NEST SITE TAPHONOMY OF MODERN ARCHOSAURS

by

Ashley Lynn Ferguson

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Earth Science

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 2016

ACKNOWLEDGEMENTS

First off, I'd like to thank my advisor Dr. David Varricchio. He has been incredible to work with and without his guidance and lightheartedness I would not have made it through this program. Second, it's been a pleasure to work with my committee members Dr. David Willey and Dr. Jack Horner. Their insight into the research has proven invaluable. I am especially grateful for my brother and Dr. Varricchio, who had to put up with me in the field on multiple occasions. Thank you to Dr. Carlos Piña for his hospitality during our stay in Argentina and for his guidance in locating and interpreting caiman nesting sites. Thank you to Rauel, a local farmer in Argentina, who assisted us in locating caiman nests and helped us avoid getting lost and walking right into gigantic spider webs. I'm very thankful for the support that I received while working at the Bowdoin National Wildlife refuge. The staff are incredibly helpful and hospitable, going so far as to let me borrow a canoe. Thank you to Mark St. John and Elisa Boyd for letting me borrow boating equipment, knowing full well that I would be hauling back dead birds. I can't begin to count how many insightful conversations I've had with Jacob Gardner, Mikayla Struble, Jack Wilson and Chris Organ about analyzing and interpreting statistics as well as understanding the taphonomy of my material. I especially thank Mikayla and Michael Holland for letting me feed the dermestid beetles and teaching me how to properly clean and prepare modern skeletal material. Thank you to Evan Chase and L.J. Krumenacker for assisting in cleaning and identifying the avian taphonomic assemblage. Last, but not least, I'd like to thank my family for believing in me when I didn't and encouraging me to continue pursuing my dream.

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CHAPTER 1

INTRODUCTION

Modern analogs have been used throughout all fields of paleontology to deduce the behavior of extinct organisms. Modern taphonomic studies in particular provide a means to interpret and understand fossil localities. However, in order to use modern nesting sites as a proxy for understanding archosaurian nesting grounds from the geologic record, a familiarity of nesting behavior, developmental strategies, parental care strategies, nest site usage, and pre- and postmortem life histories needs to be understood to determine how they influence the generation of skeletal material at modern nesting sites (McGrath 2014; Wang et al., 2014). The goal of this thesis is to investigate the taphonomic processes that affect crocodylian and modern bird nesting localities in the hope that they would shed light into the identification of fossil nesting grounds and the interpretation of juvenile developmental stage. This project in particular observed nests of American crocodiles (*Crocodylus acutus*) at the Turkey Point Power Plant in Homestead, Florida, broad snouted caiman (*Caiman latirostris*) nests in the Northern Santa Fe and Chaco Provinces of Argentina, and colonial ground nesting birds (American white pelicans, double-crested cormorants, ring-billed and California gulls) at Bowdoin National Wildlife Refuge (BNWR) east of Malta, Montana. A major component of this project is the documentation of potentially preservable components, i.e., specimens (bones, eggshell, etc.) and structures (e.g. nesting traces) that might be represented in the

fossil record. This thesis documents the agents and processes influencing bone and egg accumulations and nesting trace preservation across diverse biologies and environments.

CHAPTER TWO

FROM EGGS TO HATCHLINGS: NEST SITE TAPHONOMY OF AMERICAN CROCODILE *(CROCODYLUS ACUTUS)* AND BROAD SNOUTED CAIMAN *(CAIMAN LATIROSTRIS)*

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2 and 3

Author: Ashley L. Ferguson

Contributions: Collected and analyzed taphonomic data, wrote manuscript.

Co-Author: David J. Varricchio

Contributions: Collected data and provided discussion and substantial edits.

Co-Author: Carlos I. Piña

Contributions: Assisted in locating caiman nests, and provided edits.

Co-Author: Frankie D. Jackson

Contributions: Assisted in collecting data and provided edits.

Manuscript Information Page

Ashley L. Ferguson, David J. Varricchio, Alex J. Ferguson
Palaios
Status of Manuscript:
__x_ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

FROM EGGS TO HATCHLINGS: NEST SITE TAPHONOMY OF AMERICAN CROCODILE *(CROCODYLUS ACUTUS)* AND BROAD SNOUTED CAIMAN *(CAIMAN LATIROSTRIS)*

ASHLEY L. FERGUSON[1], DAVID J. VARRICCHIO[1], CARLOS I. PIÑA[2], and FRANKIE D. JACKSON[1]

[1]*Montana State University, Department of Earth Sciences, Bozeman, Montana 59717, USA*

[2] *Proyecto Yacaré. CICyTTP – CONICET Dr. Matteri y España. CP 3105. Diamante, Entre Ríos. Argentina.*

email: ashley.ferguson3@msu.montana.edu

ABSTRACT: The nesting behavior of extant animals can potentially serve as either analogs or as taphonomic models for the interpretation of extinct archosaurian reproduction. Past studies have examined birds with open nests and nest-bound young and turtles with buried nests and precocial young. Here we taphonomically describe nesting of two crocodylians, the American crocodile (*Crocodylus acutus*) at Turkey Point, Florida and the broad-snouted caiman (*Caiman latirostris*) from Santa Fe and Chaco provinces, Argentina. Surveys focused on eggshell abundance, orientation, distribution, and nest construction from successfully hatched nests. *Crocodylus acutus* excavate triangular or semi-circular hatching traces in organic-rich sandy clay, with associated mollusk debris, limestone pebbles and cobbles. Depths of the cavity ranged from 20-45 cm with a breadth of 50-80 cm. Eggshell orientations outside the egg chamber favor concave down (58.1%). *Caiman latirostris* construct mound nests of predominantly plant debris in forested areas with organic rich soil or on vegetation islands. Nests range in diameter from 1.2-1.6 m with a height of 0.3-0.6 m. Eggshell orientations within the egg chamber favor concave up (61.8%), whereas fragments

outside of the chamber were nearly evenly distributed with 51.8% concave-up. Eggshell orientations observed outside the egg chamber in both crocodylians differs from the 60:40 up:down ratio in both bird and tortoise nests, as well as the 20:80 ratios of hydraulically transported shell. The distribution and orientation of eggshell in these crocodylians largely results from the adult females assisting and transporting the young during hatching and this ratio may facilitate interpretations of parental assistance in the fossil record.

INTRODUCTION

Using modern analogs to deduce the behavior of extinct organisms is a common practice in all fields of paleontology. For example, extant amniotes, such as birds and crocodylians, are the closest phylogenetic and morphologic equivalents to dinosaurs and are utilized in several studies to infer the nesting behavior of non-avian dinosaurs (Seymour 1979; Coombs 1989; Horner 1994; Varricchio et al., 1997; Mueller-Töwe et al., 2002; Deeming 2006; Brazaitis and Watanabe 2011). With the exception of one study of turtle nests with buried clutches and precocial young (Jackson et al., 2015), taphonomic specific evaluations of modern nest sites focus on avian open nests with nest-bound young (Horner, 1994; Hayward et al., 1997, 2000, 2011; Cruz 2007; Wang et al., 2014; McGrath 2014; Oser and Jackson 2014; Imai et al., 2015). This information has been intended as a proxy for dinosaur nesting sites. A number of these studies have used fragmented eggshell orientation to distinguish a transported assemblage from hatched, trampled, or predated nesting sites (Hayward et al., 2000, 2011; Wang et al., 2014; Oser

and Jackson 2014; Imai et al., 2015). For example, studies of successfully hatched tortoise, gull, and common tern nests demonstrate that fragmented eggshell favored a concave up orientation, with an approximately 60:40 concave up to concave down ratio, despite differences in nesting strategies (Hayward et al., 2000, 2011; Wang et al., 2014; Jackson et al., 2015). However, gas conductance studies, eggshell morphology of eggshell, and discoveries of large clutches of dinosaur eggs, possibly laid en masse (Seymour 1979; Deeming 2006; Jackson et al., 2008; Grellett-Tinner et al., 2006), suggest that dinosaurian nesting behavior may be more closely related to crocodylians who bury their clutches, have two functioning oviducts, and display parental care (Coombs 1989; Brazaitis and Watanabe 2011; Grigg and Kirshner 2015).

Modern taphonomic studies of avian and tortoise nesting sites reveal patterns in the abundance, orientation, condition, and spatial distribution of eggs, eggshell fragments, and bone. However, a similar taphonomic study of crocodylians nesting has yet to be done, despite the fact that extinct crocodylomorphs and most non-avian dinosaurs likely buried their eggs (Seymour 1979; Deeming 2002, 2006; Hastings and Hellmund 2015). Further, parental care has also been proposed for some non-avian dinosaurs (Varricchio et al., 1997, 2008; Clark et al., 1999; Horner et al., 2000; Hastings and Hellmund 2015). Nesting sites of extinct crocodylomorphs are rare in a global context, with approximately 20 reported by the end of 2015 (Srivastava et al., 2015). A taphonomic study of extant localities may help identify crocodylomorph nesting sites in the fossil record, as well as aid in the interpretation of dinosaurian nesting sites. Here, we document the distribution of biological remains associated with successfully hatched

nests of two crocodylians, the American crocodile (*Crocodylus acutus*) and broad snouted caiman (*Caiman latirostris*). We hypothesize that (1) the parental care demonstrated by adult crocodylians will produce a recognizable signature, such as nest site disturbance by the attending female; (2) the departure of precocial young from the nest soon after hatching would leave an abundance of eggshell and lack of predated skeletal material; and (3) eggshell orientations within crocodylian nests will approximate a 60:40 hatching signature.

AMERICAN CROCODILE *(CROCODYLUS ACUTUS)*

Crocodylus acutus inhabits neotropical areas such as the coast of Florida, the islands of Cuba, Jamaica, and Hispaniola, along the coasts of Central America, and south to Ecuador and Venezuela (Ponce-Campos et al., 2012) (Fig. 1). The species was listed as endangered in 1975 under the Endangered Species Act due to increasing habitat loss, low nest success and high hatchling mortality rates (Ogden 1978; Mazzotti and Cherkiss 2003; Ponce-Campos et al., 2012). Since then conservation efforts by the National Park Service, U.S. Fish and Wildlife Service, Fish and Wildlife Conservation Commission, and Florida Power and Light Company has decreased the endangered status to "threatened" within the United States (Mazzotti and Cherkiss 2003). Crocodile nests built near the Turkey Point Power Plant (TPP), a site owned by the Florida Power and Light Company near Homestead, Florida (Fig. 1), have the highest success rate of hatched young in Florida (Mazzotti and Cherkiss 2003). Construction of the power plant

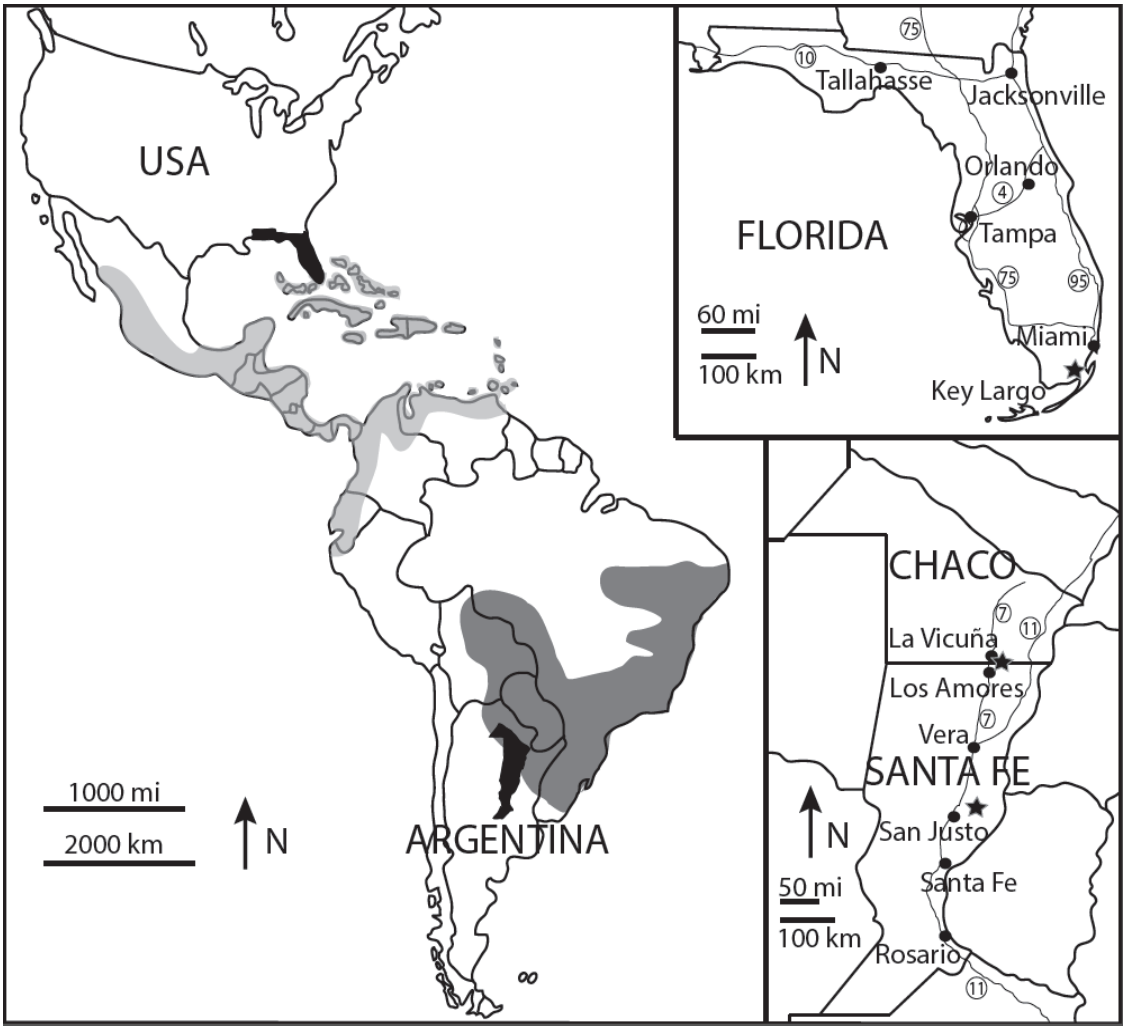

FIG. 1. —Occurrence of C. acutus (light gray) and C. latirostris (dark gray) and location of study areas. Stars indicate general locations of nest sites.

required excavation of a series of parallel canals and berms across an area 8 km long and km wide, split into five separate units. These man-made berms consist of friable organic-rich sandy clay with varying amounts of mollusk shells and pebble and cobble sized carbonate rock and support a number of plants, including Australian pine (*Casuarina spp*.), red mangrove (*Rhizophora mangle*), buttonwood (*Conocarpus erectus*), and other salt tolerant species (Mazzotti and Cherkiss 2003), as well as the crocodylian nests examined in this study.

This large crocodylian species (up to 7 m in length, with the average reproductive female measuring 2-3 m) (Throbjarnarson 1986; Trutnau and Sommerlad 2006) displays a dark gray or olive colored back with a white to yellowish belly (Trutnau and Sommerlad 2006). Unlike American alligators, which occur in the same area, the American crocodile has a long narrow snout and the fourth tooth on the dentary is visible when the mouth is closed. *Crocodylus acutus* prefers brackish water, but can be found in freshwater systems as well (Ogden 1978; Throbjarnarson 1986; Mazzotti and Cherkiss 2003; Trutnau and Sommerlad 2006). The crocodiles are extremely cautious, often retreating at the sight of people (Trutnau and Sommerlad 2006). During the reproductive season females dig cavity nests or build mound nests into loose substrate, choosing well-drained soils with stable temperatures and elevated locations (Grigg and Kirshner, 2015). Clutches range in size from 40-60 eggs with an incubation time around 85 days (Trutnau and Sommerlad 2006; Grigg and Kirshner 2015), with hatching occurring in early July at TPP (M. Cherkiss, personal communication). Females that construct mound nests will maintain primary and secondary mounds for consecutive use over several years (Ogden 1978). After egg laying the female will leave the nest, but visit more frequently when hatching time nears (Ogden 1978). Eggs are elongate (6-7.5 cm long and 4.5 cm wide) (Trutnau and Sommerlad 2006) with hard, smooth calcitic shells. Females respond to the chirping of young and will assist with hatching by digging a hole into the nest, gently breaking the eggs between her tongue and palate, and carrying the young to the water in the gular pouch (Ogden 1978; Throbjarnarson 1986). Hatching occurs synchronously with the chirping of the young possibly facilitating the synchronization, as typical of all

crocodylian species (Grigg and Kirshner 2015). Nests often become overgrown with vegetation before hatching occurs (M. Cherkiss, personal communication, 2011). The hatchlings are on their own within a few weeks (Trutnau and Sommerlad 2006). Major predators of *C. acutus* nests and hatchlings include raccoons (*Procyon lotor*) and fire ants (*Solenopsis*) (Mazzotti and Cherkiss 2003).

BROAD SNOUTED CAIMAN *(CAIMAN LATIROSTRIS)*

Caiman latirostris inhabit eastern central South America, including Uruguay, northeastern Argentina, Paraguay, Bolivia, and the southern and eastern sides of Brazil (Crocodile Specialist Group 1996; Trutnau and Sommerlad 2006) (Fig. 1). The species was listed as endangered until 1996 when it was relisted as of least concern (Crocodile Specialist Group 1996). Our study areas include two locations in Argentina: a swamp just outside of the small town of Cacique Ariacaiquin in the Santa Fe Province, ~100 km north of the city of Santa Fe (Fig. 1), and wet savannas and subtropical dry forests (Chaco Sarrano) just to the north and across the border into the Chaco Province from Los Amores (Fig. 1).

This species of caiman can reach a maximum size of 3.5 m, with reproductively active females averaging 1.5 m in length. A transverse bony ridge between the anterior corner of the eyes and a wide, short snout, possibly an adaptation for crushing shelled animals, characterize the species (Trutnau and Sommerlad 2006). Adult skin appears black on the back and white or light yellow on the ventral side (Trutnau and Sommerlad 2006). This species prefers calm, even stagnant fresh water environments with abundant

vegetation, as well as brackish swamps (Trutnau and Sommerlad 2006; Montini et al., 2006) and can be extremely aggressive if provoked. Unlike the American crocodile, *C. latirostris* only construct mound nests, either from vegetation or friable sediment (Trutnau and Sommerlad 2006; Larriera and Piña 2000). Hatchling size and clutch size (20-70 eggs) are related to the size of the female (Larriera et al., 2004; Montini et al., 2006; Trutnau and Sommerlad 2006; Grigg and Kirshner 2015), with egg width representing the limiting factor in the latter (Larriera et al., 2004). The eggs are elliptical (7 cm long and 5 cm wide) (Trutnau and Sommerlad 2006) with calcitic nodules or superficial wrinkles (Fernández et al., 2013). Females will defend the nest and assist the young when hatching occurs (Trutnau and Sommerlad 2006) approximately 70% of the time (C. Piña., in review). Predation of eggs is higher during dry years, with vegetation nests less affected than soil based nests; the most common predators include feral pigs (*Sus scrofa*), the common hawk (*Polyborus plancus*), and skunks (*Conepatus chinga*) (Larriera and Piña 2000).

METHODS

To characterize crocodylian nesting taphonomy and broaden our understanding of taphonomic processes at nesting localities we documented five *C. acutus* nests during late July of 2011 and eleven *C. latirostris* nests in early March of 2015. American crocodile nests occur on man-made berms constructed by the TPP in an attempt to expand their nesting habitat. The TPP biologists monitor all nests on the property as part of their study of the vulnerable species. In 2011, the hatching season for *C. acutus*, normally completed

by the first week of July, occurred several weeks late. As a consequence, only about half of the nests had hatched during the fieldwork interval. Once the reproductive season is over, TPP biologists collect eggs from the nests after hatching to evaluate nesting success, thereby disrupting the contents of the chamber. Three of the five egg chambers examined for our study, therefore, were considered unreliable for determining eggshell orientations. However, the number of complete or partial eggs collected by the biologists were documented. Each *C. acutus* nest is noted in chronological order (i.e. N1, N2, etc.) except for two nests dubbed Twin Nests due to their close proximity to one another. The Twin Nests are considered one data point because of the difficulty in distinguishing what eggshell material originated from which nest.

Researchers and graduate students from Diamante, Entre Ríos locate and document the broad snouted caiman nests within the Santa Fe province. A local farmer in the Chaco Province assisted in locating nests as well. The hatching season was in progress by the middle of March, 2015, with very little, if any, human activity associated with the nests. Following procedures of previous studies, we labeled each caiman nest in chronological order of nest discovery and designated its habitat by V (floating vegetation island, VN1) or F (forest, FN1). Previous studies have used these labels to distinguish different nesting habitats and for consistency we use those terms here.

After measuring height and diameter for each nest of both species, surface hatched eggs and eggshell fragments were gridded using a flexible 10 x 10 cm grid, tallied, and assessed for eggshell orientation as either concave up (CU), concave down (CD), or unknown. Eggshell designated as unknown indicates that the angle of the

eggshell exceeded 45^{o} to the horizontal plane or was disturbed upon excavation. Only eggshell fragments of 1 cm^{2} or greater were considered.

The mound nests of *C. latirostris* required careful removal of the chamber ceiling for *in situ* hatched eggshell counts. This was achieved by hand with various hand tools, such as dental picks and an oyster knife. This method is only used for *C. latirostris* since no excavations were done for *C. acutus*. Eggs and eggshell fragments within the egg chamber were tallied and their orientation documented. Any eggshell or eggshell membranes found in nearby bodies of water or in the trails left by females leading to the water were noted.

In order to test for significance, results were normalized by removing the unknown eggshell orientations and compared to 60:40 hatched, 20:80 transported, and 50:50 control eggshell ratios using a chi-square test with Yates correction. Due to an infestation of fire ants chamber counts for FC1 could not be considered for analysis. Other data collected for the eleven nests included nest composition and presence of scat or skeletal elements. Excavated material was backfilled and contoured to approximate the original nest surface.

