cell 2, fragments occurred only in hatched, predated or nests of unknown fate and none exhibited bite marks. Between the two colonies, 153 fragments remained in 12 nests; more fragments were generally found in nests were hatching occurred (Table 8). There did not appear to be a relationship between clutch size and number of fragments remaining in these nests.

Table 9 shows the combined Cell 2 and Cell 6P eggshell fragment orientation data arranged by nest fate (hatched, predated, or unknown). In the hatched nests, eggshell fragment orientation was more likely to be concave-up (64%, *N* = 65), whereas predated and unknown nest fate fragments were typically concave-down (57%, *N* = 8; and 69%, *N* = 24 respectively). When hatched and predated values are combined, however, eggshell fragment orientation favors concave-up to concave-down 61:39. This combined data was used to perform a chi-square analysis that compared the number of concave-up (*N* = 71) to concave-down (*N* = 45) eggshell fragments in hatched and predated nests to the 60:40 distribution observed by Hayward et al. (2000). The analysis demonstrated that there was not a statistically significant difference between the studies, thereby supporting Hayward et al.'s (2000) findings. In hatched and predated nests, eggshell fragments are more likely to be oriented concave-up than concave-down.

Two additional chi-square tests compared 1) combined hatched and predated concave-up (*N* = 71) to concave-down (*N* = 45) values to an expected 50:50 distribution (if the orientation was due to chance), and 2) total hatched, predated, and unknown concave-up to concave-down orientations to the expected 60:40 distribution reported by Hayward et al. (2000). The chi-square analysis for the 50:50 distribution demonstrates a statistically significant difference, and therefore the concave-up to concave-down orientation is not random.

The chi-square analysis comparing the combined hatched, predated and unknown nest fates of concave-up (*N* = 82) to concave-down (*N* = 69) to Hayward et al.'s (2000) expected 60:40 distribution was not statistically significant. These data indicate that in hatched, predated and unknown fate nests, eggshell fragments are more likely to be oriented concave-up than concave-down, and agree with Hayward et al. (2000).

Tables 6, 7 and 8 summarize the position of eggshell fragments in Cell 2 and Cell 6P. Eggshells were mostly detected in nests composed of vegetation, and most fragments were located in the nest cup center, either stacked on top of each other or pressed deep into the nest. The latter likely resulted from trampling by chicks and/or adults. Surface fragments in nests seemed to favor the concave-up orientation, and fragments embedded in the nest structure favored the concave-down orientation. The largest number of fragments per nest typically occurred in hatched nests. Eggshell fragments present within the colony but outside the nests, seemed to favor the concave-down position.

A chi-square analysis compared the total numbers of concave-up ($N$ = 33) and concave-down (N = 46) fragments buried in nest vegetation and/or in the sand substrate from Cell 2 and Cell 6P to the trampled fragment ratio (60 concave-down: 40 concave-up) reported by Hayward et al. (2011). Buried fragments at Cells 2 and 6P seemed to be pushed into the nest vegetation and/or sand substrate, indicating that trampling may have occurred. The chi-square analysis showed no statistically significant difference in the two data sets, indicating that in nests where trampling likely occurred and eggshell fragments are buried in the nest or ground substrate, fragment orientation is more likely to be positioned concave-down than concave-up. These data support Hayward (2011).

An unpaired *t*-test compared the difference of eggshell orientation (CU:CD) in hatched and predated nests. The analysis showed that there was not quite a statistically significant difference between the favored concave-up orientation observed in hatched nests vs. the favored concave-down orientation in predated nests. Only 14 eggshell fragments were collected in predated nests compared to 102 in hatched nests. This outcome may be due to the nature of avian predation, where whole eggs are often removed from the nest by predators. The small sample size from predated nests may have adversely impacted this statistical outcome. The difference between eggshell orientation in predated and hatched nests warrants further study.