RESULTS

Crocodylus acutus

The five nests consisted of cavity nests with a triangular- or semi-circular hatching trace (~ 1-2 m across) generated by the female. The term hatching trace used here is defined as the structure created by the female during excavation of the cavity or

mound nest to assist the young in hatching. Eggshell fragments and membranes were scattered in a semi-circle about the chamber (Fig. 2A). Nests were 50-80 cm in diameter with depths 20-45 cm. Each of the nests were located ~ 1.2 m in elevation above the surrounding water line with two nests (Twin Nests) located adjacent to each other (Fig. 2C). The hatching traces occurred on the downhill slope of the berms, generally in the direction of the water. Slight depressions in the soil were smooth and devoid of vegetation, representing drag traces from the female entering and exiting the water. The most obvious occurred within a meter of the water (Fig. 2B). Four of the five nests were

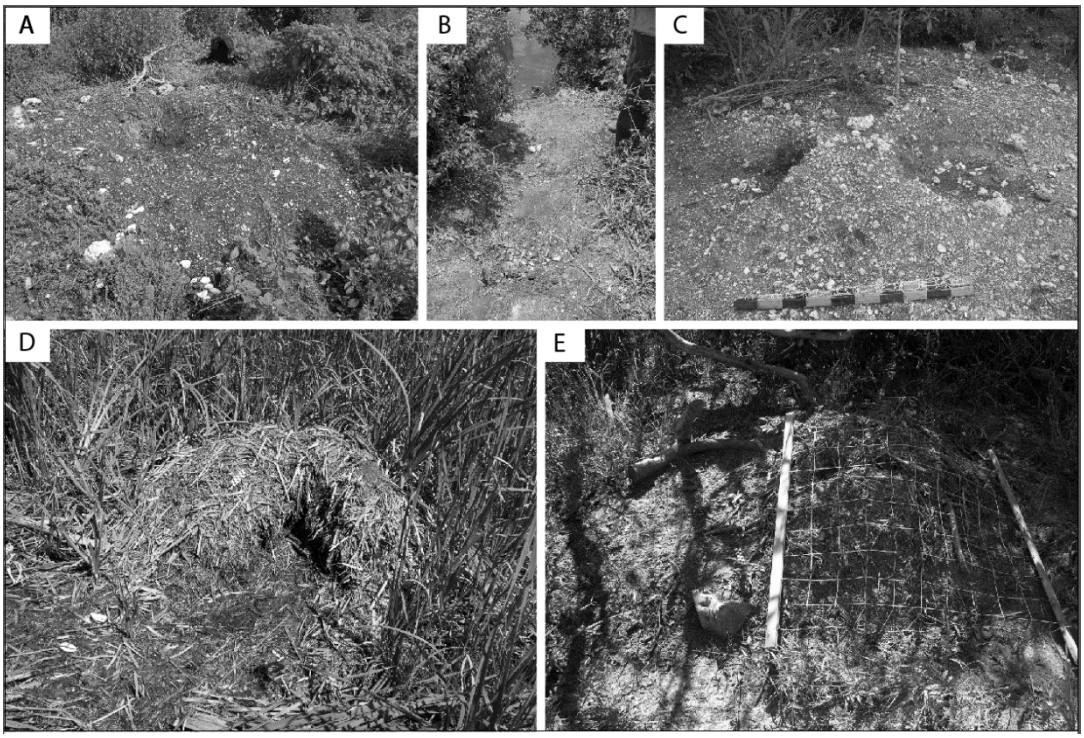

FIG. 2. — Examples of *Crocodylus acutus* (A-C) and *Caiman latirostris* (D and E) nests and traces. A is an example of a *C. acutus* cavity nest with a wide semicircular hatching trace. Backpack for scale. B) Drag trace from *C. acutus* female (N3). C) Twin Nests. Note the close proximity of the nests and numerus membranes inside the nest chamber. D) Example of a vegetation nest with a hatching trace, scale located on left side on surface of nest. Note two membranes on the trail in the bottom left corner of the picture. E) Forest nest example (FN2). Notice two holes on either side of the inflection point of the nest representing multiple attempts by the female to open the mound.

adjacent to low salinity (15 ppt) refugia pools. The nests lacked prey derived skeletal material or scat, with the exception of two marsh rabbit (*Sylvilagus palustris)* mandibles 3 m north of N3.

Among the five nests there were a total of 1764 eggshell fragments, 40.2% of which were CU (N=710), 55.7% CD (N=983) and 4.0% unknown (N=71; Table 1). Excluding the eggshell material of unknown orientation, the normalized total percentages from the surface gridded material yielded 41.9% CU and 58.1% CD, with all the nests (including the combined data from the Twin Nests) favoring CD, which ranged from 53.1-80.0%. Nests N2 and N3 yielded the two highest percentages of CD eggshell. Most of the fragmented material (96%) occurred within the semicircular hatching trace (Appendix A). A 2 x 2 x^2 with Yates correlation was used to compare the total number of CU (N=710) versus CD (N=983) eggshell from the nesting surface to 50:50, 60:40, and 20:80 CU:CD ratios. The observed values are statistically significant compared to all three ratios (50:50, $x^2(1) = 43.7$, $p < 0$; 60:40, $x^2(1) = 229.396$, $p < 0$; 20:80, $x^2(1) = 507.851$, $p < 0$), and therefore the eggshell distribution differs from previously reported hatched and transported assemblages (Hayward et al., 2000, 2011; Imai et al., 2015; Jackson et al., 2015).

A total of 70 egg membranes occurred in the hatching traces. These varied in quantity within individual nests and ranged from complete to fragments (Table 1). Eggs collected from the Twin Nests, N1, and N2 came from the nest cavity, and generally consisted of partial specimens (N=43). Only N3 included whole and partial eggs within the hatching trace (Table 1). The partial eggs had a section from one of the poles missing

TABLE 1. —Surface grid values for fragmented eggshell, membranes, and eggs for *Crocodylus acutus* nests. Includes CU, CD and unknown (UK) eggshell counts, normalized percentages (NCU% and NCD%), egg membranes (M), and whole (WE) and partial (PE) eggs.

	CU (%)	CD (%)	UK (%)	Total	NCU%	NCD%	M	WE	PE
TN	309 (45.8)	350 (51.9)	16 (2.4)	675	46.9	53.1	44	1	33
N1	219 (39.9)	290 (52.8)	40 (7.3)	549	43.0	57.0	18	0	6
N2	175 (35.1)	315 (63.1)	9 (1.8)	499	35.7	64.3	6	1	4
N3	7 (17.1)	28 (68.3)	6 (14.6)	41	20.0	80.0	2	2	2
Total	710 (40.2)	983 (55.7)	71 (4.0)	1764	41.9	58.1	70	4	45
Mean	177.5 (34.5)	245.8 (59.0)	18 (6.5)	441.0	36.4	63.6	17.5	1	11.3

as a result of hatching. Whole eggs included three infertile and one with a desiccated embryo.

Caiman latirostris

Two types of *C. latirostris* nests were documented: vegetation (N=8) (Fig. 2D) and forest nests (N=3) (Fig. 2E) all hatched successfully. Both types of nests consisted of mounds 30-60 cm in height and 1.2-1.6 m in diameter. Vegetation nests occurred on floating vegetation islands of reeds and grasses within marshes. The nests were composed entirely of the available floating vegetation. The forest nests were located along the banks of small bodies of water in the Chaco Province. These nests were composed of large pieces of grass, reeds, and palm leaves supported by a silt and clay matrix. Hatching traces in both types of nests were semi-circular or triangular gouges within the center of the nest, with the opening in the direction of the closest body of water. Forest nests exhibited more difficult to identify hatching traces compared to the vegetation nests. With the exception of VN7, which occurred ~ 14-16 m from the water, most nests were within 1-2 m or less of the water. Drag traces for both nest types were made by the female and display areas of flattened sediment or vegetation extending from the hatching trace to the water. Few of the nests had associated skeletal material, with a few large mollusk shells and fish bones found near FN2. A few pieces of scat were found associated with three nests.

In contrast to the *Crocodylus acutus* surface grid counts, total eggshell counts for *Caiman latirostris* nests are significantly lower (N=428) with an average 39.5 eggshell pieces per nest. Within the caiman nests 48.8% of the assemblage favors CU (N=212),

with 45.4% CD (N=197) and 5.8% unknown (N=25). Normalized grid percentages for CU and CD are more variable when compared to *C. acutus*, ranging from 35.3-64.7% for CU (Table 2). The normalized total percentages for *C. latirostris* surface material favor CU at 51.8% and 48.2% CD. Chi-square test with Yates correction demonstrates that the grid CU (N=212) and CD (N=197) observed values differ significantly from hatched ($x^2(1) = 11.027$, $p = 0.000898$) and transported ($x^2(1) = 257.061$, $p < 0$) values, but not from a 50:50 ratio ($x^2(1) = 0.479$, $p = 0.4889$).

Chamber counts are limited to nests VN2-4 and FN2-3 due to the abundance of fire ants within the egg chamber or removal of the chamber by the female during hatching. The number of eggshell fragments collected from within the nesting chamber is higher than the surface material, with a total of 574 eggshell pieces among the five nests (Table 2). Chamber counts favor CU, with a total of 47.4% (N=272) and 29.3% (N=168) CD. However, the number of unknown eggshell pieces increased, with a total of 23.3% (N=134). Normalized total percentages favor CU over CD with 61.8% and 38.2%, respectively. A 2 x 2 x^2 test with Yates correlation shows significant difference compared to a 50:50 ($x^2(1) = 24.111$, $p < 0.0001$) and 20:80 ($x^2(1) = 478.299$, $p < 0.0001$); however, no statistical significance exists between the observed CU:CD ratio and the 60:40 hatched ratio ($x^2(1) = 0.533$, $p = 0.4653$) for chamber eggshell values.

Combining the two datasets together (surface material and chamber material) yielded 484 CU (55.8%) and 365 CD (44.2%) fragments. This combined value is also not statistically different in comparison to a 60:40 ratio ($x^2(1) = 3.043$, $p = 0.08109$) but does differ significantly when compared to 50:50 ($x^2(1) = 16.4$, $p < 0.0001$) and 20:80 ($x^2(1) =$

TABLE 2. —Grid and chamber eggshell, egg, and membrane counts for *Caiman latirostris*. Percentages of eggshell indicated by parentheses. Includes CU, CD and unknown (UK) eggshell counts, normalized percentages (NCU% and NCD%), egg membranes (M), and whole (WE) and partial (PE) eggs.

	Grid Count						Chamber Count								
	CU(%)	CD(%)	UK(%)	Total	NCU%	NCD%	CU(%)	CD(%)	UK(%)	Total	NCU%	NCD%	M	WE	PE
VN1	10(50.0)	9(45.0)	1(5.0)	20	52.6	47.4	-	-	-	-	-	-	3	0	0
VN2	16(55.2)	10(34.5)	3(10.3)	29	61.5	38.5	52(44.8)	28(24.1)	36(31.0)	116	65	35	7	0	0
VN3	3(50.0)	2(33.3)	1(16.7)	6	60	40	97(52.2)	64(34.4)	25(13.4)	186	60.2	39.8	5	1	0
VN4	33(43.4)	38(50.0)	5(6.6)	76	46.5	53.5	64(49.2)	52(40.0)	14(10.8)	130	55.2	44.8	7	0	0
VN5	10(52.6)	9(47.4)	0(0.0)	19	52.6	47.4	-	-	-	-	-	-	3	0	0
VN6	38(52.8)	28(38.9)	6(8.3)	72	57.6	42.4	-	-	-	-	-	-	4	0	0
VN7	12(33.3)	22(61.1)	2(5.6)	36	35.3	64.7	-	-	-	-	-	-	1	0	0
VN8	11(64.7)	6(35.3)	0(0.0)	17	64.7	35.3	2(28.6)	2(28.6)	3(42.9)	7	50	50	0	2	3
FN1	23(47.9)	22(45.8)	3(6.3)	48	51.1	48.9	-	-	-	-	-	-	-	-	-
FN2	40(58.8)	25(36.8)	3(4.4)	68	61.5	38.5	41(46.6)	9(10.2)	38(43.2)	88	82	18	0	0	0
FN3	16(37.2)	26(60.5)	1(2.3)	43	38.1	61.9	16(34.0)	13(27.7)	18(38.3)	47	55.2	44.8	1	0	0
Total	212(48.8)	197(45.4)	25(5.8)	434	51.8	48.2	272(47.4)	168(29.3)	134(23.3)	574	61.8	38.2	31	3	3
Mean	19.3(49.6)	17.9(44.4)	2.3(6.0)	39.5	52.9	47.1	45.3(42.6)	28.0(27.5)	22.3(29.9)	95.7	61.3	38.7	3.1	0.3	0.3

724.44, $p < 0.0001$). Two nests (VN3 and VN9) include minor amounts of eggshell (N =15) present in the drag trace left by the female. A total of 31 membrane fragments were found among the nests; eggs are uncommon, with only 3 partial hatched eggs and 3 infertile complete eggs. One membrane associated with VN7 included 26 attached eggshell fragments still attached (13 CU, 7 CD, and 6 unknown).

DISCUSSION

The nesting biology of these two species of crocodylians display significant differences, despite both burying their eggs and providing post-hatching parental assistance to the young. The *Crocodylus acutus* nests were dug cavity nests in organic rich sandy clay (Fig. 2A, C). Though *C. acutus* construct mound nests, none were observed in this study. The female excavated a semicircular or triangular hatching trace originating from the egg chamber and widening toward the closest shoreline. This hatching trace was accompanied by a drag trace from the water to the nest (Fig. 2B).

Whole eggs were rare, with only four associated with the five nests. Only N3 included eggs and partial eggs outside of the egg chamber. The hatching trace was littered with membranes and eggshell fragments (Appendix A). During hatching the hard yet brittle eggshell flakes off of the tough membrane leaving behind fragmented eggshell. The number of partial eggs in the nest chambers is extremely variable, ranging from 2-33 (Table 1). The brittle eggshell, along with the digging and transport of eggs by the female, likely contributed to the amount of fractured eggshell and the lack of partial eggs in three of the five nests.

In contrast, the caiman *(C. latirostris)* built mound nests out of vegetation or organic rich silt and clay (Fig. 2D, E). The vegetation nests exhibited a distinct semicircular or triangular hatching trace (Fig. 2D); the female in some cases (N=3) completely removed the chamber during excavation. Recognizing the hatching trace in the forest nests was difficult due to the more diffuse morphology of the trace. Two small pits on either side of nest FN2 (Fig. 2D) resulted from the female's may have attempt to dig in multiple places to free the young. The drag traces to and from the water are extremely similar to those associated with *C. acutus* nesting sites. Whole and partial eggs are rare, with only three of each among the 11 nests, with VN8 contributing five of the six whole and partial eggs (Table 2). The total number of membrane specimens represent less than half of the amount found in the crocodile nests; similarly, hatched eggs with attached eggshell pieces are rare due to the hard yet brittle eggshell and tough membranes. Most of the eggshell fragments occurred within the egg chamber. No apparent difference was found between the amount of eggshell material and its distribution between the vegetation and forest nests (Appendix B). Smaller hatching traces in the mound nests, and higher vegetation content of the nest structure, likely contributed to higher eggshell content inside the egg chamber.

In both species the nests exhibit a lack of prey derived skeletal material despite nest defense documented in both species. FN2 had associated fish elements and a large gastropod shell; however, branches occurring above the nest would provide a suitable location for birds to roost and drop prey material on top of the caiman nest. *Crocodylus acutus* females often leave the nest after eggs are laid, only visiting on occasion with

more frequent visits as the hatching time nears (Ogden, 1978). This would explain a lack of prey skeletal material left by the female. American alligators have been known to go without food during the incubation period (Grigg and Kirshner 2015) and if *Caiman latirostris* females display similar behavior this would also explain the lack of skeletal material associated with the nests. This may also be attributed to the precocial nature of the young in that they do not spend time gathering prey materials around the nest itself and require little parental care after hatching. Juvenile crocodiles mainly feed on terrestrial and aquatic invertebrates and none of the nests showed clear signs of the associated gastropods preyed on by *C. acutus* juvniles. Most prey captured by crocodylians is swallowed whole (Grigg and Kirshner 2015) which could also account for a lack of skeletal material associated with the nests as well as the fact that most feeding occurs in the water (Grigg and Kirshner 2015).

Eggshell Distribution

In *Crocodylus acutus* nests approximately 96% of the eggshell occurs inside the semicircular hatching trace (Appendix A), whereas most of the eggshell on the surface in *C. latirostris* nests is contained in the hatching trace and the trails leading towards the water (Appendix B). The crocodile (*C. acutus*) and caiman nests (*C. latirostris*) nests average, respectively, 89.6 and 33.4 eggshell pieces per meter on the surface. This distribution may result from a more compact substrate and the female digging into a cavity, rather than a more accessible mound nest. The eggshell distribution of caiman forest nests differs little from the vegetation nests (Appendix B) and therefore the mound nesting strategy appears to dictate the distribution. Almost all of the membrane fragments

associated with the caiman nests are found outside of the egg chamber and in the trails leading to the water (N=30, 96.8%). In contrast, most of the eggshell found in the caiman nests were concentrated in the egg chamber (57%). Although not assessed, given the amount of eggshell and partial eggs present in Twin Nests, we would expect similar amounts in *C. acutus* chambers.

Taphonomic study of Agassiz's desert tortoise (*Gopherus agassizzi)* nests showed that a significant amount of eggshell material associated with *in situ* eggs occurred inside the eggs, (N=106) as well as the surrounding matrix of the underground chamber (N=79) (Jackson et al., 2015). Tortoise nests had no significant amount of eggshell or hatched eggs above the egg chamber. Though the desert tortoise and both species of crocodylian have precocial young, the eggshell spatial distribution differs significantly due to the parental care exhibited by the crocodilian females.

It has been suggested that eggshell from successfully hatched eggs that are buried within sediment would remain inside the eggs, rather than within the surrounding sediment (Mueller-Töwe et al., 2002, pg. 158). This assumption has been applied to large spherical eggs from China examined by computed tomography. However, the data Mueller-Töwe et al., (2002) collected are from eggs in museum collections without taphonomic or sedimentologic context. Therefore the number of eggshell fragments occurring outside of the eggs remains unknown. Jackson et al.'s. (2015) tortoise research, as well as our research presented here, suggests that the large amount of eggshell fragments outside the nest and around the eggs in the egg chamber may

represent a more useful indicator of hatching, especially with animals that assist young out of eggs.

Eggshell Orientation

Studies of avian eggshell orientation provide valuable information in discerning *in situ* hatched, predated, or trampled assemblages versus transported eggshell. Hayward et al., (2000, 2011) have noted that a predominance of CU eggshell is associated with successfully hatched gull, chicken, and predated sites (63-79%). A common tern nesting site on Poplar Island, Chesapeake Bay, Maryland yielded similar results for eggshell fragments found on the nesting surface of hatched and predated sites (68:32) (Wang et al., 2014). However, material in the subsurface of the tern nests yielded a 42:58 ratio, more closely matching an experimental 40:60 ratio at trampled sites reported by Hayward et al., (2011). Hydraulically and wind transported assemblages favor CD, with only ~20% CU (Hayward et al., 2011; Imai et al., 2015). These finding have been applied to dinosaur nesting sites such as Devils Coulee in Alberta, Canada; Augusta Site in

TABLE 3. —Comparison between crocodilian, tortoise, and avian nesting ratios where distinctions were made between the surrounding sediment and inside the nest or egg. * Refers to eggshell orientations in the surrounding sediment. ** Indicates burial post hatching. References: 1) this study, 2) Jackson et al., 2015, 3) Wang et al., 2014.

	Surface/Surrounding Sediment	Chamber/Inside Egg	Surface and Chamber	References
American crocodile	42:58	N/A	N/A	1
Broad snouted caiman	52:48	61:39	56:44	1
Tortoise	38:62*	69:31	57:43	2
Common tern	68:32	42:58**	54:46	3

Montana, U.S.A (Hayward et al., 2000); and Jackknife Creek in Idaho, U.S.A. (Simon 2014). These Mesozoic nesting sites yielded a similar CU:CD ratio to avian hatched assemblages (56-60% CU). Further, Jackson et al., (2015) examined the Agassiz's desert tortoise (*Gopherus agassizzi)* and reported that fragments inside the egg and the immediate surrounding sand yielded an approximate 60:40 hatched ratio (57:43) (Table 3), similar to that found in avian assemblages. However, it is important to note that the sample size and CU:CD ratios varied across the individual tortoise nests (CU percentages from 14-78%) and the orientation depended on the location relative to inside and outside of the egg. They conclude that assessing fossil assemblages require large sample sizes (e.g., N > 100) to accurately represent an entire locality.

The *Crocodylus acutus* surface material CU:CD ratio for all nests in this study was 42:58 (N=1693) (Table 3), suggesting a trampled assemblage. This ratio may reflect trampling by the female as she transported the young from the nest to the water. However, the tortoise eggshell orientations display a similar ratio in the sediment around the egg chamber (Table 3). Therefore, this signature does not appear unique to the American crocodile.

In contrast to the *Crocodylus acutus* CU:CD ratio, *Caiman latirostris* CU:CD surface material on and around the nest was 53:47, matching a 50:50 CU to CD ratio. The surface values may represent a transition from a hatched assemblage ratio towards a trampled assemblage caused by the female removing the eggs and young. Influence from storms isn't likely as the nests we examined hatched within days of our arrival and no storms occurred during the two weeks of collection. Chamber eggshell material was

61:39 (Table 3), closely matching the expected 60:40 hatched ratio seen in tortoise and avian nests. The chamber ratio matches the CU:CD ratio reported in avian assemblages, despite the difference in nesting strategy and behavior. This also reflects the CU:CD ratio seen in dinosaur nesting sites interpreted as non-transported nesting assemblages (Hayward et al., 2000; Simon 2014) and tortoise nesting sites (Jackson et al., 2015). However, there are important factors to take into consideration when analyzing these numbers. The number of eggshell pieces associated with the surface material ranged from 6-76 with the percentage of CU eggshell varying from 38-64% in normalized total values. For the chamber eggshell fragments the amount of material in each chamber was substantially different, ranging from 7-186, while the percent of CU material varied from 50-82% in normalized values. However, the surface and chambers are influenced by one outlier and therefore we believe the total ratio still reflects the overall nesting assemblage.

In order to make these values comparable to the tortoise dataset for surface and chamber material we have been combined the data yielding a ratio of 56:44 (Table 3). This ratio is very similar to the tortoise data and statistically indistinguishable from the 60:40 ratio found in avian nesting sites. The scattered assemblage seen in *C. acutus* nests may be a product of the female digging out young from a hole instead of removing a smaller section of material from a mound. The trampling signature may be a more clear result of the female traveling back and forth from the nest. Chamber values, or the combined chamber and surface values, are likely more representative of *C. latirostris* nests than evaluating the surface material alone, as well as in interpreting fossil assemblages. Considering material found in the chamber is less likely to be influenced by

transportation and erosion, this increases the likelihood of preserving *in situ.* The missing chamber counts from the *C. acutus* nests leaves room for speculation as to how different the *C. acutus* nests are from *C. latirostris* nests; however, surface orientations and distributions are still important in interpreting fossil nesting sites and possible modes of parental care.

Limitations

The first and most obvious limitation to our study is the small number of *C. acutus* nests. This increases the likelihood of overestimating the effect size and decreases the reproducibility of results. Second, eggshell orientations were not counted inside the egg chamber for *C. acutus* contributing to the difficulty of accurately comparing the two species. Therefore, *C. acutus* nests and *C. latirostris* forest nests represent preliminary results and a larger dataset of nests are necessary in order to more accurately describe the population. Lastly, several chamber counts from *C. latirostris* could not be taken due to fire ant colonies directly on the egg chamber. Increasing the sample size would increase the chances of finding nests without the ant colonies but we recommend taking precautions before embarking to collect data from *C. latirostris* nesting sites. Despite these limitations, this study provides the first in depth evaluation of crocodylian nesting sites and can be used as a stepping stone for further analyses.

CONCLUSIONS

Crocodylus acutus and *Caiman latirostris* nesting sites yielded 5 and 11 successfully hatched nests, respectively. Large amounts of eggshell were associated with

the nests with little to no skeletal material. *C. acutus* eggshell was scattered throughout the hatching trace with ~4% found above the egg chamber, whereas *C. latirostris* eggshell material was found predominately inside the egg chamber (57%), despite only 6 nests with available chamber data. Surface eggshell counts in *C. acutus* nests closely match a trampled assemblage (42:58), differing from the ~50:50 surface assemblage documented in *C. latirostris* (53:47). Chamber material associated with the *C. latirostris* nests statistically matches the 60:40 CU vs CD ratio (61:39) reported in bird and tortoise nesting assemblages and combining chamber and surface material statistically matches this ratio as well (56:44). These crocodylian nests have a recognizable hatching trace and a lack of biological material (besides eggshell) confirms our hypothesis proposed for an absence of prey material associated with precocial young. However, only *C. latirostris* nests match the 60:40 hatched ratio reported from avian and tortoise nesting sites. The increased amount of digging required in order to free young from a cavity nest versus a mound may influence the distribution and orientation in *C. acutus* nests.

These modern taphonomic investigations provide important insights into interpreting nesting sites in the fossil record. A lack of prey bones could denote adult feeding habits, such as hunting in the water and generally swallowing prey whole, and a short residence time by precocial young at nesting sites. Large spatial distributions and quantities of eggshell associated with buried nests may indicate hatching assistance by a parent. Eggshell orientations can distinguish a solely transported assemblage from a hatched or trampled signature. Continued work in this area will lead to a better understanding of the type and distribution of biological remains that may be found in

fossil localities and whether they reflect the behavior of adults and the behavior and developmental stage of young.

ACKNOWLEDGMENTS

A very special thank you goes to the National Science Foundation Division of Earth Sciences for providing funding for this field work (grant number 0847777 to DJV). Thank you to J. Gardner, J. Wilson, and C. Organ for discussion and mathematical insight. We sincerely thank J. R. Lindsay, J. Gless, M. Aldecoa, J. Wasilewski and the Florida Power and Light Company for sparing their time to assist us in locating American crocodile nests and M. Cherkiss and the USGS for introducing us to the crocodile nests. We'd like to extend a very special thank you to Rauel who located the elusive caiman forest nests and helped us evade monstrously sized spiders. We would also like to thank CONICET and the Centro de Investigacion Cientifica y Transferencia Tecnologica a la Produccion in Diamante for letting us stay in their institution and the Montana State University Earth Sciences department for field equipment and support for this project.

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CHAPTER 3

NEST SITE TAPHONOMY OF COLONIAL GROUND NESTING BIRDS AT BOWDOIN NATIONAL WILDLIFE REFUGE

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2 and 3

Author: Ashley L. Ferguson

Contributions: Collected majority of biologic material, obtained appropriate permits, collected and analyzed data, wrote manuscript.

Co-Author: David J. Varricchio

Contributions: Assisted in data collected and provided discussion and substantial edits.

Co-Author: Alex J. Ferguson

Contributions: Assisted in the majority of data collection and provided edits.

Manuscript Information Page

Ashley L. Ferguson, David J. Varricchio, Alex J. Ferguson
Palaios
Status of Manuscript:
__x_ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

NEST SITE TAPHONOMY OF COLONIAL GROUND NESTING BIRDS AT BOWDOIN NATIONAL WILDLIFE REFUGE

ASHLEY L. FERGUSON[1], DAVID J. VARRICCHIO[1], ALEX J. FERGUSON
[1]*Montana State University, Department of Earth Sciences, Bozeman, Montana 59717, USA*
email: ashley.ferguson3@msu.montana.edu

ABSTRACT: Taphonomy of extant birds in combination with studies of modern reptiles provides a range of models for interpreting reproduction in ancient archosaurs. Here we describe reproductive assemblages generated by nesting American white pelican (*Pelecanus erythrorhynchos*), double-crested cormorant (*Phalacrocorax auritus*), and two gulls (*Larus*). A total of 25 gull, 25 cormorant, and 20 pelican nests yielded 171 invertebrate exoskeletons, 7667 bones, and 2174 eggshell fragments. Gulls constructed nests of sticks and grass ranging from 19-67 cm in diameter and 3-5 cm in height. Associated avian elements were common (65.4%) with almost half consisting of skeletally mature gull bones. Cormorant nests were 20-30 cm in height, 34-50 cm in diameter and made from sticks, bones, and man-made debris. Prey items dominate the assemblage (72.4%), followed by juvenile cormorant elements (15.2%). Pelicans made simple scratch nests 40-77 cm in diameter and 3-4 cm in height dominated prey material (51.3-76.9%) and juvenile pelicans (3.5%). Most elements associated with pelican and cormorant nests occurred outside the nest (46-82%), whereas most gull nesting debris was found inside the nests where 81% of the eggshell was predated pelican eggshell. Eggshell concave up (CU) and concave down (CD) orientations on the surface of gull nests characterized a predated assemblage, whereas pelican and cormorant surface

orientations were approximately 50:50 (CU:CD), suggesting alteration by trampling altricial young. Weathered bones in the subsurface of cormorant and pelican nesting sites, and layers of predated eggshell in gull nests, suggest an accumulation of material over several years. The amount of material associated with the nests, as well as the relative age of the nester skeletal material, provides a means of distinguishing altricial and semiprecocial nesting sites.

INTRODUCTION

Dinosaur eggs span almost every continent and represent the bulk of ootaxa diversity suggesting a variety of dinosaur taxa (Carpenter and Alf 1994; Mikhailov 1997). Several studies have found that some small carnivorous dinosaurs share a multitude of reproductive traits with that of extant birds, including; an asymmetric egg shape, large egg to body size, rimmed open nests, (Varricchio 1997; Clark et al., 1999; Varricchio et al., 1999), a rigid two layered calcite structure (Mikhailov 1997), and water vapor conductance rates or porosity consistent with an egg structure exposed in an open nest and of an avian egg of similar size (Deeming 2006; Varricchio et al., 2013). Discoveries of adult theropod skeletons on top of egg clutches support the vapor conductance data and reinforces the inference of avian brooding behavior in maniraptorans. Additionally, several behaviors have been attributed to dinosaurs that are also avian-like, such as high nest site fidelity (Horner, 1982), pre-and post-hatching parental care (Horner 1982; Varricchio 1997, 2011; Varricchio et al., 2013; Clark et al., 1999), and colonial nesting (Horner 1982, Carpenter 1999). Considering these

similarities, modern avian nesting sites may be a relevant analog into inferring dinosaurian reproduction and nest site taphonomy.

Studies documenting fragmented eggshell have demonstrated that particular ratios of concave up and concave down fragments characterize hatched, predated, or transported assemblages (Wang et al., 2014; Hayward et al., 2000, 2011; McGrath 2014; Imai et al., 2015; Jackson et al., 2015). For example, successfully hatched gull, common tern, turtle, and caiman nests show that fragmented eggshell favors a concave up orientation with an approximate 60:40 concave up versus concave down ratio, despite different nesting strategies (Jackson et al., 2015; Hayward et al., 2011; Wang et al., 2014; Chapter 2). However, the subsurface orientations of common tern nests (42:58) and the lack of eggshell material found in the subsurface underneath great blue heron nests (McGrath 2014), suggests the mechanisms of eggshell burial or subsurface processes affect eggshell orientation (Wang et al. 2014) and abundance. Flume tests of fragmented chicken, gull, goose, ostrich and emu eggs suggest that hydraulic processes skew eggshell to a more stable concave down orientation (over 80%) (Hayward et al., 2011; Imai et al., 2015), allowing recognition of hydraulically transported eggshell assemblages.

Studies of material found outside of the nest are relatively rare (Horner 1994, Cruz 2007; Wang et al., 2014, McGrath 2014; Jackson et al., 2015). In 1994, Horner compared the size range and distribution of American white pelican (*Pelecanus erythrorhynchos)* and double-crested cormorant (*Phalacrocorax auritus)* nests at the Bowdoin National Wildlife Refuge (BNWR) in northern Montana to dinosaur nesting sites in the Upper Cretaceous Two Medicine Formation. He found that juvenile elements

are concentrated in nesting grounds and proposed that juvenile material. Here, we expand on this study by returning to BNWR and gathering quantitative observations from colonial ground nesting birds, including pelicans, cormorants, California gulls (*Larus californicus*) and ring-billed gulls (*Larus delawarensis*). We test (1) the practicality of eggshell orientation in determining a successfully hatched or predated assemblage on the surface as well as the subsurface and (2) if the types and abundance of biological material left behind after nesting reflect semiprecocial versus altricial young. We would expect birds with altricial nests to leave behind more prey items for the young and a trampling eggshell orientation signature to denote a longer residence time in the nest.

OVERVIEW OF NESTING BEHAVIOR AND BIOLOGY

Ring-billed Gull

Ring-billed gulls exhibit a high fidelity to a particular colony site, generally consisting of islands, and even specific areas within that colony (Ludwig 1974; Pollet et al., 2012). Nests are constructed by both parents from sticks, grass, leaves, moss, and molted feathers in low open areas with sparse vegetation or under trees. Clutch sizes range from 2-4 eggs (Table 1), average of three eggs (Berger and Gotchfeld 1996), with the eggs varying in color from olive gray, smoke gray, pale pearl gray, or a burnt umber color with irregular splotches. Parents will often try to retrieve eggs that have rolled out or will extend the nest around displaced eggs.

Chicks are born asynchronous (Brown and Morris 1996) with a few documented cases of young hatching synchronously (Southern 1987) and semiprecocial, leaving the

TABLE 1. —General biology of the four species of birds in this study

Species	Diet	Nest Builder	Nest Type	Clutch Size	Young Developmental Stage	Fledging Age (days)	Incubation Period (days)
Ring-billed gull	Omnivore	Male and Female	Vegetation	2-4	Semiprecocial	40-45	20-31
California gull	Omnivore	Male and Female	Scratch or Vegetation	1-4	Semiprecocial	40-60	22-28
American white pelican	Mostly fish	Male and Female	Scratch	2	Altricial	63-70	~30
Double-crested cormorant	Mostly fish	Male and Female	Arboreal or Elevated Vegetation	2-7	Altricial	72-84	25-28

nest after around 40-45 days (Pollet et al., 2012). However, by four days old the chicks begin leaving the confines of the nest travel with the parents up to 40 m away from the nest site on foot. Diets of adult gulls consist of fish, insects, worms, rodents, vegetation, and garbage (Pollet et al., 2012).

California Gull

California gulls have a typical gull diet of insects, invertebrates, vertebrates and garbage. The gulls create scratch nests in sand or soil, often with vegetation, feathers, and bones as a nest lining, although lining can be absent. Clutch size is between 1-4 eggs, averaging 2-3 eggs depending on location (Berger and Gotchfeld 1996), and colors range from buff to greenish with dark spots, speckles, and splotches (Winkler, 1996). California gull chicks are also born asynchronously and semiprecocial, leaving the nest around 40-60 days old. By around 4 days old the chicks are already moving short distances around and outside of the nest (Winkler, 1996). By 9-20 days old the chicks will run as much as 7 m to hide under cover at the sound of alarm calls (Winkler, 1996). Between 40 and 60 days the young abandon the nest and young move toward the water with some young able to fly short distances. Chicks are fed until fledging age (Table 1).

American White Pelican

The American white pelican creates large scratch nests with little to no insulation with both sexes using their bills to shuffle the sediment (Knopf and Evans 2004). Females lay two eggs with a uniform chalky appearance. The young are altricial and hatch asynchronously with older chicks often harassing the younger sibling to the point

where the younger chick dies of starvation, exposure, or predation (Knopf and Evans, 2004). The young fledge between 63-70 days. The adult diet consists of fish such as minnows, carp, rainbow and cutthroat trout, and suckers and they will often eat bottom feeders (Elliot 1996; Knopf and Evans 2004). American white pelicans have been recorded consuming small birds such as duck chicks and pigeons but no formalized documentation of why or how often pelicans consume birds.

Double-crested Cormorant

Double-crested cormorants are arboreal and ground nesters and will often share nesting grounds with pelicans. Like other ground nesting birds, they prefer islands with sparse vegetation (Sullivan et al 2006). This species has some site fidelity and will often build nests that are re-used in subsequent years (Sullivan et al 2006). The ground nests are often 4-17 inches high and made by both adults with sticks, seaweed, and grass (Sullivan et al., 2006; Dorr et al., 2014). Cormorants lay 1-7 eggs, averaging 3-4 (Orta 1992) (Table 1) that are a distinct pale blue color. Chicks are altricial and require the care of their parents and hatch asynchronously. Younger chicks usually perish due to the insistent and more vocal begging activities of the older chicks (Sullivan et al., 2006). Chicks may stay in the nest until 6-7 weeks of age. The adult diet is almost exclusively fish with the occasional insect, crustacean or amphibian (Dorr et al., 2014).

NESTING LOCALITY AND METHODS

The study site is located on three separate islands (Woody, Long, and the northern Pelican Island) within BNWR in the Milk River Valley of Phillips County, approximately

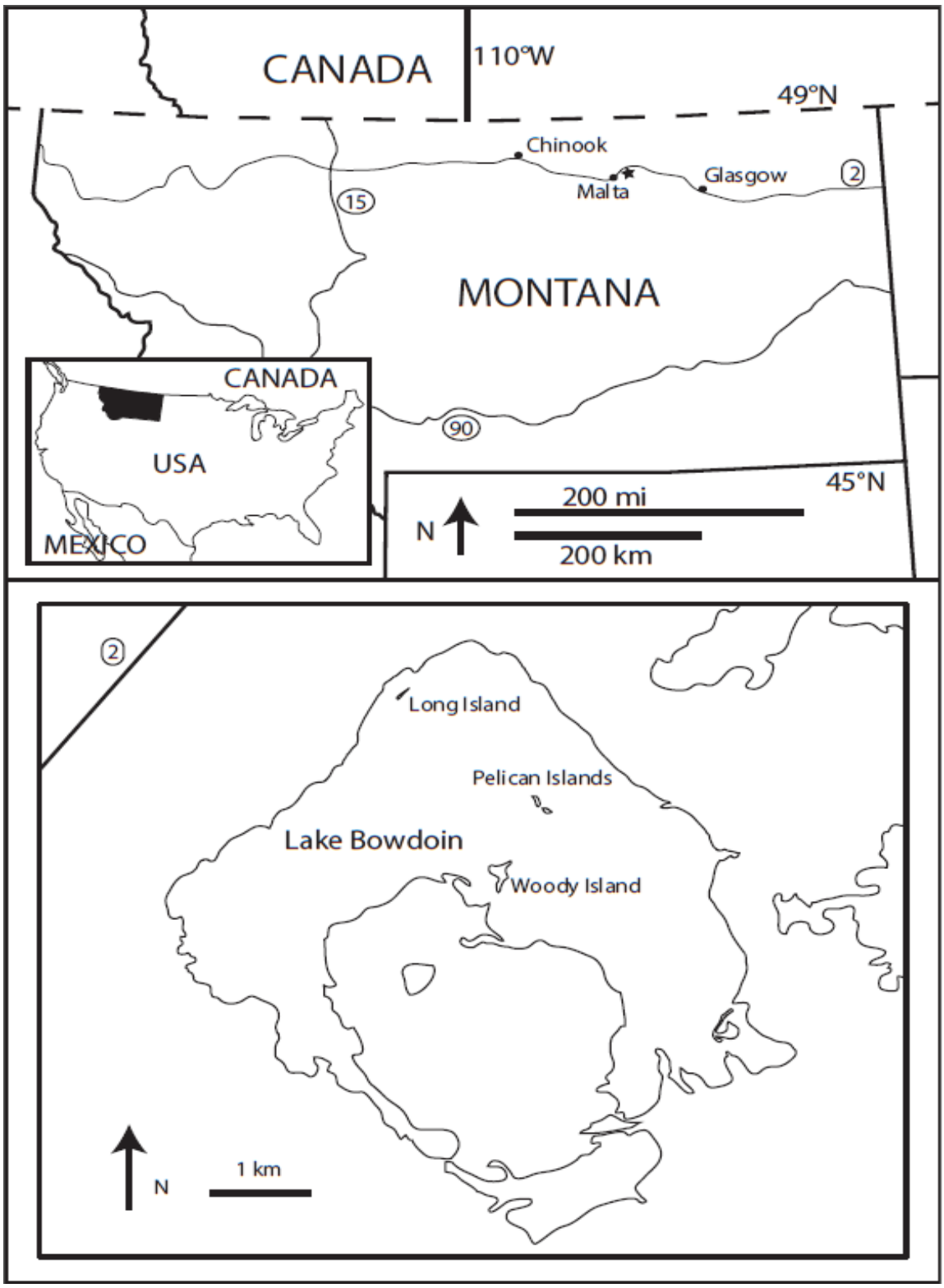

FIG. 1. —Location of Bowdoin National Wildlife Refuge in Montana. Material was collected from Long, Woody, and the northern Pelican Island.

eleven kilometers east of Malta, Montana (Fig. 1). Woody Island is the only natural island in Lake Bowdoin and consists predominantly of alkaline silt and clay. Long Island and the Pelican Islands comprise a mix of alkaline silt and clay together with siliciclastic and limestone gravel and boulders. The northern Pelican Island is mostly composed of boulders on the northern side. Long and Woody Island were largely covered by dense vegetation and the Pelican Islands were mostly bare. Due to the high salinity of Lake Bowdoin (reaching an average pH of 9.4 in September of 2015) no fish, except for the occasional minnow, live in the lake. Fish remains are predominately derived from the Nelson Reservoir, a top fishing destination in Montana located ~6 km to the northeast, and the Milk River ~12 km to the northeast (J. Larson, personal communication). BNWR provides a prime breeding habitat for thousands of migratory birds making an ideal location to study colonial ground nesting birds with high nest site fidelity and dense populations.

The nest surveys were done in September of 2014 and September of 2015, following the reproductive season so as not to disturb eggs and young. Nests were designated in chronological order and by the common name of each species (i.e. Nest Gull 1 (NG1) etc.) with a total of 25 gull, 25 cormorant, and 20 pelican nests described. Due to the similarity between *L. delawarensis* and *L. californicus* nests and eggs we use gull to indicate a mixture of nests and eggshell from both species. Documentation included the distribution, density, and orientation of eggshell and animal remains within and outside of the nest, as well as nest size and composition. Each nest was photographed

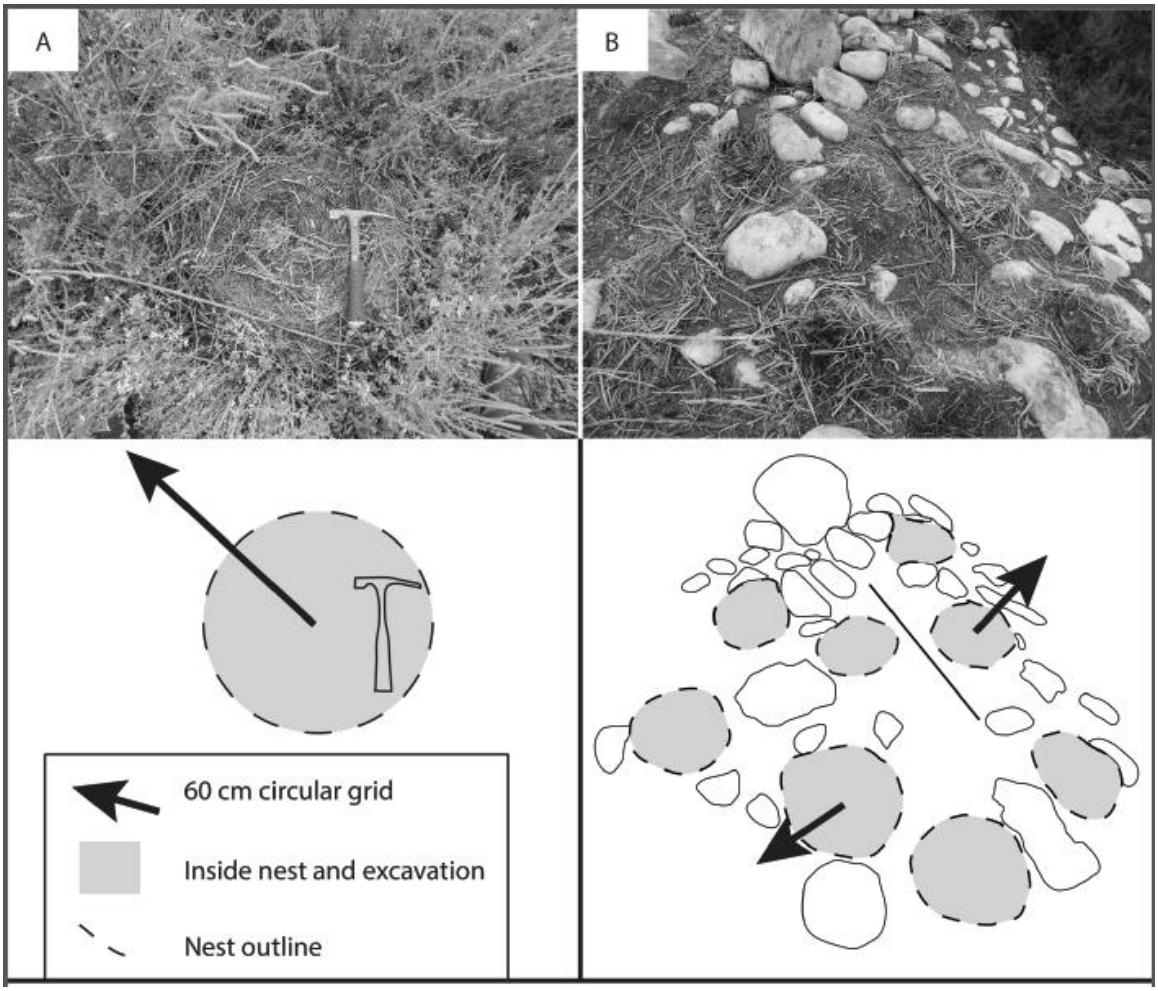

FIG. 2. —Example of sample collection from a gull nest (A) and cormorant cluster of nests (B). Arrow in A indicates 60 cm from the center of the nest and around the nest. Arrows in B indicate 60 cm from nests on outside perimeter of cluster.

and plotted onto a field map (Appendix C) and their location documented using a Global Positioning System.

The collection of animal remains are split into three designations, inside the nest cup and cup edges (IN), gridded material outside the perimeter of the nest (ON), and excavations in the nest proper (Fig. 2A). IN and ON consist of surface material only. A 60 cm circular grid measured from the center of each nest was used as a guideline for ON counts, with the exception of NP3 where an 80 cm grid was used. In addition to the 60

cm circular grid, traditional gridding methods using a 1x1 m^2 grid were also employed. NG1-12, recorded in September of 2014, are documented in this fashion since permission to collect salvage material was not yet acquired. The size of the grid in these nests were limited to ~0.5 m from the large amount of vegetation that grew around the nests (see Appendix D for grids). Therefore, the ON counts for these nests are not representative of the assemblage and are not included in calculations. In addition, NP1-2 were gridded along with five additional grids in between the two nests to highlight the amount of material scattered in between (Appendix E). However, the square grids did not encompass the area around the entire nest, therefore NP1-2 also could not be utilized for ON counts. No cormorant nests were gridded due to time constraints. Due to the close proximity of the nests to each other the 60 cm grid was not practical in identifying material derived from each of the cormorant nests. A new grid was established using nest clusters as a guide. These grids broke down to areas between nests and a 60 cm perimeter around the nest cluster (Fig. 2B).