### Caribbean Flamingo (*Phoenicopterus ruber*)

Caribbean Flamingo nest taphonomy was studied at the NZP as a comparison to the Common Tern. The Caribbean Flamingo nests are dramatically different from that of the Common Tern in composition, size, and distribution. Flamingo nests are typically constructed of mud and small stones. At the NZP, topsoil and peat are added to the mud residue left from the previous year; this may influence the texture and weathering of the nests. Compared to the variation that occurs in Common Tern nests, the flamingo nests are remarkably similar to each other in structure and size, and are considerably closer together. The mean distance to the nearest neighbor nest in the flamingo colony is less than half the average wingspan of the Caribbean Flamingo (Table 10); compared to the mean nearest neighbor distance in the Common Tern colony that is approximately five times the adult wing span (Table 2). Two-and-half weeks after the flamingo's terminated nest maintenance, weathering was visibly evident, not only at the nest cone (Table 10) but also in the nest height. Caribbean Flamingo construct nests of 30 – 40 cm height; the nests at the NZP appeared to weather by ~5 cm in height.

Of the 32 nests in the flamingo colony, only six contained biologic material (feathers and eggshell fragments) at the surface (Table 11). Eggshell fragments present on nest surfaces and on the colony surface favored concave-down orientation. The Fisher's exact test comparing the number of concave-down ($N = 9$) to concave-up ($N = 1$) eggshell fragments on the colony surface (representing a trampled area) to an expected

50:50 distribution (if the orientation was random) was not statistically significant. These data indicate that the concave-down to concave-up orientation may represent random distribution. This statistical outcome may have been adversely impacted by the very small sample size (*N* = 10). The observations from this preliminary study of flamingo colony eggshell fragments may have favored the concave-down orientation and warrants further investigation. If the eggshell between nests is considered trampled and/or transported, and the dominant concave-down orientation is shown to be non-random, the data would agree with the Common Tern study and with Hayward et al. (2011).

All excavated nests contained eggshell fragments embedded in the nest substrate, most of which were stratigraphically $\leq$ 6 cm below the surface (Table 13) and in the nest cup center, as observed in the Common Tern nests. The nests where hatching occurred also contained eggshell membrane within this region; some of the membranes contained eggshell fragments positioned vertically with the concave surface facing into the nest.

The Fisher's exact test comparing the number of concave-down (*N* = 8) to concave-up (*N* = 2) eggshell fragments in nests to an expected 50:50 distribution if the orientation was random was not statistically significant. This indicates that the orientation of concave-down to concave-up eggshell may again represent a random distribution and the statistics may be impacted by the small sample size. If the eggshell fragments in the nests are considered trampled, the observed concave-down orientation may support Hayward's (2011) findings, but further study is needed to make this correlation.

The colony ground surface displays significant trampling by parents, chicks, and other adults. Hayward et al.'s (2011) experimental study of fragment orientation indicated that trampling by domestic chicks favored the concave-down to concave-up orientation of 60:40, compared to nests where hatching and predation had occurred. In the latter, a concave-up orientation was favored (Hayward et al., 2000). The preliminary flamingo data collected from nests and the colony surface may support Hayward et al.'s (2011) trampling hypothesis. After flamingo chicks leave the nest at NZP, adults and their offspring spend time on the nesting island walking over and on top of nests. This trampling behavior occurs not only on the ground surface between nests, but also on the nests themselves.

## CONCLUSIONS

Studies to assess evidence of hatching and/or predation in modern nesting colonies are not typically performed by biologists. Taphonomic studies, therefore, may be useful in determining nest fate in modern avian nesting sites. Visual examination for the presence of eggshell fragments and their orientation in modern colonial sites may provide more accurate interpretation for nests of unknown fate. In addition, this study builds upon the work of Hayward et al. (2000, 2011), providing observations and quantitative data that may increase the understanding of the reproductive behavior and paleobiology of extinct taxa, including non-avian dinosaurs. Factors to consider at fossil nesting localities are provided below.