Excavations were done to a maximum depth of 5 cm in gull and pelican nests and 7 cm for cormorants. Depths are dependent on the depth of the soil before hitting rocks or a lack of animal remains. Excavations were done manually with simple hand tools to avoid disturbing *in situ* material. Surface eggshell fragments were tallied indicating the eggshell orientation as either concave up (CU), concave down (CD) or unknown. Eggshell fragments designated as unknown indicates that the angle of the eggshell exceeded 45^o to the horizontal plane or was disturbed upon excavation. Only eggshell fragments of 1 cm^2 or greater were considered. Eggshell counts were then compared to a

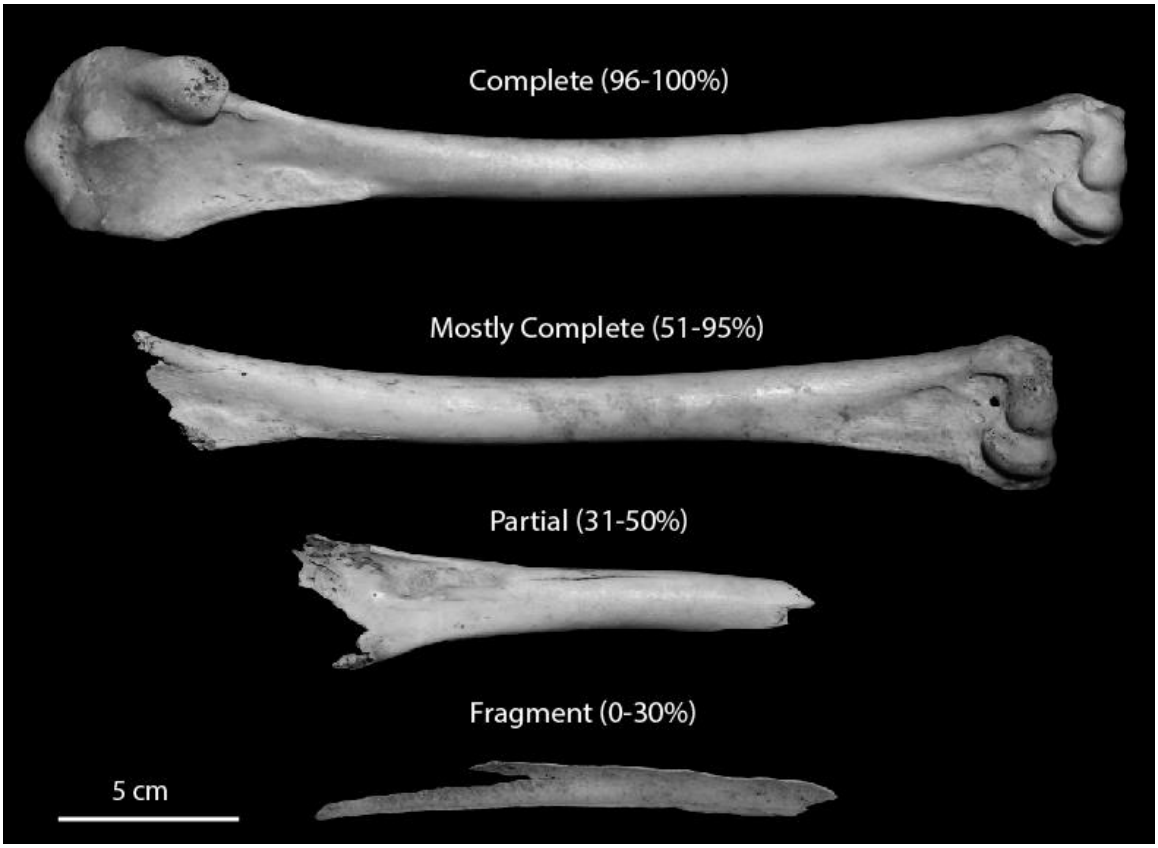

FIG. 3. —Examples of completeness classes used in this study. All four elements are *P. erythrorhynchos* (American white pelican) humeri.

null hypothesis of 50:50, as well as a 60:40 hatched/predated ratio (Hayward et al., 2000, 2011; Wang et al., 2014; Jackson et al., 2015) and 20:80 transported ratio (Hayward et al., 2011; Imai et al., 2015) using a chi-square test with Yates correction. The trend and plunge of any *in situ* long bone material was recorded as well. All excavated material was backfilled and returned to its original shape.

Material collected from the four taxa were cleaned and examined for weathering stage (Behrensmeyer 1978; Behrensmeyer et al., 2003), skeletal maturity (classified as either adult or juvenile) using the development of epiphyses for mammals and the periosteum texture and definition of articular ends for birds, abrasion (Shipman 1981),

element completeness and corresponding fracturing (Lyman 1994), and identification down to species if possible. Completeness is divided into four categories: complete (≥96%), mostly complete (51-95%), partial (31-50%), and fragment (0-30%) (Fig. 3). The completeness of articulated elements was determined by the amount of the entire limb preserved or animal in the case of articulated axial skeleton. For example, if an articulated animal was collected, that was counted as one specimen. Skeletal elements refers to vertebrate bones as well as the exoskeleton of crayfish. Any unknown skeletal elements are not included in final totals and percentages due to the inability to properly assess element completeness. Fish scales are also not included as measuring completeness seems inappropriate to properly assess their relation to the nesting sites. The minimum number of individuals (MNI) for each class and order was determined by identifying the highest number of taxon elements and counting the left or right side with the most elements represented. Weathering of avian bones could only be determined on skeletally mature elements due to the difficulty of differentiating the degree of ossification from weathering. Four skeletally mature birds from each species and one juvenile pelican were collected in the field and brought back to be cleaned by dermestid beetles to aid in element identification.

RESULTS

The combined elements of the four species yielded 7838 elements, of which 99.6% were identifiable by taxa (NISP, N=7803) and only 0.42% were either uncertain of

their taxon or entirely unidentifiable. Therefore, only 38 skeletal elements have been removed from calculations.

Gulls

Nest Descriptions

Gull nests, all collected from Long Island, are distributed along the south-west side providing protection from winds originating from the north-east. In September of 2014 the gull nests were much more abundant and closer together, whereas in 2015 the park staff informed us that the number of nesting pairs had decreased, which is reflected in a more scattered nest distribution (Appendix C). Gull nests on Long Island are constructed of sticks and grass, often lined with down feathers. NG18 to contained at least two layers of down and vegetation with eggshell concentrated in the deeper layer and another nest (NG11) had a crushed egg just outside the nest rim (Appendix D). The damaged nature of the egg made it difficult to determine whether it successfully hatched or was predated. Nests range in size from 19-67 cm in diameter and 3-5 cm in height.

Skeletal Remains

The 25 nests and grids produced only 213 skeletal remains. Removing fish scales and unidentified material, as well as material collected from outside the nest rims from NG1-12 yields 182 elements. Avian elements are the most common (62.3%, N=119), 55 of which come from gulls (Fig. 4A). Skeletally mature elements dominate the assemblage with 55.9% (N=57), most of which consist of California gull elements (N=30), with only four ring-billed gull element represented (Appendix F). Juvenile gull elements are

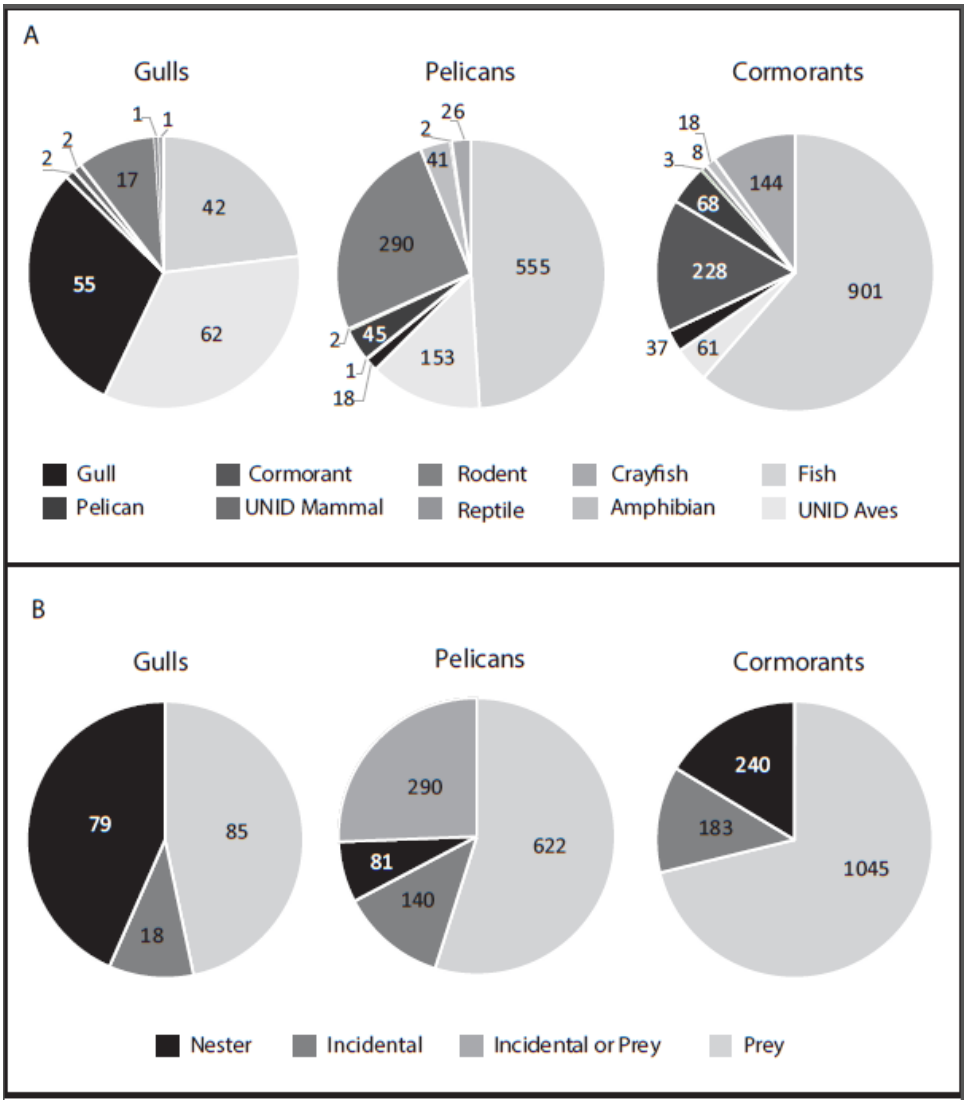

FIG. 4. – A) Number of identifiable elements per taxon per nesting site, not including fish scales. UNID refers to unidentified beyond family. B) Interpretations of skeletal elements per nesting site.

uncommon, consisting of only 10 elements out of the total 44. Within the juvenile elements, 5 complete and one mostly complete element's morphology clearly does not match gulls and 4 elements are too fractured to identify. The remaining elements are too underdeveloped to properly identify. The assemblage is composed of 22.3% Actinopterygii elements and 14.2% from mammals, including rodents (N=14). Two of

the mammal ribs collected are clearly cut by humans and were likely salvaged by the birds. The bulk of the identified elements are found inside of the nest (40.6%) and 50.3% fall in the complete category (Table 2). Despite excluding NG1-12 ON values the amount of material found in the nest is still significantly higher (40.4%) even excluding NG1-12 entirely, which consist of 6 IN elements and 8 excavated elements. This changes the ON percentage from 26.9 to 29.2.

Gull nest skeletal remains include an MNI of 3 common carp (*Cyprinus,* order Cypriniformes) represented by the right operculum, 2 rodents (order Rodentia) represented by the right mandible, and 9 Aves represented by the right tibiotarsus, including one California gull and 2 ring-billed gulls. A reptile and crayfish dorsal vertebrae and walking leg segment, respectively, are represented as well.

Of the skeletally mature specimens of Aves and Mammalia, 82.5% (N=33) fall within weathering stage 0 with Aves consisting of 77.5% of the material in this category (Appendix G). The largest portion of stage 0 avian material is buried in the subsurface (37.5%). Weathering stages 1-5 consist of only 17.5% of the skeletally mature material. The mammals included in Appendix G in gull nests are represented by Rodentia only.

Eggshell

Within the gull nests and the perimeter around them, a total of 422 eggshell pieces were collected. Despite the nests being constructed by gulls the eggshell fragments found in the nests are dominantly pelican eggshell (87%) with only 13% original gull material (Appendix J). All of the eggshell outside of the nests belongs to pelican eggs, 81% in the

TABLE 2. —Number of elements inside, excavated, and outside the nest and their corresponding completeness. Abbreviations: C – complete, MC – mostly complete, P – partial, F – fragment, IN – inside, ON – outside, EX – excavation.

Gull Nests						
	Complete	Mostly Complete	Partial	Fragment	Total	Mean
IN	28	29	8	9	74	40.7
ON	24	11	12	2	49	26.9
EX	37	13	6	3	59	32.4
Total	89	53	26	14	182	100
Mean	48.9	29.1	14.3	7.7	100	
Cormorant Nests						
	Complete	Mostly Complete	Partial	Fragment	Total	Mean
IN	54	47	18	12	131	8.9
ON	499	410	184	113	1206	82.2
EX	43	59	16	13	131	8.9
Total	596	516	218	138	1468	100
Mean	40.6	35.1	14.9	9.4	100	
Pelican Nests						
	Complete	Mostly Complete	Partial	Fragment	Total	Mean
IN	51	67	100	23	241	23.3
ON	141	173	89	73	476	46
EX	64	65	134	55	318	30.7
Total	256	305	323	151	1035	100
Mean	24.7	29.5	31.2	14.6	100	

nest cup, and 88% buried in the nests themselves. Unfortunately, we cannot tease apart the pelican and gull shell in the orientations. The number of eggshell pieces outside of the nest (N=14) for NG13-25 is significantly less than material found inside (N=64) or excavated (N=316) within the thirteen nests (Appendix H). Across the 25 nests the totals are 92 (IN) and 424 (excavation). Eggshell of unknown orientation make up 24.4% of the excavated assemblage (N=77) with IN and ON unknown percentages less than 10. Total values outside of the nest varied from no eggshell (N=9) up to 10 pieces (Appendix H).

IN eggshell counts varied from 0-19 pieces, with 13 of the nests without any eggshell on the surface. Only 6 of the 25 nests had no eggshell in the excavation and the highest amount for one nest was 86 pieces. Seven of the nests were completely devoid of eggshell in any of the three areas and 6 other nests contained only excavated material.

The total normalized values favor CU in all regions, with ON 53.8%, IN 56.3%, and 52.4% in the excavation (Fig. 5). The ON totals for NG13-25 are not statistically significant compared to either a 50:50, 60:40, or 20:80 CU:CD ratio (Table 3). However, IN values are significant compared to a 20:80 transported ratio and excavation values are significant compared to a 60:40 and 20:80 ratio. Weighting the 13 nests with ON values against the 25 nests with IN and excavation eggshell values the CU percentage equals 54.3% across the three locations. Surface weighted values (IN and ON) equal 52.2% CU.

Pelicans

Nest Descriptions

Woody Island is an elongate natural island oriented in a north south direction on the south western side of Lake Bowdoin (Fig. 1). The island was littered with dead pelicans, concentrated along the islands shoreline during September of 2015, with botulism and West Nile virus as the main culprits. The largest concentration of nests we observed occurred on the very southern portion of Woody Island (Appendix C). Pelican nests here consisted of simple scratch nests dug into organic rich alkaline soil. In some cases sticks would accumulate around the rim of the nests. Regurgitated material consolidates the soil preserving the scratch nests (Horner 1994). Nests range in size from

TABLE 3. — Summary of chi-square results with Yates correction for eggshell orientation and total eggshell pieces.

Gull	50:50	60:40	20:80	N
IN	$x^2(1) = 0.698$, $p = 0.403$	$x^2(1) = 0.242$ $p = 0.623$	$x^2(1) = 24.319$, $p = 8.16 \times 10^{-7}$	87
ON	$x^2(1) = 0.039$, $p = 0.844$	$x^2(1) = 0.1$, $p = 0.751$	$x^2(1) = 3.197$, $p = 0.074$	13
EX	$x^2(1) = 0.417$, $p = 0.519$	$x^2(1) = 4.019$, $p = 0.045$	$x^2(1) = 79.079$, $p = 5.97 \times 10^{-19}$	347
IN+ON	$x^2(1) = 0.723$, $p = 0.395$	$x^2(1) = 0.328$, $p = 0.567$	$x^2(1) = 27.504$, $p = 0$	100
Pelican	50:50	60:40	20:80	N
IN	$x^2(1) = 1.928$, $p = 0.165$	$x^2 = 18.917$, $p = 0.000014$	$x^2 = 63.643$, $p = 1.49 \times 10^{-15}$	437
ON	$x^2(1) = 0.046$, $p = 0.831$	$x^2 = 9.493$, $p = 0.002062$	$x^2 = 110.416$, $p = 7.94 \times 10^{-26}$	537
EX	$x^2(1) = 0.755$, $p = 0.385$	$x^2(1) = 0.974$, $p = 0.324$	$x^2 = 43.752$, $p = 3.73$x10-11	170
IN+ON	$x^2 = 0.594$, $p = 0.441$	$x^2 = 27.058$, $p = 1.97 \times 10^{-7}$	$x^2 = 172.942$, $p = 1.69 \times 10^{-39}$	974
Cormorant	50:50	60:40	20:80	N
IN	$x^2(1) = 0.059$, $p = 0.808$	$x^2(1) = 3.605$, $p = 0.058$	$x^2 = 24.572$, $p = 7.16 \times 10^{-7}$	136
ON	$x^2(1) = 0.018$, $p = 0.893$	$x^2 = 5.648$, $p = 0.017$	$x^2 = 47.485$, $p = 5.54 \times 10^{-12}$	249
EX	$x^2(1) = 0.174$, $p = 0.676$	$x^2(1) = 0.300$, $p = 0.584$	$x^2 = 11.618$, $p = 0.000653$	46
IN+ON	$x^2 = 0.064$, $p = 0.801$	$x^2 = 9.24$, $p = 0.002368$	$x^2 = 72.047$, $p = 2.10 \times 10^{-17}$	385

40-77 cm in diameter and 3-4 cm in height and distances between nests can vary from several meters to ~30 cm. One pelican nest had a yearling gull associated with it (NP1; Appendix E).

Skeletal Remains

These nests and grids contain the most biological material compared to the other nesting sites with a total of 5087 elements with Actinopterygii scales accounting for 3614 (71%) of animal remains collected. Excluding scales and unidentified material the total comes to 1133 identifiable elements which includes 3 articulated juvenile pelicans and 28 crayfish remains. Actinopterygii elements are the most common composing 49.0% (N=555; Fig. 4A) of the total skeletal elements, including common carp, northern pike or muskellunge, bass, and perch material. Rodentia is the second most abundant order with 290 elements (25.6%), including one possible Lagomorph and one unidentified mammal, followed by Aves (N=217, 19.2%; Fig. 4A). Among Aves, juvenile material is more common (72.7%, N=128) (Appendix F). Pelican material accounts for 20.1% (N=45) of the avian material, with 44 of the elements complete enough to determine skeletal maturity (Appendix F, I). Only 4 of the pelican elements are skeletally mature. Within the unidentified avian material, 12 of the juvenile elements may also belong to young pelicans, however the material is too fragmented, falling in the partial (N=9) and fragment (N=3) completeness classes. Most of the skeletally mature material associated with pelican nests comes from rodent material (39.1%, N=120).

Pelican nests and grids generated an MNI of: 16 Actinopterygii, including 12 common carp and 3 Percidae, represented by the left operculum; 10 Aves, including 3

pelican juveniles, one California gull and one ring-billed gull, represented by the right tibiotarsus; 22 Rodentia represented by the right tibia; and 9 crayfish represented by the right cheliped claw. *Ambystoma tigrinum* (tiger salamander) trunk vertebrae are also represented (N=41) as well as reptile trunk vertebrae (N=2).

The majority of the elements are located outside the nest perimeter (46.0%, N=476) with partial elements more common overall (31.2%, N=323). ON completeness categories favor complete and mostly complete, whereas excavation and IN completeness categories favor partial elements (Table 2). Like the gull nesting material, weathering in avian and mammal material falls into weathering stages 0 (84.0%, N=21) and 1 (12.0%, N=3), with only one element classified as stage 4 (Appendix G). The majority of the stage 0 material occurs on the surface outside of the nest (Appendix G).

Eggshell

Out of a total of 1252 eggshell fragments 549 were found outside of the nest perimeter (NP3-20) with IN consisting of 444 fragments and excavation values at 259 across all twenty nests (Appendix H). Almost all of the eggshell collected belonged to pelican eggs (99%) leaving 1% for a thin, tan to olive green eggshell with dark brown spots, possibly gull eggshell, and a grayish blue unknown shell. Only two nests (NP2 and NP20) have no eggshell material in the excavation. Total normalized eggshell orientations inside the nests favor CD (54.7%, 45.3% CU) while ON and excavation material favored CU, 50.7% and 54.7% respectively (Fig. 5).

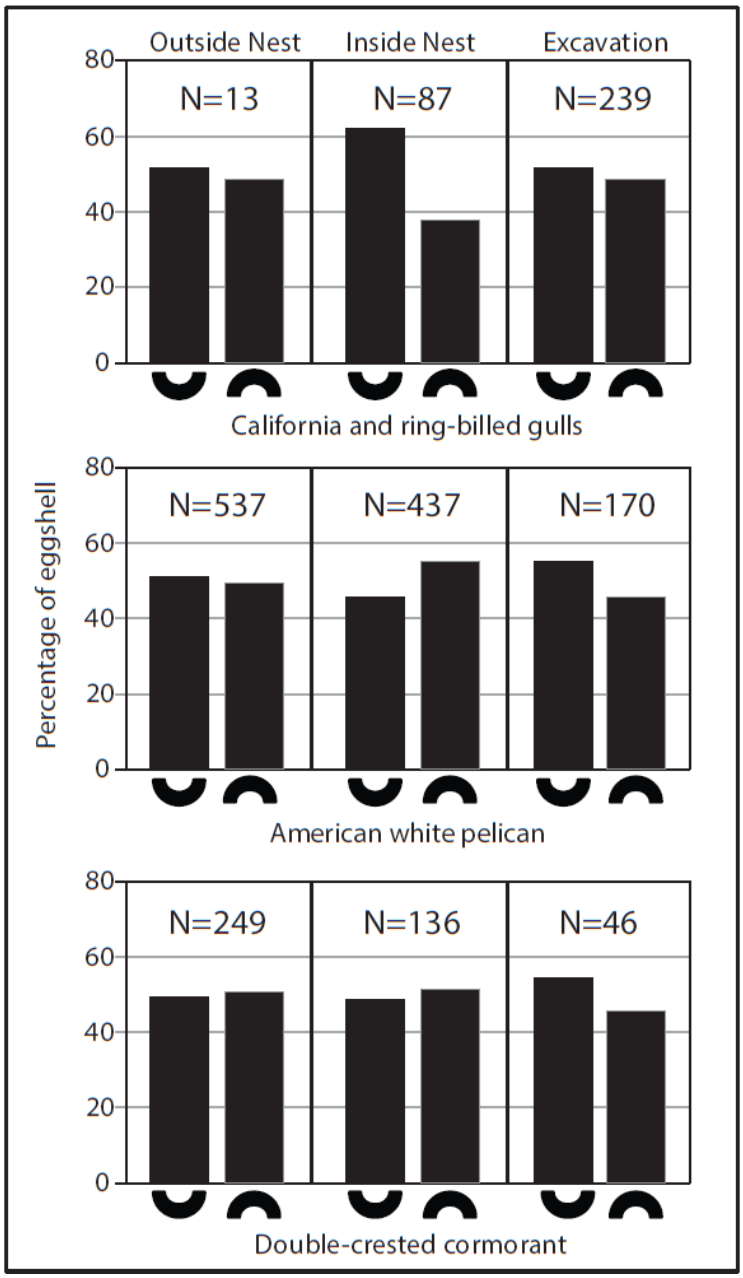

FIG. 5. —Eggshell concavity normalized total ratios between collection locations and species. Black bars represent CU eggshell, and gray CD eggshell. Outside nest values for the two species of gull include NG13-25 only.

Weighting the ON values from NP3-20 against the IN and excavations values between all the nests the CU value equals 43.1%. Weighted surface CU values equal 46.9%. Total ON eggshell counts are not statistically different compared to a 50:50 ratio,

but are when compared to a 60:40 and 20:80 transported assemblage (Table 3). Similarly, the IN ratio is significantly different from a 60:40 hatched/predated and a 20:80 transported assemblage ratio (Table 3). Excavated eggshell is only significantly different from a transported assemblage.

Cormorants

Nest Descriptions

All the material collected from the cormorant nests were collected from the northern Pelican Island (Fig. 1). The cormorants on this island built elevated platform nests ~20-30 cm tall, 34-50 cm in diameter, constructed from long sticks, bones, and man-made debris. The birds nest in clusters often next to large boulders and against other cormorant nests (Fig. 2B). Cormorant young are often found flattened by trampling and even incorporated into the nest along with long pelican elements. Dead cormorants were scattered throughout the island, found concentrated among the nesting clusters. The yearling cormorant collected for osteological comparison had large amounts of feathers in the crop and stomach.

Skeletal Remains

The 25 cormorant nests and surrounding material contained 2538 total elements, 1468 excluding unknown elements and scales. Actinopterygii elements dominate the assemblage (67.7%, N=736), including common carp, northern pike and muskellunge, catfish, bass, perch, and walleye. Cormorant elements (17.1%, N=228) are the second most abundant, followed by crayfish (9.8%, N=144; Fig. 4A) and unidentified avian

elements consist of 61 specimens. Juvenile elements far outnumber adult material (75.9%, N=281), skewed by the abundance of cormorant young (N=223, 63.8%; Appendix F) with only 13 specimens classified as adult cormorants, though there are a number of ring-billed gull (N=37) and pelican elements (N=65) as well. Seven juvenile specimens classified as unidentified Aves could belong to cormorants, however the elements are too fragmented or underdeveloped to properly identify.

MNI counts for the cormorant nests and surrounding grids yielded: 21 Actinopterygii, including 3 *Cyprinus*, 1 *Esox* and 15 *Perciformes* represented by the left operculum; 14 Aves, including 1 ring-billed gull, 7 pelicans, and 15 cormorants represented by the right humerus and individuals; 1 rodent represented by a left mandible; and 25 crayfish left cheliped claws. *Ambystoma tigrinum* (tiger salamander) trunk vertebrae are also represented (N=18).

As with the pelican nests and grids the majority of the skeletal remains are found outside of the nest (82.2%, N=1206) (Table 2). Elements collected from the nests and grids favor mostly complete (35.1%, N=516) and complete (40.6, N=596) categories (Fig. 4A).Weathering of avian and mammalian elements favor 0 (68.8%, N=53) and 1 (22.1%, N=17). Avian elements with higher weathering stages are found outside of the nest and in excavation. Only two mammals were found large enough to determine weathering (Appendix G). About half of the stage 0 material (N=53) occurs outside of the nest (N=30).

Eggshell

The cormorant nests and surrounding areas contained 500 eggshell fragments, all coming from cormorant eggs. As with the skeletal elements, most of the eggshell is also found outside of the nest perimeter (N=275) with 151 pieces in the nest cup and only 74 in the subsurface. A complete egg was found on the north east side of NC10. The egg was fertilized but failed early in development. Eggshell orientations for surface assemblages are almost 50:50 for normalized total eggshell counts (Fig. 5) with excavation favoring CU (54.3%). As with pelican nest values, ON eggshell counts differ significantly compared to a 60:40 hatched and 20:80 transported assemblage (Table 3). IN and excavated nest values are only significant compared to a transported ratio (Table 3).

DISCUSSION

This research builds on the work of Horner (1994) and Hayward et al., (2000, 2011) by evaluating the types of preservable material found in colonial nesting grounds and testing the reproducibility of a hatched or predated eggshell orientation in nesting sites. Here we discuss overall trends observed between the three groups of birds and any correlation between altricial and precocial young that may be useful in applications toward non-avian and avian taphonomic nesting signatures.

Gull Nesting Sites

Gull nesting sites consist of well-developed vegetation nests with at least one nest with several layers. Ring-billed gulls have been documented to reuse nests over multiple

years (Berger and Gotchfeld 1996) and multiple layers of down and eggshell suggest taphonomic evidence of this. Skeletal elements in an around the nests are dominated by skeletally mature gull bones and unidentified juvenile bird elements (Appendix F). Many of these juvenile unidentified bird elements could belong to gulls as they fall within the correct size range, however, the bones are too underdeveloped to determine any recognizable homologous features. Other skeletal elements include fish, pelican, mammals, reptiles, and crayfish. The diets of both gull species are very diverse, including garbage, fish, arthropods, birds, rodents, etc. (Brousseau et al., 1996; Knopf and Evans 2004). Given the dietary data for these birds, the fish, crayfish, mammal, and at least 6 juvenile Aves elements are consistent with gull prey items. Due to the uncertainty of the species of unidentified birds, we consider the skeletally mature elements as incidental material and interpret the remaining juvenile material as gull elements (Fig. 4B). In addition, eggshell pieces inside the nests are dominated by pelican eggshell. Unattended pelican eggs and young are often preyed on by gulls (Schaller 1964; Knopf and Evans 2004), therefore we interpret the abundant pelican eggshell and the few juvenile pelican bones as prey items as well.

Based on our observations here, we would expect to find very little skeletal remains incorporated in the nest or on the surface (Table 2; 4) of a typical gull nest. The bones associated with the nests would mostly be found on the nest surface (40.7%) and this likely represents material congregating over several years. Weathering stages on the surface (IN and ON) are up to stage 3, meaning they would have been exposed on the surface up to 4-15 years (Behrensmeyer 1978). The skeletal and eggshell material found

TABLE 4. —Average amount of skeletal material and eggshell that can be expected per nest (surface material and excavation) and on the nesting surface (inside and outside). *Over 80% predated pelican eggshell.

	Bone/Nest	Bone/Surface Grid	Eggshell/Nest	Eggshell/Surface Grid
Gulls	7.3	4.9	16.9*	4.24*
Pelicans	41.4	28.7	50.1	39.7
Cormorants	58.7	53.5	20	17

in the excavations also represents the incorporation of material over the course of several years as most of the predated pelican shell was incorporated in the nest along with skeletal elements (Table 2; 4). The skeletal elements found in the subsurface are not weathered indicating they were incorporated into the nest quickly, preventing weathering. However, the likelihood of this material preserving is low, considering the elements are buried in the vegetation made to construct the nests, not sediment. Most of the skeletal material is also complete or mostly complete and is also found on the nest surface or buried in the nest itself (Appendix I).

Pelican Nesting Sites

Pelicans make scratch nests in silt or clay with a ring of gathered sticks occasionally making the rim of the nest. Compared to the gull nests, the pelican nests contain a significantly higher number of skeletal remains (1133 vs 213). These remains include fish of various species, unidentified birds, gulls, one cormorant element, unidentified mammals, rodents, tiger salamanders, reptiles, crayfish, and pelican bones. The pelican remains found at the nests are dominated by juvenile elements (Appendix F). Pelicans will eat whatever aquatic species they can catch, including amphibians and crayfish, though their main diet consists of fish (Knopf and Evans 2004). Taking into

consideration the typical diet of pelicans, we interpret the fish, salamander, and crayfish elements as prey items.

A high percentage of rodent material were associated with the pelican nesting sites, however, the origin of this material remains unclear. The abundance of rodent material (N=290) may result from the proximity of Woody Island to the shoreline of the lake. If the water is low enough a small land bridge will form on the south-western side of the island and connect to the edge of Lake Bowdoin. This would allow easy access for rodents to travel to the island and take advantage of the abundant food left behind by the nesting birds. However, the water levels have not been low enough to create a land bridge for several years (J. Larson, personal communication) and the weathering of the rodent elements suggests lack of exposure. This also only explains how the rodents got to the island, not how they died. Pelicans have been documented eating young birds (Elliot 1992) and it may be possible that the pelicans were eating rodents. However, considering most of the rodent species identified were small (*Peromyscus, Microtus)* it's hard to imagine pelicans actively feeding on such quick mammals. It is possible that the rodents became stuck on the island, breeded, and subsequently experienced a die off as most of the rodent material consisted of subadult individuals. In Fig. 4B we compare the possibility of rodent material as prey materiel as well as incidental material.

At least 9 of the unidentified Aves juvenile elements clearly belong to an unknown species, and the other unidentified material, besides the skeletally mature elements, are too fragmented to determine a species. Therefore, we interpret the skeletally mature unknown avian elements as incidental and the fragmented juvenile

elements as young pelicans, with the other fragmented material included as incidental. We regard the other skeletal material (unknown mammal and reptile) as incidental as well, meaning material not directly associated with the activity of the nesting birds.

Most of the skeletal remains (Table 2) and eggshell material (Appendix H) is found outside of the nest rim and on the surface. A large portion of the skeletal assemblage consists of partial material, predominately found IN and in the excavation. This can be explained by the young trampling the material in the nest, especially since pelicans are such large birds. One element found on the surface had a weathering stage of 4, meaning, as with the gull nests, the surface material represents an accumulation of material over at least 6-15 years (Behrensmeyer 1978). Excavated material also appears to have accumulated material from 0-3 years, with one element with a weathering stage of 1 recovered from the subsurface. Preservation in the subsurface of pelican nests seems more likely than in gull or cormorant nests in that the material becomes pressed into soil and regurgitate solidifies the material instead of becoming incorporated into a vegetation nest.

Cormorant Nesting Sites

In contrast to the gull and pelican nests, cormorants here build elevated vegetation nests out of large sticks, bones, and even human debris such as tent stakes. These nests are situated among large boulders and are even built butting up next to each other. Skeletal remains are dominated by fish and juvenile cormorant elements with other remains including unidentified birds, gulls, pelicans, unidentified mammals, rodents, amphibians, and crayfish. Cormorants feed almost exclusively on fish (Findholt 1988;

Sullivan et al., 2006). However, the abundance of crayfish and the proximity of the amphibian elements to the nests leads us to believe the birds were consuming these animals as well. Gull and rodent elements almost exclusively occur outside of the nests, as well as most of the unidentified birds. Of the unidentified birds, three of the juvenile elements may be different species, with the remaining 12 juvenile elements possibly fragmented cormorant elements. We interpret the remaining fragmented and skeletally mature unidentified avian elements as incidental, as well as the gull elements since several young gulls were found dead on the island and the material wasn't used to construct the cormorant nests (Fig. 4B). Mammal elements were likely brought on the island by the gulls as the island is in the middle of the lake making it metabolically expensive for rodents to swim across. The pelican bones were predominately used to construct the elevated nests and are therefore considered incidental nesting material.

As with the pelican nests, a large portion of the skeletal elements (Table 2) occur outside of the nest and the nest surface. Less than 25% of the collected material falls in the partial and fragment classes (Appendix I). Cormorants have been documented building their elevated nests over consecutive years (Sullivan et al., 2006). This is reflected in the weathered elements found in the excavated material. One element inside the nest was found to be stage 5 indicating around 6 years of weathering or more (Behrensmeyer 1978; Appendix G). High weathering stages (up to stage 4) outside of the nest also indicates an accumulation of material over several years. Most eggshell is found outside of the nest as well (Appendix H). Buried material inside the nests would be unlikely to preserve since the material, like in gull nests, is contained within the

vegetation of the nest itself. However, the material that accumulates around the nests may have a high enough density and enough sediment and regurgitated material to preserve the elements outside of the nests.

Taphonomy of Skeletal Remains

There is a trend between the amount of material found associated with each of the nests and surrounding material between the semiprecocial and altricial birds. Both the cormorant and pelican nests and grids, have significant amounts of skeletal material, despite the advantageous nature of the gull diet (Table 1). This fits our hypothesis that altricial nests would be correlated with larger amounts of prey material due to the increase in parental care associated with that developmental stage. Gull nests favor gull and avian elements, a pattern also seen in common tern and penguin nests (Wang et al., 2014; Cruz 2007) which are also semiprecocial birds. Gull young fledge between 40-60 days after hatching (Table 1) and wander outside of the confines of the nest by 4 days old (Winkler 1996; Pollet et al., 2012). The rate of feeding by adult ring-billed gulls declines after 3-4 days (Evans 1970) whereas pelican young are brooded at least 2 weeks (Schaller 1964) and adults begin to leave chicks unattended when the young reach 17-25 days old (Knopf and Evans 2004). Cormorant young will remain in nests until about 28 days old (Dorr et al., 2015), similar to the pelicans. Bird species with longer periods of care therefore leave more biological material behind as a result of extended parental care.

Most elements in gull nesting grounds were located on the surface of the nest cup (40.7%, N=74) whereas pelicans and cormorants have most of their prey items outside of the nest, 46.0% and 82.2% respectively. This may be due to the sheer amount of material

associated with the altricial nests and in order to maintain cleanliness, material was thrown out. However, specific examples of this occurring in pelicans and cormorants has not been documented.

No clear pattern persists between the altricial and semiprecocial birds for element completeness. Most of the complete material for cormorants is found outside of the nest and belongs to fish and cormorant material (Appendix I), which includes articulated young and fish as well. Only one articulated juvenile cormorant was found inside of the nest with the rest occurring in between the nests within the nest clusters. The articulated nature of the elements may be a result of less trampling by adults and young whereas the higher number of partial elements associated with the pelican nests could be caused by adults and crèches of young birds walking across the island.

Fossil nesting sites of birds are extremely rare (Leggitt, 1996; Dyke et al., 2012), however, a few groups of birds, such as the clade Enantiornithes, have been interpreted as precocial or superprecocial birds (Chiappe et al., 2002) based on the degree of ossification in limb bones. Dyke et al., (2012) reported thousands of eggshell fragments, seven near-complete eggs, and neonatal and adult avialan skeletal elements in a lens of calcareous mudstone. They also report any other fossils being entirely absent. If the amount of prey related skeletal material found associated with the nests holds true to the developmental strategy utilized by the birds, then the lack of other skeletal material associated with the breeding colony described by Dyke et al., (2012) may provide more evidence towards a precocial mode of development in enantiornithine birds.

Nester Age

Horner (1994) noted that elements in dinosaur and modern pelican nesting grounds contained an abundance of juvenile material, elements that are extremely rare in other locations. This study corroborates the sheer amount of juvenile material found in colonial avian nesting sites. However, with our distinction between juvenile and skeletally mature material there is an interesting dynamic between the semiprecocial gulls and altricial pelicans and cormorants. The amount of juvenile bones per nest in altricial birds is much higher than the amount recovered per nest from the semiprecocial gulls. Therefore, the semiprecocial gulls appear to have a lower mortality rate for younger nestlings when compared to altricial young. Gulls lay 1-4 or 2-4 eggs, with an average of three eggs (Berger and Gotchfeld 1996; Winkler 1996; Pollet et al., 2012) whereas pelicans only lay two eggs (Knopf et al., 2004; Elliot 1992) and cormorants lay 2-7 eggs (Orta 1992; Dorr et al., 2014). With pelicans only laying two eggs, this alone does not explain the amount of juvenile material. This supports a study by Emlen Jr. in 1956 that showed ring-billed gull juvenile mortality rates peak in older young. He attributes this to the young being old enough to wander long distances from the nest but not old enough to defend themselves. The juvenile mortality rate in pelicans could be the result of West Nile that has been shown to increase the mortality of chicks from 4-44% after the arrival of the virus (Sovada et al., 2008). However, most double-crested cormorant chicks die less than two weeks old (DesGranges 1982) with each nest producing an average of two young (Sullivan et al., 2006). A study by Knopf (1980) found that 69% (29 out of 42) of the young observed in American white pelican nests where both eggs hatched died during

the nestling period. The incidence of both chicks surviving declines with an increase in the interval between hatching of the eggs (Knopf 1980). This difference between the mortality rates of nestlings in semiprecocial and altricial birds may be a subtle taphonomic distinction between these two modes of development.

Eggshell Orientation and Distribution

Previous studies have shown that eggshell orientations related to hatching and predation were marked by a predominance of CU eggshell in gull, chicken, common tern, and turtle sites (Hayward et al., 2000, 2011; Wang et al., 2014; Jackson et al., 2015). We found similar results in the gull surface material, with 54% CU outside the nest and 56% CU inside the nest. However, these values are not statistically distinguishable when compared to 50:50 and 60:40 ratios in a chi-square test. ON counts for the gulls are also not distinguishable from a transported assemblage, this may be due to the smaller sample size (N=13) produced from the 12 available nesting sites, NG13-25. The surface assemblage of the gulls is similar to the common tern surface assemblage observed by Wang et al., (2014). However, the subsurface material from the gulls is closer to a 50:50 ratio than a 40:60 ratio found in the subsurface of common tern nests (Table 4).

Hayward et al., (1997, 2000) combined values for the surface assemblages to get an approximate 60:40 hatched/predated ratio. Weighted averages comparing IN and ON yield a 54:46 ratio. A combined surface assemblage applied to pelican nests favors a 50:50 ratio (48:52) (Table 4). Excavated material for pelican nests can only be distinguished from a transported assemblage. Cormorant shell orientation signals are similar to the pelicans, with surface values 49:51 and subsurface material 54:46. The

combined surface values of the two altricial species, the cormorants and pelicans, are almost 50:50. The semiprecocial gulls are closer to a 60:40 assemblage which is similar to a predation signature also seen in common tern nests. We suspect the 50:50 ratio seen in the pelican and cormorant nest cups is due to the trampling of the altricial young causing the number of more stable CD eggshell to increase. Very few eggshell pieces in the gull areas are gull eggshell, making it difficult to compare ratios between the gulls and altricial birds. Experimental work of chick trampling has CU eggshell pieces ranging from 42-66%, making it difficult to narrow down a particular pattern. However, we suggest trampling because if weather was a factor then the gull nests should have a similar surface assemblage as well. Though most of the material is not distinguishable from a 50:50 and 60:40 ratio this confirms the suggestion that hatched or predated nesting sites can be distinguished from a transported assemblage. Eggshell distributions across the four species mirror those found in the bone and chitin elements. We suspect the lower percentages of eggshell found inside the nest cup in the altricial species is also due to trampling by the young as both the altricial species have lower amounts of material inside the nest relative to material outside the nest perimeter. The fact that eggshell is found inside the nest at all is surprising, considering some species remove eggshell to deter predators and prevent pathogens and parasites (Sordahl 1994; Sundar and Choudhury 2003). The abundance of pelican eggshell over gull eggshell is likely due to the more robust thickness of pelican eggs (~0.6 mm) compared to those of gull eggs (~0.2 mm).

CONCLUSIONS

This study proposed that the taphonomic signatures left behind at nesting sites could determine a pattern between semiprecocial and altricial young. Our findings suggest that a signature is evident, with the most telling evidence driven by the amount of skeletal material and juveniles associated with the species with altricial young. Eggshell orientations on the nesting surface in gulls, composed of over 80% predated pelican eggshell, were close to a 70:30 predation signature, and pelican and cormorant nests more closely resemble a 50:50 ratio on the surface, proposed as a result of trampling from the young. Eggshell orientations, though differing from a 60:40 ratio in pelicans and cormorants, are still able to differentiate a transported assemblage from a hatched or predated site.

Modern studies of nesting sites provide important information in regards to the type of material associated with nests and the subsequent interpretation of fossil nesting localities. The stage of juvenile development upon hatching determines the amount of parental care and therefore the types of material associated with nests which can provide a better understanding of element distribution and preservation in fossil localities. Continued work on modern taphonomic nesting signatures will provide an increased understanding of the type, spatial arrangement, and condition of biological remains in fossil nesting sites and whether patterns observed between altricial and precocial young can be observed in a predictable manner in the fossil record.

ACKNOWLEDGMENTS

We thank the staff of the Bowdoin National Wildlife Refuge, in particular J. Larson and T. Boonstra, for their generosity in allowing us to study the birds, for providing details about the refuge and general information about the birds and islands, and for letting us borrow a canoe when ours failed. We thank J. Dixon for providing a pH monitor as well as E. Boyd and M. St. John for providing life jackets and various boats/ boating equipment. Thank you to J. Wilson, J. Gardner, C. Organ, and D. Willey for insightful discussion and mathematical assistance. A special thank you goes to M. Struble for letting us feed our birds to her dermestid beetles and last, but not least, thank you to E. Chase and L.J. Krumenacker for helping sort through and identify the collected material. Research was supported by NSF grant #0847777 to DJV.

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CHAPTER 4

CONCLUSIONS

This thesis includes the first taphonomic work on crocodylians, as well as a comparison between the developmental stages of birds, crocodylians, and tortoises from my work and previously published literature. Our findings suggest that a signature between precocial and altricial animals is evident, with the most telling evidence driven by the amount of skeletal material and juveniles associated with the species with altricial young. Crocodylian nests are extremely clean with large amounts of eggshell and little to no skeletal material or scat associated. These crocodylian nests have a recognizable hatching trace and a lack of biological material besides eggshell and support our hypothesis proposed for precocial young. Gull nesting sites contain small amounts of prey material (e.g. fish and small mammals), whereas pelican and cormorant nesting sites are dominated by prey material. Evidence suggests the abundance of prey is correlated to the developmental stage and residence time of young (Table 1). The two altricial species of birds (pelicans and cormorants) contribute vast amounts of organic material to their nesting locale increasing preservation potential. Among the nesting animals, the altricial species had the most nester skeletal material, dominated by juveniles, whereas the semiprecocial gull nesting sites contained more skeletally mature gull elements. No nester skeletal material was associated with precocial crocodylian nests (Table 1).

Surface eggshell counts in *C. acutus* nests closely match a trampled assemblage (42:58) differing from the ~50:50 surface assemblage seen in *C. latirostris* (53:47).

TABLE 1. —Comparison between precocial (crocodylians *C. acutus* and *C. latirostris* and tortoise), semiprecocial, and altricial archosaurs. Surface ratios include inside the nest and surrounding sediment. Note adult element age refers to skeletally mature. *Ratios from *C. latirostris* and tortoise are from one nesting season, whereas bird nests incorporate multiple years. References – 1) this thesis, 2) Jackson et al. 2015, 3) Wang et al. 2014.