1) *Eggshell Concentration* – Eggshell fragments may show greater abundance at nest centers, particularly for nests constructed of vegetation and/or mud and subaerial exposed during incubation. Eggshells and eggshell membrane may also be more common in hatched than predated nests, especially with the predominance of aerial predators within an area.

2) *Eggshell Orientation* – Abundant distribution of concave-up fragments may indicate hatching and/or nest predation, whereas a greater abundance of concave-down fragments may suggest trampling by chicks, juveniles, and/or adults. Concave-down fragment orientation in a linear arrangement on a single horizon may indicate direction of water flow and/or flooding conditions. In some circumstances, however, flooding may leave no evidence of nests, eggs, or young at the nesting site after the waters subside. Layering of fragments within the strata (i.e., small, concave-down fragments beneath larger, concave-up fragments) may also indicate nest location and active trampling within the nest structure. Further studies comparing concave-up to concave-down orientation between hatching and predation sites at avian colonies may provide additional information.

3) *Random Eggshell Scatter* – Scattered eggshell fragments across a colony may indicate transport by the wind; alternatively, these fragments may be carried in the beak or attach to feet or claws and dropped by young and/or adults.

4) *Whole Eggs in a Substrate* – Eggs buried in a substrate may indicate nest abandonment by the adult, with subsequent burial to wind or water transport of sediment. At fossil localities this may be mistakenly interpreted as underground incubation.

5) *Multi-species Nesting* – Some modern colonial nesting grounds typically include more than one avian species. In the Common Tern colonies, USGS biologists documented scattered nests of the Least Tern (*Sternula antillarum*) in Cells 2 and 6. Further, nest structure and success of the nests may vastly differ both among and within species.

6) *Nest Size* – Interpreting the original size of trace fossil nests constructed from fine-grained sediments requires caution because rapid weathering may occur once the adults terminate nest maintenance.

7) *Nest Elevation* – Nests may occur at different elevations within the same or adjacent colonies during the same nesting season; therefore, interpretations of a single nesting event or inferences of site fidelity require caution, particularly given the problem of time resolution in the rock record.

8) *Nest Density* & *Distribution* – Variations in nest structure may contribute to differential preservation of nests in the fossil record, thereby leading to misinterpretation of nest density and distribution. In addition, topographic features that influence nest location in modern nesting sites (e.g., vegetation, small gullies, and marshy areas) may not be easily identified in the rock record and therefore may account for nest-free areas at fossil egg sites.

## FUTURE WORK

Flamingo nests may serve as a valuable model for studying non-avian theropod fossil localities. Flamingo mud-mound nests are large (30 – 40 cm in height), densely distributed within the colony (just beyond pecking distance), and contain a single large egg (90 mm x 55mm). Because the chicks stay in nests for 6 – 8 days, and fledging does not occur for 9 – 13 weeks, trampling within the nests and between nests may increase preservation potential by forcing eggshell fragments into the muddy substrate.

The nest construction behavior of flamingos may also be of interest. Flamingos construct nests by dragging the tip of the bill through the mud and pulling it toward them, pressing it into place with the bill and feet. Females often sit on the partially built nest and scoop the mud towards her body with the beak, tucking it up and under her wings to produce a raised rim around the nest (Figure 4A). Flamingo mud nests are baked to a hard and compact structure in the sun and last for many months or even years, thereby increasing the potential for preservation in the fossil record. Feces are abundant in the nest structure and may be a factor in cementing sediments. Birds returning to the same colony in subsequent years refurbish and re-build old nests. In addition, more than one group of adults may use the nests in a single season (Ogilvie & Ogilvie, 1986).

Although the above mentioned characteristics may be important for behavioral inferences at dinosaur nesting sites, other considerations suggest this analog warrants caution. For example, this study shows that erosion occurs rapidly once the adult abandons nest maintenance. Because of erosional processes, preservation of topographic relief in the rock record requires unusual circumstances such as a flood event that buries the structure in sediment. Nevertheless, documentation of these nests and the associated behavior of the adults and young may provide important insight into controversial inferences of nesting strategy and behavior in some dinosaurs.

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