	Surface	Subsurface	# of Elements				Nester Element Age	References
	CU:CD	CU:CD	Total	Nester	Prey	Incidental		
American crocodile	37:64	N/A	Minimal	None	None	Minimal	N/A	1
Broad-snouted caiman	53:47	61:39*	Minimal	None	None	Minimal	N/A	1
Tortoise	38:62	69:31*	None	None	None	None	N/A	2
Common tern	68:32	42:58	Minimal	Moderate	None	None	Juvenile	3
Gulls	N/A	N/A	Minimal	Moderate	Moderate	Moderate	Adult	1
Pelicans	47:53	55:45	High	High	High	Moderate	Juvenile	1
Cormorants	48:52	54:46	High	High	High	Minimal	Juvenile	1

Chamber material associated with the *C. latirostris* nests statistically matches the 60:40 CU vs CD ratio (61:39) seen in bird and turtle nesting assemblages and combining chamber and surface material statistically matches this ratio as well (56:44). The increased amount of digging required in order to free young from a cavity nest versus a mound nest may influence the spread and orientation seen at *C. acutus* nests. Eggshell orientations on the nesting surface in gulls are close to a 70:30 predation signature, and pelican and cormorant nests more closely resemble a 50:50 ratio on the surface, proposed as a result of trampling from the young. Eggshell orientations, though differing from a 60:40 ratio in pelicans and cormorants, are still able to differentiate a transported assemblage from a hatched or predated site.

Modern studies of nesting sites provide important information in regards to the type of material associated with nests and the subsequent interpretation of fossil nesting localities. The stage of juvenile development upon hatching determines the amount of parental care and therefore the types of material associated with nests which can provide a better understanding of element distribution and preservation in fossil localities. Continued work on modern taphonomic nesting signatures will provide an increased understanding of the type, spatial arrangement, and condition of biological remains in fossil nesting sites and whether patterns observed between altricial and precocial young can be observed in a predictable manner in the fossil record.

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APPENDICES

APPENDIX A

CROCODYLUS ACUTUS GRIDS/EGGSHELL DISTRIBUTION

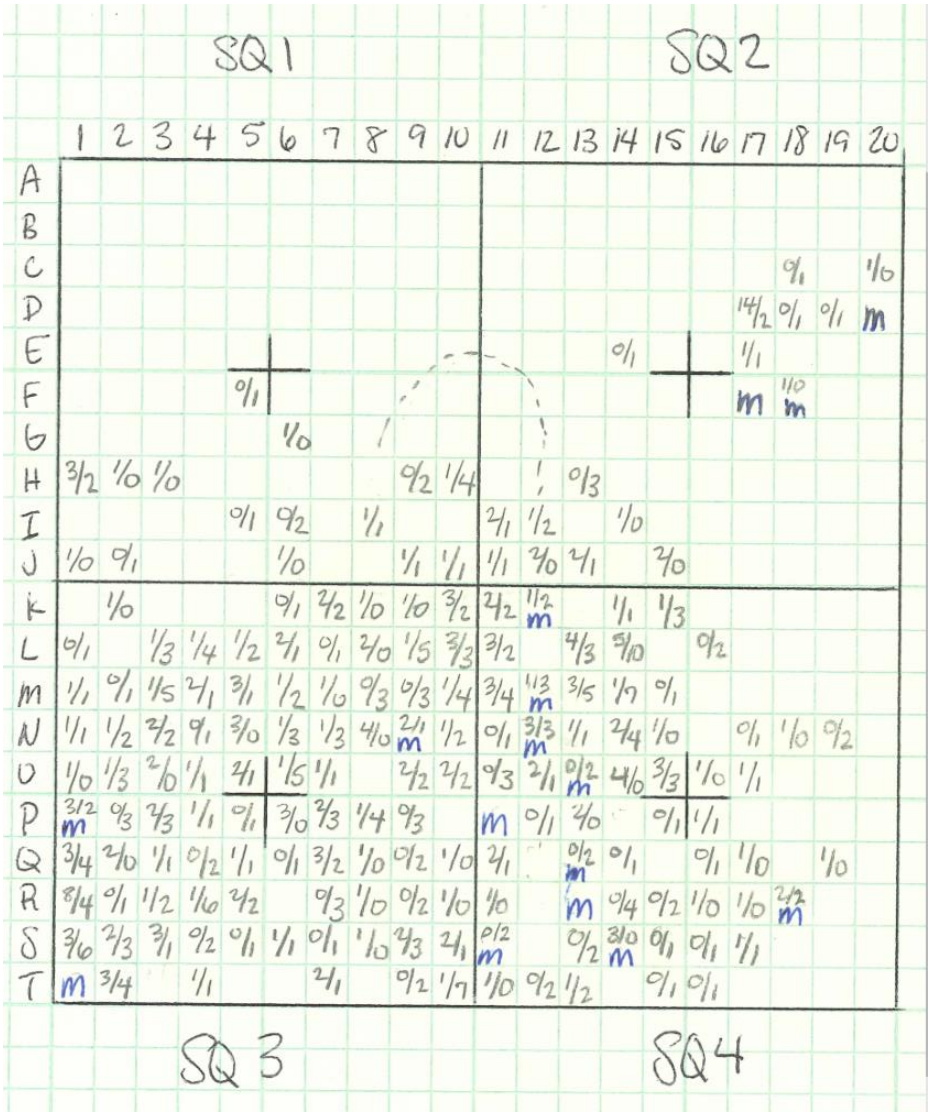
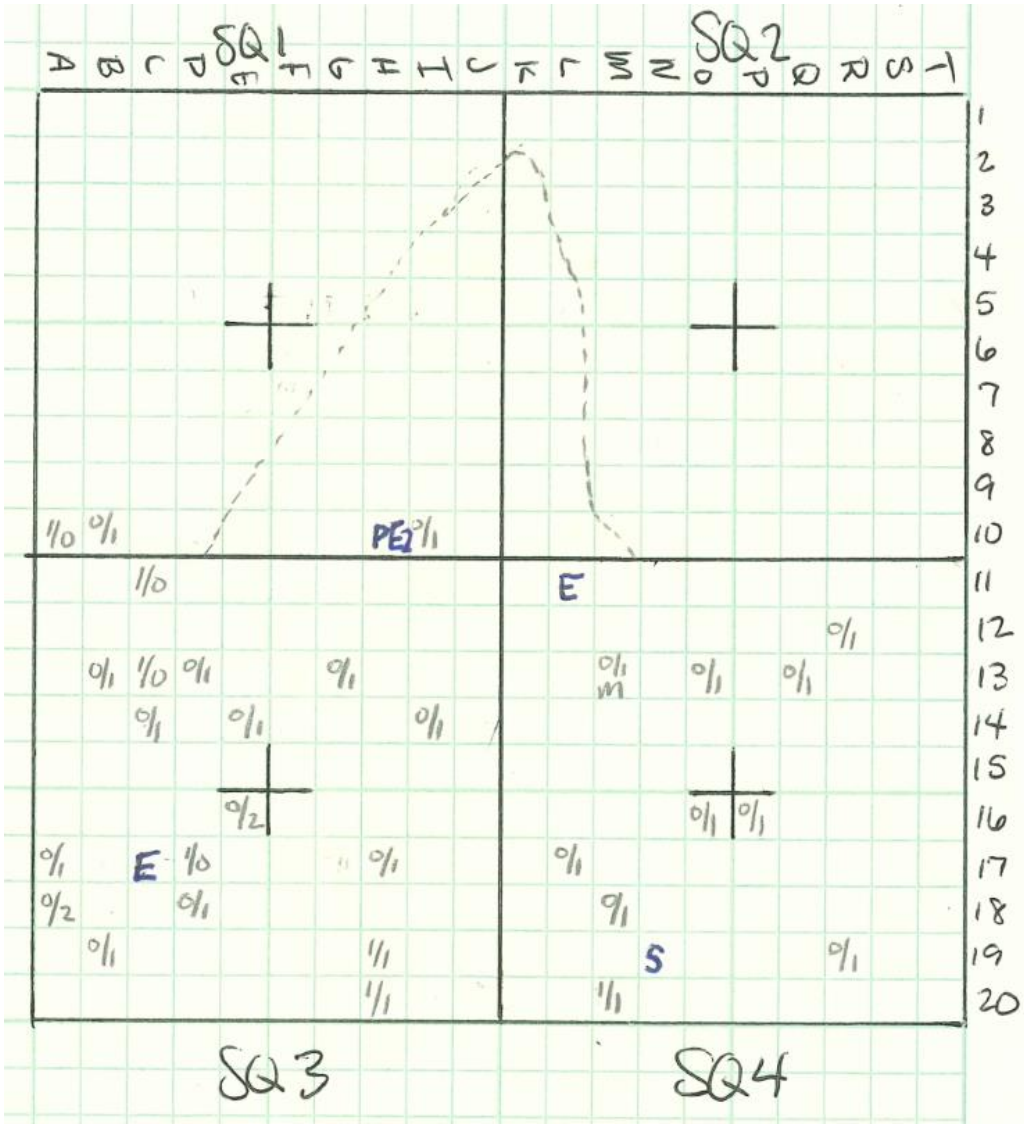
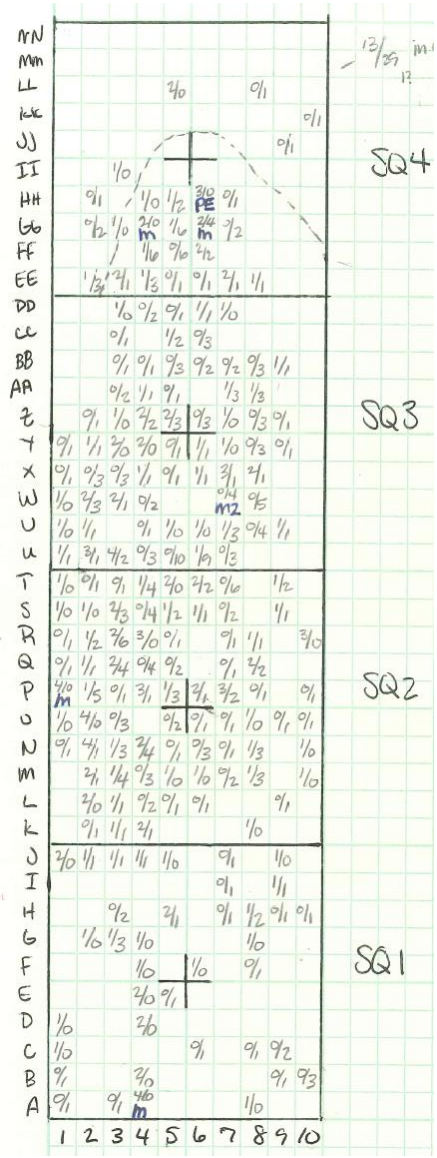


FIG. 1. – Eggshell distribution and orientation of N1.



S	Small membrane <50%		
M	Membrane	PE	Partial egg
E	Egg	#/#	U/D number
- \ `	Egg chamber boundary	SQ #	Grid number

FIG. 2. – Eggshell distribution and orientation of N3.



M	Membrane	PE	Partial egg
		#/#	U/D number
- \ \	Egg chamber boundary	SQ #	Grid number

FIG. 3. – Eggshell distribution and orientation of N2.

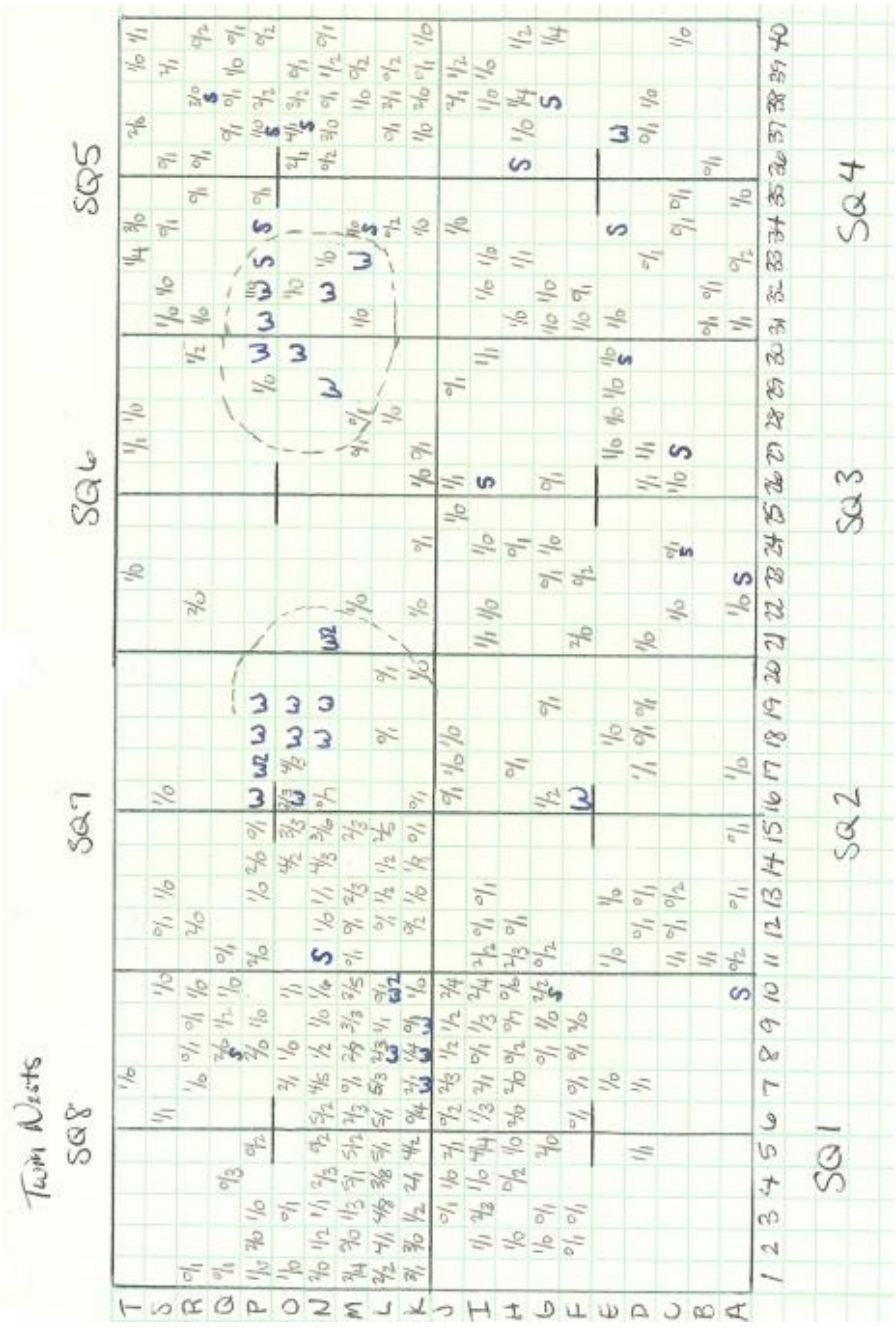
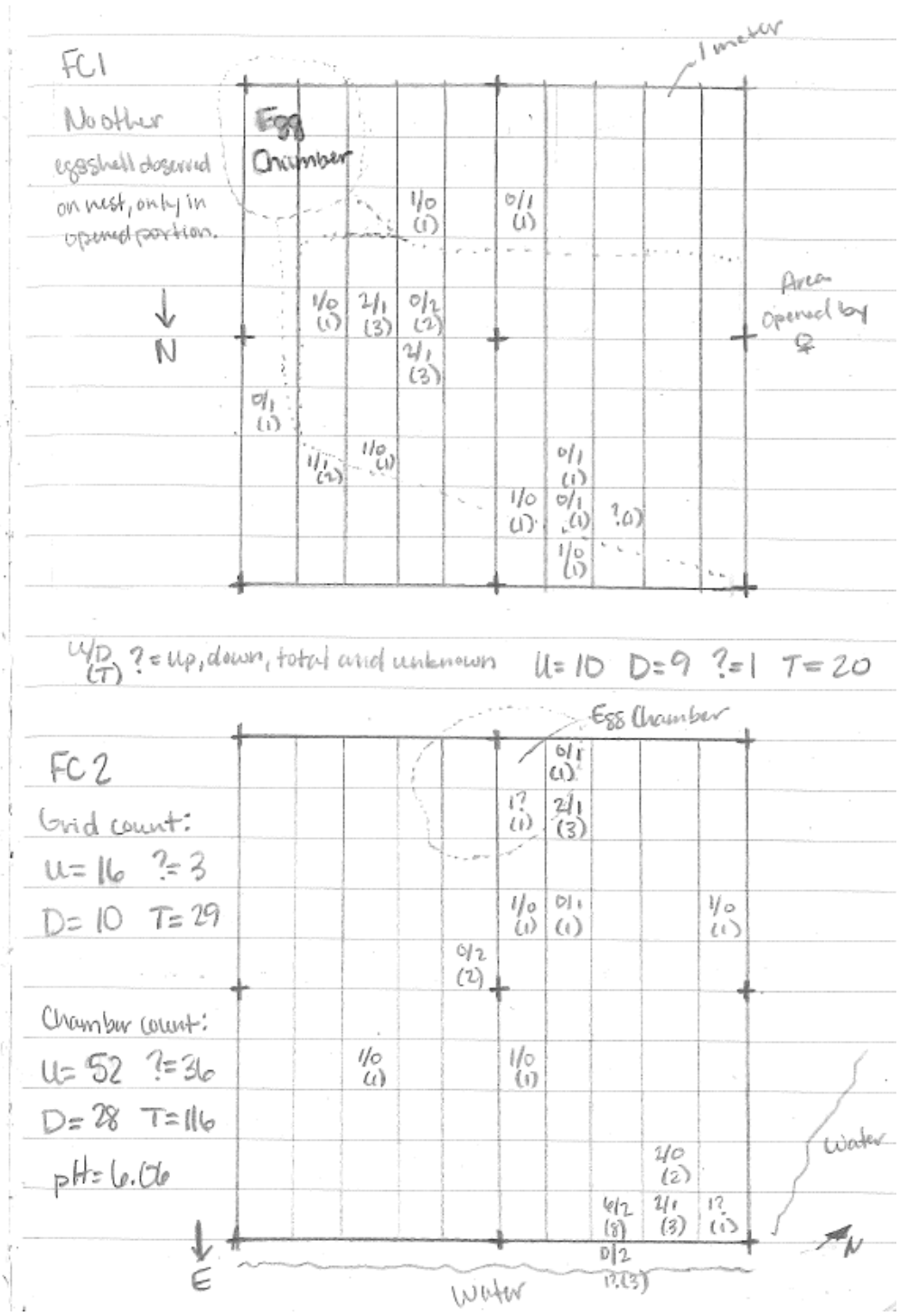


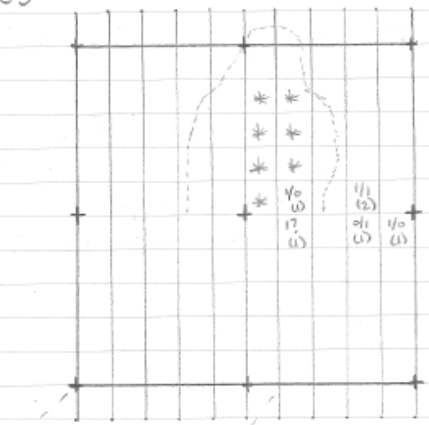
FIG. 4. – Eggshell distribution and orientation for the Twin Nests.

APPENDIX B

CAIMAN LATIROSTRIS GRIDS/EGGSHELL DISTRIBUTION


FC1
No other eggshell observed on nest, only in opened portion.
Egg Chamber
1 meter
Area opened by ♀
N
1/0 (1)
0/1 (1)
2/1 (3)
0/2 (2)
1/1 (2)
?.0)
U/D (T) ?= up, down, total and unknown U=10 D=9 ?=1 T=20
FC2
Grid count:
U=16 ?=3
D=10 T=29
Chamber count:
U=52 ?=36
D=28 T=116
pH=6.06
Egg Chamber
1? (1)
2/1 (3)
0/2 (2)
2/0 (2)
4/2 (8)
1? (1)
0/2 1?.(3)
Water
E
N

FC 3

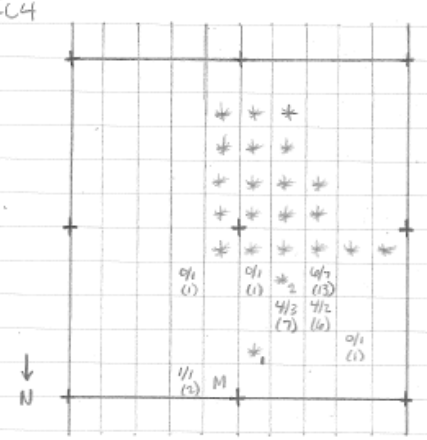


* = Chamber count
U = 97 ? = 25
D = 64 T = 186

? = vertical pieces or disturbed by excavation

Trail count: U = 4 D = 5 ? = 0 T = 9
Grid count: U = 3 D = 2 ? = 1 T = 6

FC4



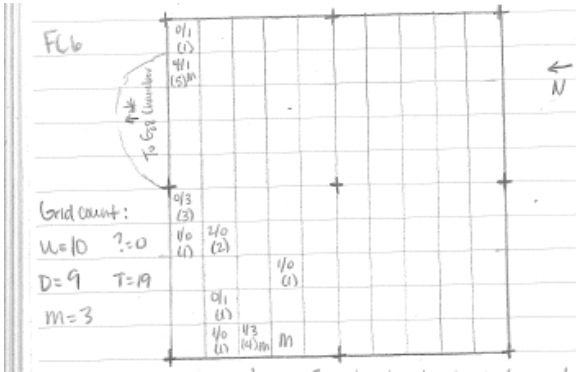
M = membrane
Split tails to water

*1 count: U = 9 D = 14 ? = 5 T = 29
*2 count: U = 9 D = 10 ? = 0 T = 19

Grid count + *1 + *2: U = 33 D = 38 ? = 5 T = 76
* Chamber count + spill over: U = 64 D = 52 ? = 14 T = 130

FC 5 - Unmatched nest, not counted.

FC6

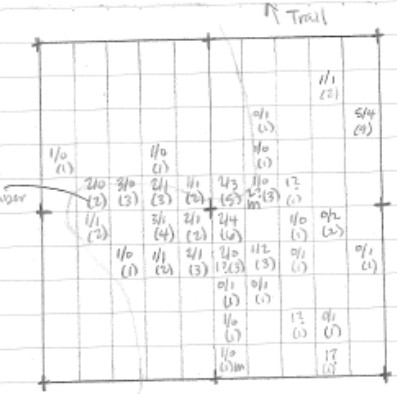


Grid count:
U=10 ?=0
D=9 T=19
m=3

Egg chamber has been dug out.

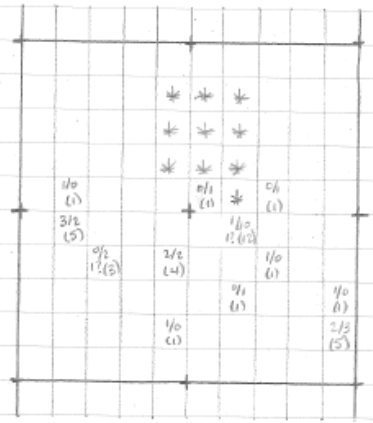
Trail

FC7



Grid Count: U=38 D=28 ?=6 T=72

FC8



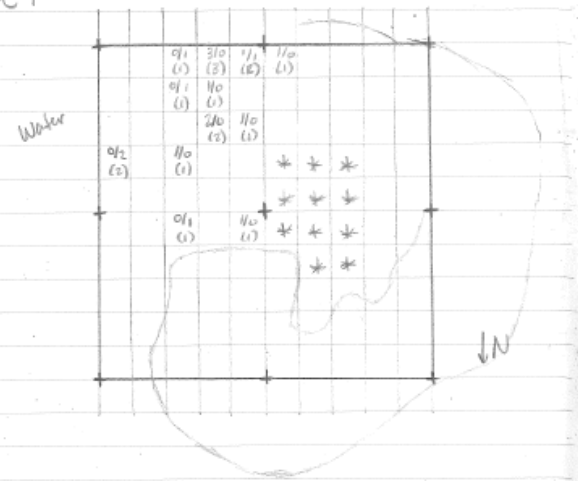
Membrane found in trail with eggshell

Membrane Count: U=13 D=7 ?=6 T=26

* Chamber: "1 membranes, possibly more. Too many ants to do an accurate count. They were partial eggs, usually with bottoms more or less intact - lots of shell skipped.

Grid Count:
U=12 ?=2
D=22 T=36

FC 9



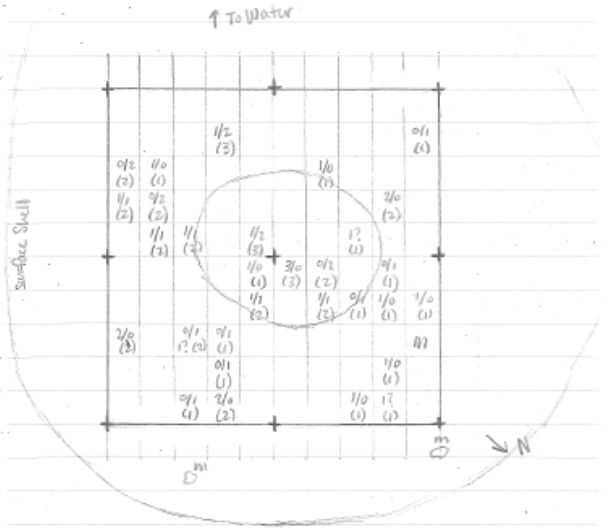
Outside grid count: *Chamber count:

U=5 ?=0 U=2 ?=3

D=1 T=6 D=2 T=7

Membranes: 3 Hatched: 3 Bad eggs: 2

Grid Count: U=11 D=6 ?=0 T=17

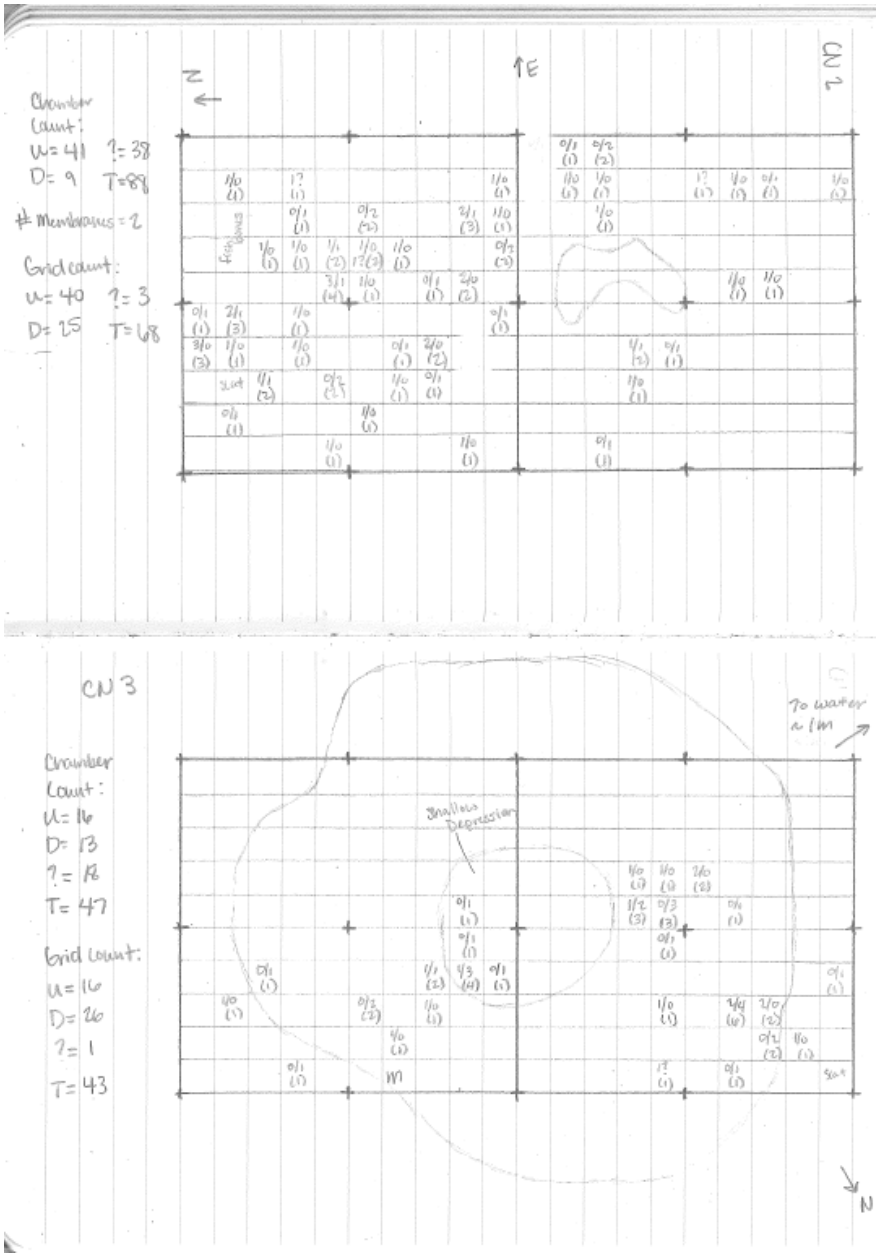


Chamber Excavation: U=56 D=39 ?=75 T=170

Grid count: U=23 D=22 ?=3 T=48

Upper 3-4 cm of nest. Not representative of entire egg chamber, represents small subsample from the upper portion only.

Found 2 membranes inside with eggshell attached, CH.


CN 2
N
E
Chamber Count:
U= 41 ?= 38
D= 9 T=88
# Membranes = 2
Grid count:
U= 40 ?= 3
D= 25 T= 68
CN 3
To water n fm
Smaller Depression
Chamber Count:
U= 16
D= 13
?= 18
T= 47
Grid count:
U= 16
D= 26
?= 1
T= 43
N

APPENDIX C

BOWDOIN NEST LOCATION MAPS

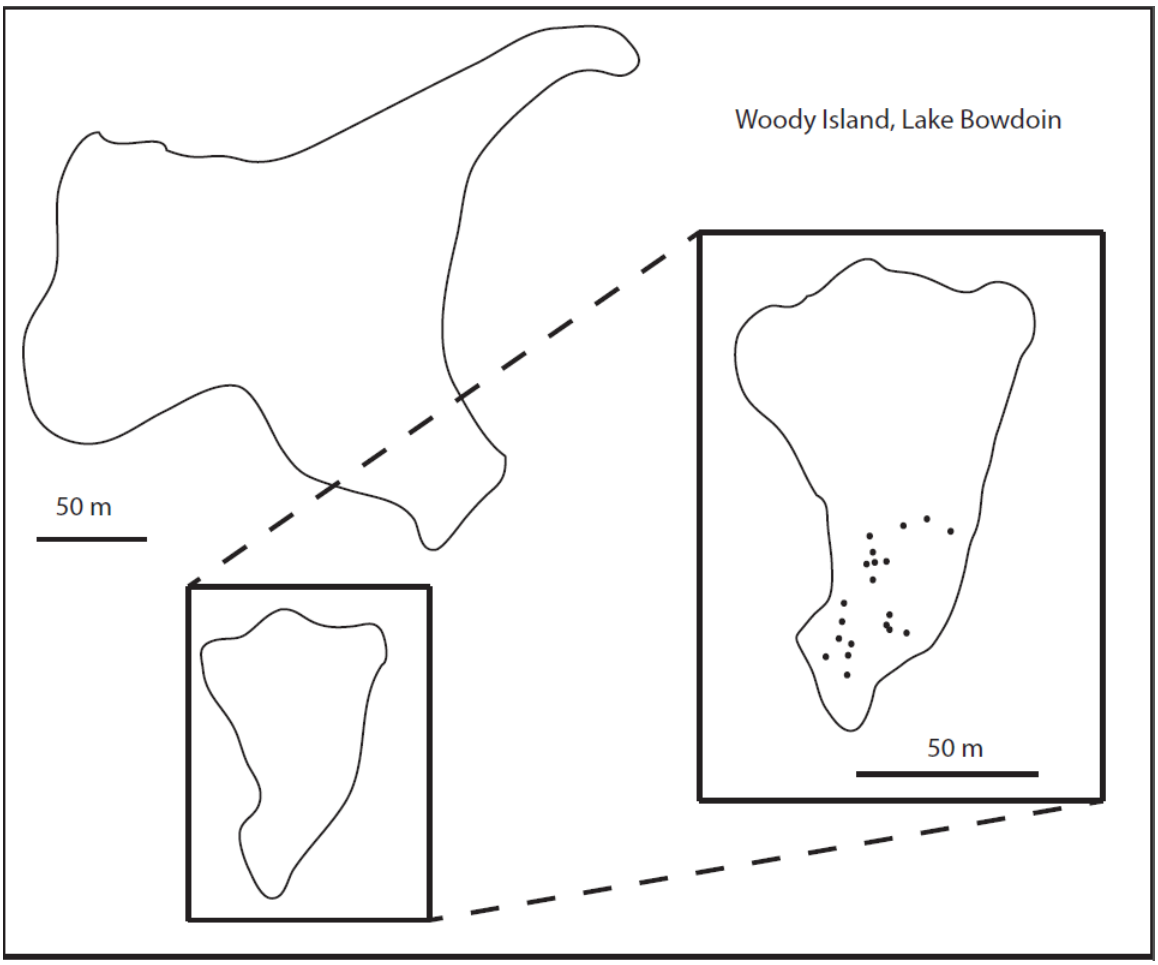


FIG. 1. – American white pelican nest distribution on Woody Island.

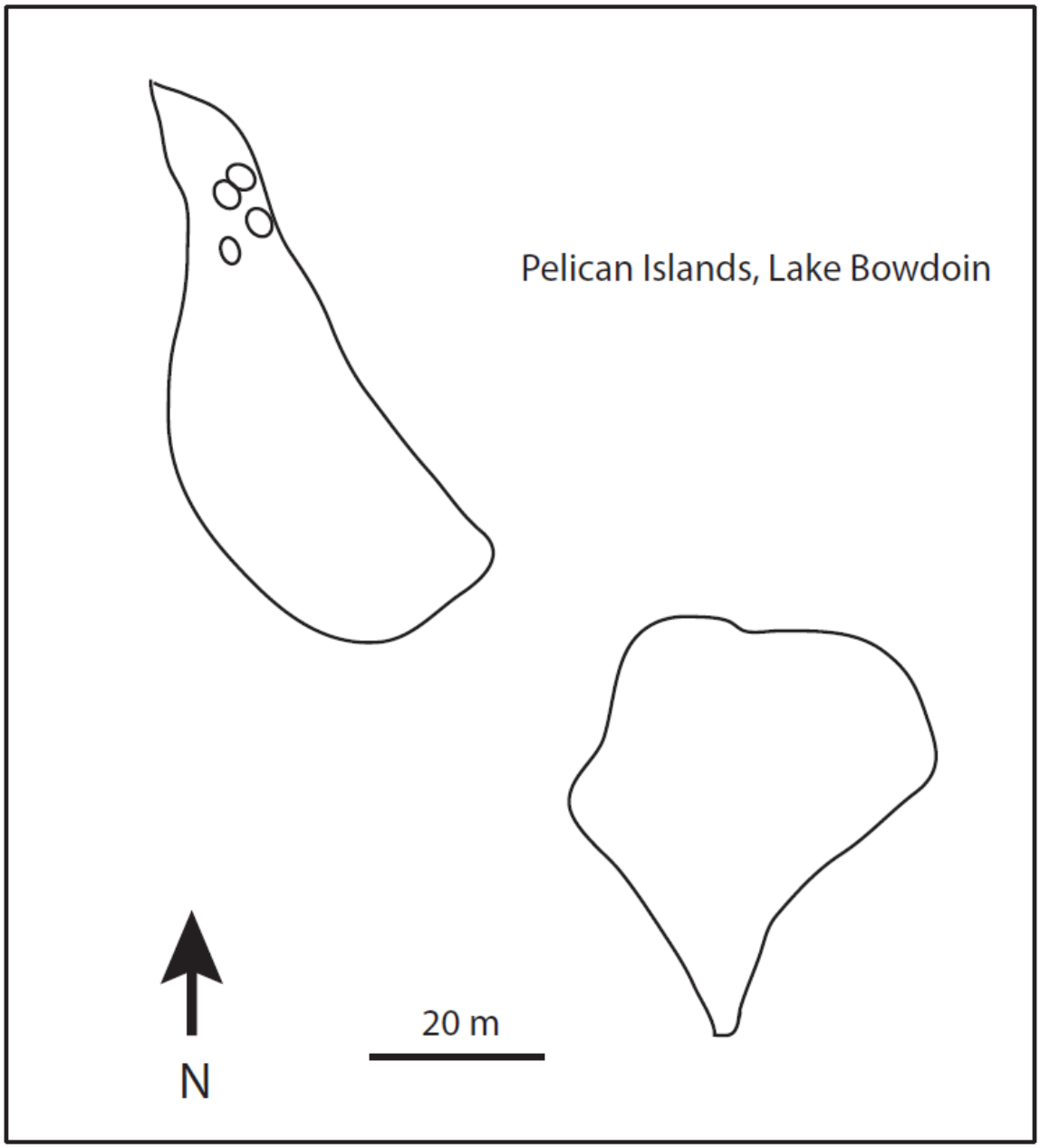


FIG. 2. – Double-crested cormorant nest distribution on the Pelican Islands. Circles represent clusters of nests.

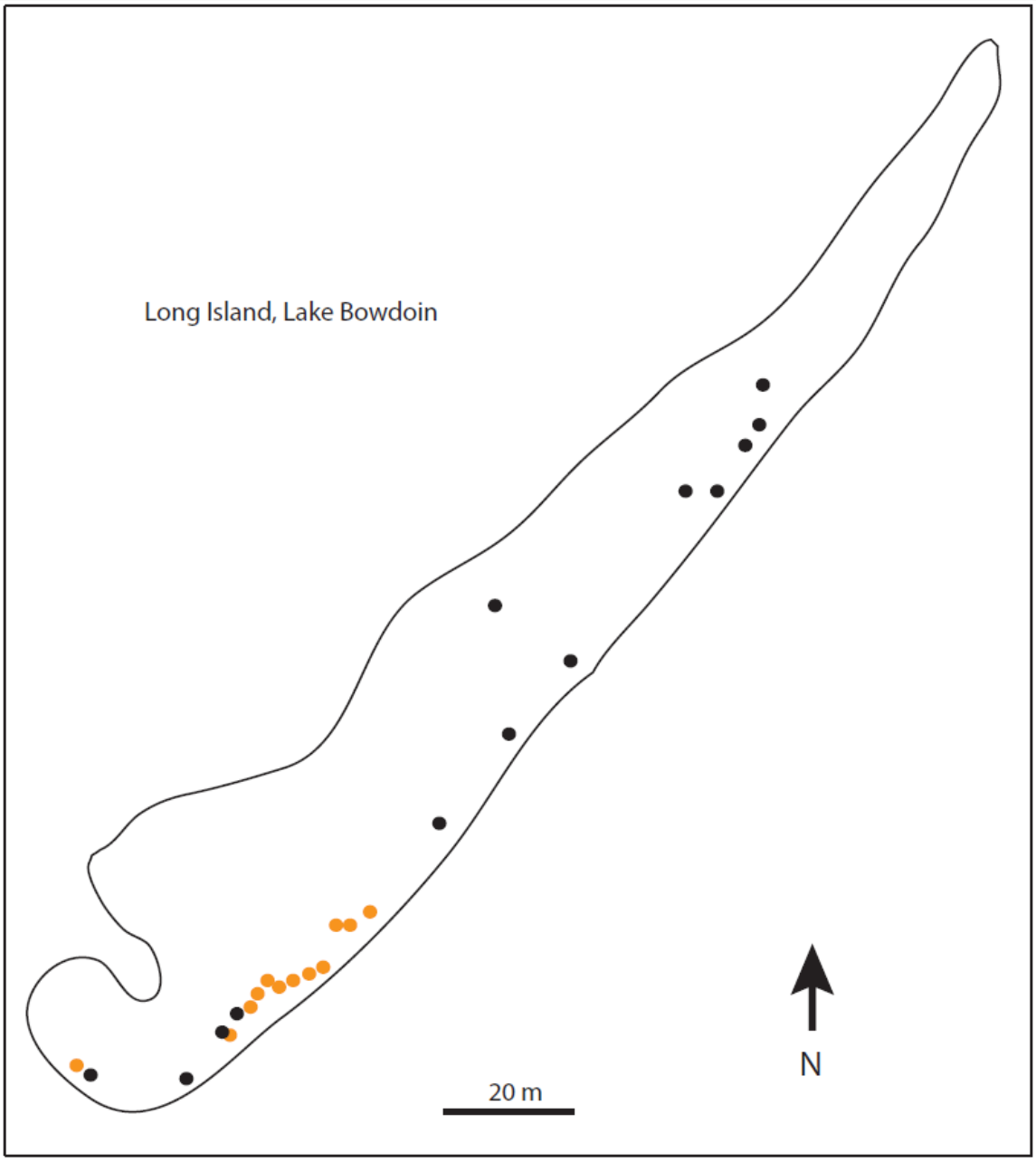
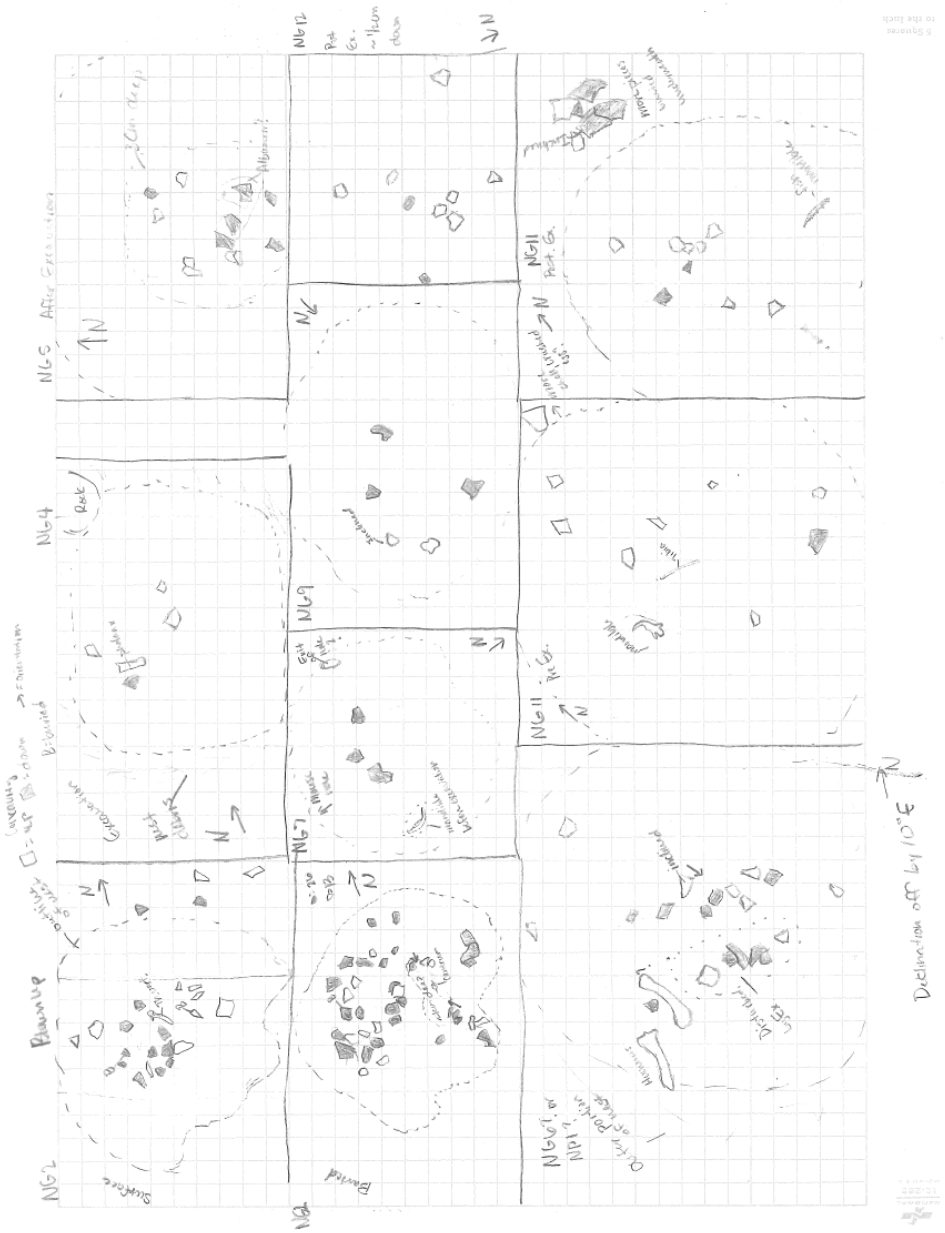


FIG. 3. –Gull nest distribution on Long Island. Orange dots are nests collected from September 2014 and black dots are from September 2015.

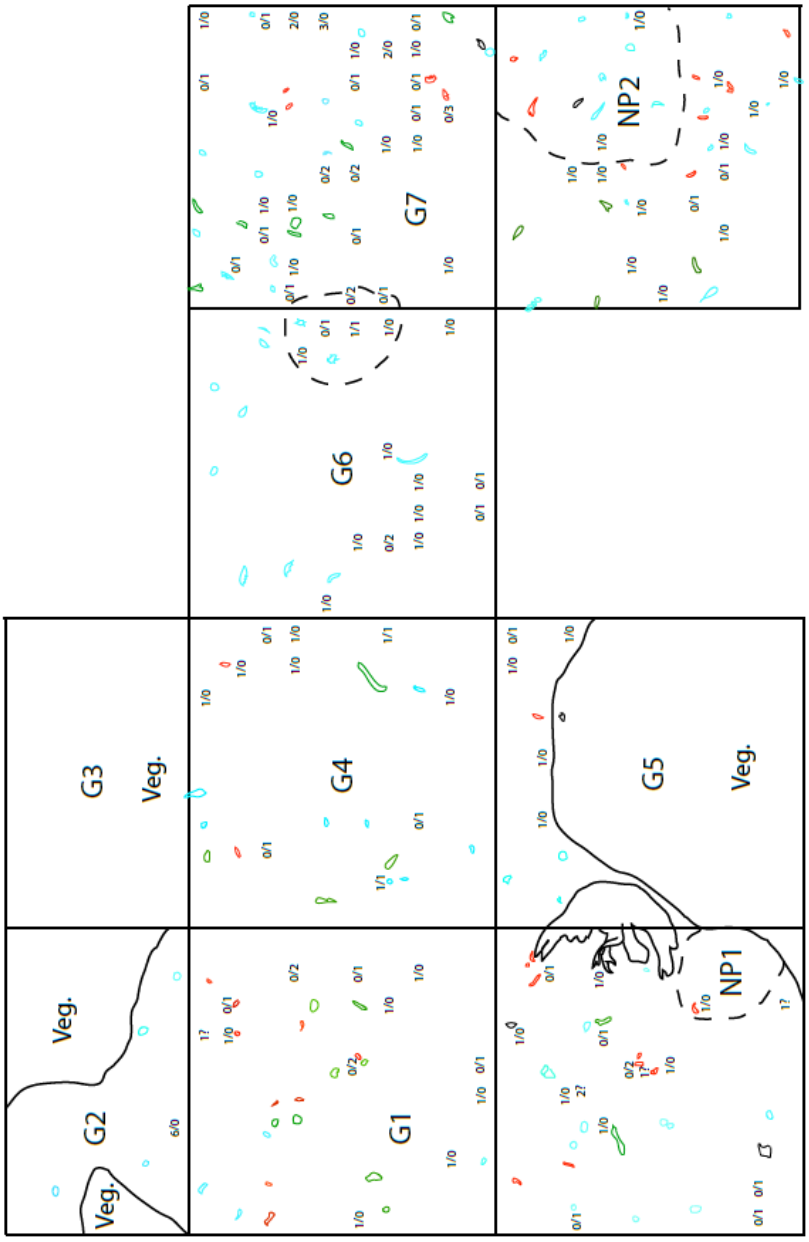
APPENDIX D

GULL NEST GRIDS NG1-12



APPENDIX E

PELICAN NEST GRIDS NP1-2


G1
G2
G3
G4
G5
G6
G7
NP1
NP2
Veg.
Veg.
Veg.
Veg.

APPENDIX F

SKELETALLY MATURE AND JUVENILE MATERIAL

ACROSS THE NESTING SITES

Gull

	Skeletally Mature	Juvenile	Total	Mean
UNID Aves	17	30	47	46.1
Larus	34	10	44	43.1
P. erythrorhynchos	0	2	2	2.0
Rodentia	6	3	9	8.8
Total	57	45	102	
Mean	55.9	44.1		

Pelican

	Skeletally Mature	Juvenile	Total	Mean
UNID Aves	21	45	66	21.5
Larus	10	7	17	5.5
P. auritus	0	1	1	0.3
P. erythrorhynchos	4	40	44	14.3
Rodentia	122	57	179	58.3
Total	157	150	307	
Mean	51.1	48.9		

Cormorant

	Skeletally Mature	Juvenile	Total	Mean
UNID Aves	9	15	24	6.5
L. delawarensis	22	15	37	10.0

P. auritus	13	223	236	63.8
P. erythrorhynchos	37	28	65	17.6
UNID Mammalia	8	0	8	2.2
Total	89	281	370	
Mean	24.1	75.9		

APPENDIX G

WEATHERING STAGES OF SKELETALLY MATURE ELEMENTS

Gulls	**Weathering Stage**	**0**	**1**	**2**	**3**	**4**	**5**	**Total**	**Mean**
Aves	Excavation	15	0	0	0	-	-	**15**	**37.5**
	Inside	10	3	1	1	-	-	**15**	**37.5**
	Outside	6	2	0	0	-	-	**8**	**20.0**
Mammalia	Excavation	1	0	0	0	-	-	**1**	**2.5**
	Inside	1	0	0	0	-	-	**1**	**2.5**
	Outside	0	0	0	0	-	-	**0**	**0.0**
	Total	**33**	**5**	**1**	**1**	-	-	**40**	
	Mean	**82.5**	**12.5**	**2.5**	**2.5**	-	-		

Pelicans	Weathering Stage	0	1	2	3	4	5	Total	Mean
Aves	Excavation	2	1	0	0	0	-	**3**	**12.0**
	Inside	0	0	0	0	0	-	**0**	**0.0**
	Outside	9	2	0	0	1	-	**12**	**48.0**
Mammalia	Excavation	1	0	0	0	0	-	**1**	**4.0**
	Inside	3	0	0	0	0	-	**3**	**12.0**
	Outside	6	0	0	0	0	-	**6**	**24.0**
	Total	**21**	**3**	**0**	**0**	**1**	-	**25**	
	Mean	**84.0**	**12.0**	**0.0**	**0.0**	**4.0**	-	**100.0**	

Cormorants	Weathering Stage	0	1	2	3	4	5	Total	Mean
Aves	Excavation	9	6	1	0	0	1	**17**	**22.1**
	Inside	14	1	0	0	0	0	**15**	**19.5**

	Outside	30	9	0	1	3	0	**43**	**55.8**
Mammalia	Excavation	0	1	0	0	0	0	**1**	**1.3**
	Inside	0	0	0	0	0	0	**0**	**0.0**
	Outside	0	0	1	0	0	0	**1**	**1.3**
	Total	**53**	**17**	**2**	**1**	**3**	**1**	**77**	
	Mean	**68.8**	**22.1**	**2.6**	**1.3**	**3.9**	**1.3**		

APPENDIX H

EGGSHELL ORIENTATIONS AND LOCATIONS PER NEST

Nest # **Location** **Outside Nest**

		#CU	%CU	#CD	%CD	(?)	%?	**Total**	N. CU%	N. CD%
NG1	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG2	L. Is.	2	50.0	2	50.0	0	0	**4**	50.0	50.0
NG3	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG4	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG5	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG6	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG7	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG8	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG9	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG10	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG11	L. Is.	8	66.7	4	33.3	0	0	**12**	66.7	33.3
NG12	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG13	L. Is.	1	50.0	1	50.0	0	0	**2**	50	50
NG14	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG15	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG16	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG17	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!

NG18	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG19	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG20	L. Is.	5	50.0	4	40.0	1	10	**10**	55.6	44.4
NG21	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG22	L. Is.	1	100.0	0	0.0	0	0	**1**	100	0
NG23	L. Is.	0	0.0	1	100.0	0	0	**1**	0	100
NG24	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG25	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
Totals		**7**	**50**	**6**	**42.9**	**1**	**7.1**	**14**	**53.8**	**46.2**
Mean		**0.5**	**50.0**	**0.5**	**47.5**	**0.1**	**2.5**	**1.1**	**51.4**	**48.6**

Nest # **Location** **Inside Nest**

		#CU	%CU	#CD	%CD	(?)	%?	**Total**	N. CU%	N. CD%
NG1	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG2	L. Is.	8	42.1	9.0	47.4	2.0	10.5	**19.0**	47.1	52.9
NG3	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG4	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG5	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG6	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG8	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!

NG9	L. ls.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG10	L. ls.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG11	L. ls.	7	87.5	1	12.5	0	0	**8**	87.5	12.5
NG12	L. ls.	1	100	0	0	0	0	**1**	100	0
NG13	L. ls.	4	50	4	50	0	0	**8**	50	50
NG14	L. ls.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG15	L. ls.	7	46.7	8	53.3	0	0	**15**	46.7	53.3
NG16	L. ls.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG17	L. ls.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG18	L. ls.	1	14.3	3	42.9	3	42.9	**7**	25	75
NG19	L. ls.	1	50	1	50	0	0	**2**	50	50
NG20	L. ls.	3	60	2	40	0	0	**5**	60	40
NG21	L. ls.	2	100	0	0	0	0	**2**	100	0
NG22	L. ls.	4	57.1	3	42.9	0	0	**7**	57.1	42.9
NG23	L. ls.	8	88.9	1	11.1	0	0	**9**	88.9	11.1
NG24	L. ls.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG25	L. ls.	3	33.3	6	66.7	0	0	**9**	33.3	66.7
Totals		**49**	**53.3**	**38**	**41.3**	**5**	**5.4**	**92**	**56.3**	**43.7**
Mean		**2.0**	**60.8**	**1.5**	**34.7**	**0.2**	**4.4**	**3.7**	**62.1**	**37.9**

Nest # **Location** **Nest Excavation**

	#CU	%CU	#CD	%CD	(?)	%?	**Total**	N. CU%	N. CD%

NG1	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG2	L. Is.	13	33.3	25	64.1	1	2.6	**39**	34.2	65.8
NG3	L. Is.	3	33.3	6	66.7	0	0.0	**9**	33.3	66.7
NG4	L. Is.	3	75.0	1	25.0	0	0.0	**4**	75.0	25.0
NG5	L. Is.	6	50.0	6	50.0	0	0.0	**12**	50.0	50.0
NG6	L. Is.	7	36.8	6	31.6	6	31.6	**19**	53.8	46.2
NG8	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG9	L. Is.	1	25.0	2	50.0	1	25.0	**4**	33.3	66.7
NG10	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG11	L. Is.	7	77.8	2	22.2	0	0.0	**9**	77.8	22.2
NG12	L. Is.	7	77.8	2	22.2	0	0.0	**9**	77.8	22.2
NG13	L. Is.	8	38.1	8	38.1	5	23.8	**21**	50.0	50.0
NG14	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG15	L. Is.	18	37.5	13	27.1	17	35.4	**48**	58.1	41.9
NG16	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG17	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG18	L. Is.	36	41.9	34	39.5	16	18.6	**86**	51.4	48.6
NG19	L. Is.	4	50.0	0	0.0	4	50.0	**8**	100.0	0.0
NG20	L. Is.	11	39.3	15	53.6	2	7.1	**28**	42.3	57.7
NG21	L. Is.	0	0.0	3	50.0	3	50.0	**6**	0.0	100.0
NG22	L. Is.	36	49.3	25	34.2	12	16.4	**73**	59.0	41.0
NG23	L. Is.	14	42.4	10	30.3	9	27.3	**33**	58.3	41.7
NG24	L. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NG25	L. Is.	8	61.5	4	30.8	1	7.7	**13**	66.7	33.3

Totals		**182**	**57.6**	**165**	**52.2**	**77**	**24.4**	**316**	**52.4**	**47.6**
Mean		**7.3**	**42.7**	**6.6**	**40.9**	**3.1**	**16.4**	**17.0**	**51.2**	**48.8**

Nest # **Location** **Grid Counts**

		#CU	%CU	#CD	%CD	(?)	%?	**Total**	N. CU%	N. CD%
NP1	W. Is.	-	-	-	-	-	-	-	-	-
NP2	W. Is.	-	-	-	-	-	-	-	-	-
NP3	W. Is.	16	51.6	13	41.9	2	6.5	**31**	55.2	44.8
NP4	W. Is.	10	66.7	4	26.7	1	6.7	**15**	71.4	28.6
NP5	W. Is.	3	33.3	6	66.7	0	0.0	**9**	33.3	66.7
NP6	W. Is.	6	31.6	11	57.9	2	10.5	**19**	35.3	64.7
NP7	W. Is.	10	52.6	8	42.1	1	5.3	**19**	55.6	44.4
NP8	W. Is.	7	58.3	5	41.7	0	0.0	**12**	58.3	41.7
NP9	W. Is.	27	57.4	20	42.6	0	0.0	**47**	57.4	42.6
NP10	W. Is.	21	43.8	27	56.3	0	0.0	**48**	43.8	56.3
NP11	W. Is.	14	43.8	18	56.3	0	0.0	**32**	43.8	56.3
NP12	W. Is.	27	46.6	28	48.3	3	5.2	**58**	49.1	50.9
NP13	W. Is.	27	40.3	39	58.2	1	1.5	**67**	40.9	59.1
NP14	W. Is.	20	50.0	20	50.0	0	0.0	**40**	50.0	50.0
NP15	W. Is.	10	90.9	1	9.1	0	0.0	**11**	90.9	9.1
NP16	W. Is.	8	47.1	7	41.2	2	11.8	**17**	53.3	46.7
NP17	W. Is.	24	45.3	29	54.7	0	0.0	**53**	45.3	54.7
NP18	W. Is.	26	57.8	19	42.2	0	0.0	**45**	57.8	42.2
NP19	W. Is.	8	57.1	6	42.9	0	0.0	**14**	57.1	42.9
NP20	W. Is.	8	66.7	4	33.3	0	0.0	**12**	66.7	33.3

Totals		**272**	**49.5**	**265**	**48.3**	**12**	**2.2**	**549**	**50.7**	**49.3**
Mean		**15.1**	**52.3**	**14.7**	**45.1**	**0.7**	**2.6**	**30.5**	**53.6**	**46.4**

Nest #	**Location**	**Inside Nest**								
		#CU	%CU	#CD	%CD	(?)	%?	**Total**	N. CU%	N. CD%
NP1	W. Is.	1	50.0	0	0.0	1	50.0	**2**	100.0	0.0
NP2	W. Is.	2	100.0	0	0.0		0.0	**2**	100.0	0.0
NP3	W. Is.	7	29.2	17	70.8	0	0.0	**24**	29.2	70.8
NP4	W. Is.	5	45.5	5	45.5	1	9.1	**11**	50.0	50.0
NP5	W. Is.	14	58.3	10	41.7	0	0.0	**24**	58.3	41.7
NP6	W. Is.	10	37.0	17	63.0	0	0.0	**27**	37.0	63.0
NP7	W. Is.	9	42.9	11	52.4	1	4.8	**21**	45.0	55.0
NP8	W. Is.	4	40.0	6	60.0	0	0.0	**10**	40.0	60.0
NP9	W. Is.	10	43.5	13	56.5	0	0.0	**23**	43.5	56.5
NP10	W. Is.	13	43.3	16	53.3	1	3.3	**30**	44.8	55.2
NP11	W. Is.	10	41.7	13	54.2	1	4.2	**24**	43.5	56.5
NP12	W. Is.	12	46.2	13	50.0	1	3.8	**26**	48.0	52.0
NP13	W. Is.	27	54.0	23	46.0	0	0.0	**50**	54.0	46.0
NP14	W. Is.	7	30.4	15	65.2	1	4.3	**23**	31.8	68.2
NP15	W. Is.	7	23.3	23	76.7	0	0.0	**30**	23.3	76.7
NP16	W. Is.	7	41.2	10	58.8	0	0.0	**17**	41.2	58.8
NP17	W. Is.	13	56.5	10	43.5	0	0.0	**23**	56.5	43.5
NP18	W. Is.	29	50.0	29	50.0	0	0.0	**58**	50.0	50.0
NP19	W. Is.	10	58.8	7	41.2	0	0.0	**17**	58.8	41.2
NP20	W. Is.	1	50.0	1	50.0	0	0.0	**2**	50.0	50.0
Totals		**198**	**44.6**	**239**	**53.8**	**7**	**1.6**	**444**	**45.3**	**54.7**

Mean		**9.9**	**47.1**	**12.0**	**48.9**	**0.4**	**4.0**	**22.2**	**50.2**	**49.8**

Nest #	**Location**	**Nest Excavation**								
		#CU	%CU	#CD	%CD	(?)	%?	**Total**	N. CU%	N. CD%
NP1	W. Is.	5	41.7	3	25.0	4	33.3	**12**	62.5	37.5
NP2	W. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NP3	W. Is.	2	16.7	5	41.7	5	41.7	**12**	28.6	71.4
NP4	W. Is.	2	100.0	0	0.0	0	0.0	**2**	100.0	0.0
NP5	W. Is.	7	29.2	7	29.2	10	41.7	**24**	50.0	50.0
NP6	W. Is.	6	66.7	1	11.1	2	22.2	**9**	85.7	14.3
NP7	W. Is.	4	50.0	1	12.5	3	37.5	**8**	80.0	20.0
NP8	W. Is.	3	30.0	3	30.0	4	40.0	**10**	50.0	50.0
NP9	W. Is.	10	62.5	4	25.0	2	12.5	**16**	71.4	28.6
NP10	W. Is.	7	29.2	5	20.8	12	50.0	**24**	58.3	41.7
NP11	W. Is.	10	66.7	3	20.0	2	13.3	**15**	76.9	23.1
NP12	W. Is.	5	22.7	8	36.4	9	40.9	**22**	38.5	61.5
NP13	W. Is.	3	18.8	5	31.3	8	50.0	**16**	37.5	62.5
NP14	W. Is.	5	27.8	8	44.4	5	27.8	**18**	38.5	61.5
NP15	W. Is.	1	7.7	7	53.8	5	38.5	**13**	12.5	87.5
NP16	W. Is.	2	33.3	1	16.7	3	50.0	**6**	66.7	33.3
NP17	W. Is.	5	35.7	5	35.7	4	28.6	**14**	50.0	50.0
NP18	W. Is.	12	40.0	8	26.7	10	33.3	**30**	60.0	40.0
NP19	W. Is.	4	50.0	3	37.5	1	12.5	**8**	57.1	42.9
NP20	W. Is.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
Totals		**93**	**35.9**	**77**	**29.7**	**89**	**34.4**	**259**	**54.7**	**45.3**

Mean		**4.7**	**40.5**	**3.9**	**27.7**	**4.5**	**31.9**	**13.0**	**56.9**	**43.1**

Grid # **Location** **Outside Grid**

		#CU	%CU	#CD	%CD	(?)	%?	**Total**	N. CU%	N. CD%
GC1	P. Is. N.	12	52.2	8	34.8	3	13.0	**23**	60.0	40.0
GC2	P. Is. N.	5	33.3	9	60.0	1	6.7	**15**	35.7	64.3
GC3	P. Is. N.	5	27.8	12	66.7	1	5.6	**18**	29.4	70.6
GC4	P. Is. N.	11	42.3	13	50.0	2	7.7	**26**	45.8	54.2
GC5	P. Is. N.	9	56.3	7	43.8	0	0.0	**16**	56.3	43.8
GC6	P. Is. N.	9	36.0	7	28.0	9	36.0	**25**	56.3	43.8
GC7	P. Is. N.	18	46.2	19	48.7	2	5.1	**39**	48.6	51.4
GC8	P. Is. N.	7	38.9	10	55.6	1	5.6	**18**	41.2	58.8
GC9	P. Is. N.	3	60.0	2	40.0	0	0.0	**5**	60.0	40.0
GC10	P. Is. N.	20	48.8	19	46.3	2	4.9	**41**	51.3	48.7
GC11	P. Is. N.	1	16.7	4	66.7	1	16.7	**6**	20.0	80.0
GC12	P. Is. N.	9	56.3	5	31.3	2	12.5	**16**	64.3	35.7
GC13	P. Is. N.	3	42.9	4	57.1	0	0.0	**7**	42.9	57.1
GC14	P. Is. N.	11	55.0	7	35.0	2	10.0	**20**	61.1	38.9
Total		***123***	***44.7***	***126***	***45.8***	***26***	***9.5***	***275***	***49.4***	***50.6***
Mean		***8.8***	***43.7***	***9.0***	***47.4***	***1.9***	***8.8***	***19.6***	***48.1***	***51.9***

Nest # **Location** **Inside Nest**

		#CU	%CU	#CD	%CD	(?)	%?	**Total**	N. CU%	N. CD%
NC1	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!

NC2	P. Is. N.	2	66.7	1	33.3	0	0	**3**	66.7	33.3
NC3	P. Is. N.	3	50	2	33.3	1	16.7	**6**	60	40
NC4	P. Is. N.	0	0	2	100	0	0	**2**	0	100
NC5	P. Is. N.	6	31.6	13	68.4	0	0	**19**	31.6	68.4
NC6	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC7	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC8	P. Is. N.	2	40	3	60	0	0	**5**	40	60
NC9	P. Is. N.	1	50	1	50	0	0	**2**	50	50
NC10	P. Is. N.	1	50	1	50	0	0	**2**	50	50
NC11	P. Is. N.	11	55	8	40	1	5	**20**	57.9	42.1
NC12	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC13	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC14	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC15	P. Is. N.	6	28.6	7	33.3	8	38.1	**21**	46.2	53.8
NC16	P. Is. N.	8	66.7	4	33.3	0	0	**12**	66.7	33.3
NC17	P. Is. N.	1	33.3	1	33.3	1	33.3	**3**	50	50
NC18	P. Is. N.	4	57.1	3	42.9	0	0	**7**	57.1	42.9
NC19	P. Is. N.	0	0	1	100	0	0	**1**	0	100
NC20	P. Is. N.	1	100	0	0	0	0	**1**	100	0
NC21	P. Is. N.	1	100	0	0	0	0	**1**	100	0
NC22	P. Is. N.	4	26.7	9	60	2	13.3	**15**	30.8	69.2
NC23	P. Is. N.	1	20	4	80	0	0	**5**	20	80
NC24	P. Is. N.	3	60	2	40	0	0	**5**	60	40
NC25	P. Is. N.	11	52.4	8	38.1	2	9.5	**21**	57.9	42.1
Total		**66**	**43.7**	**70**	**46.4**	**15**	**9.9**	**151**	**48.5**	**51.5**

Mean		**2.6**	**46.7**	**2.8**	**47.2**	**1**	**6.1**	**6.04**	**49.7**	**50.3**

Nest #	**Location**	**Nest Excavation**								
		#CU	%CU	#CD	%CD	(?)	%?	**Total**	N. CU%	N. CD%
NC1	P. Is. N.	1	100	0	0	0	0	**1**	100	0
NC2	P. Is. N.		0		0	2	100	**2**	#DIV/0!	#DIV/0!
NC3	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC4	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC5	P. Is. N.	0	0	1	100	0	0	**1**	0	100
NC6	P. Is. N.	2	100	0	0	0	0	**2**	100	0
NC7	P. Is. N.	1	100	0	0	0	0	**1**	100	0
NC8	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC9	P. Is. N.	0	0	1	100	0	0	**1**	0	100
NC10	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC11	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC12	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC13	P. Is. N.	1	100	0	0	0	0	**1**	100	0
NC14	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC15	P. Is. N.	11	32.4	8	23.5	15	44.1	**34**	57.9	42.1
NC16	P. Is. N.	1	20	2	40	2	40	**5**	33.3	66.7
NC17	P. Is. N.	0	0	1	100	0	0	**1**	0	100
NC18	P. Is. N.	1	50	1	50	0	0	**2**	50	50

NC19	P. Is. N.	1	50	0	0	1	50	**2**	100	0
NC20	P. Is. N.	1	100	0	0	0	0	**1**	100	0
NC21	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC22	P. Is. N.	0	0	1	50	1	50	**2**	0	100
NC23	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC24	P. Is. N.	0	#DIV/0!	0	#DIV/0!	0	#DIV/0!	**0**	#DIV/0!	#DIV/0!
NC25	P. Is. N.	5	27.8	6	33.3	7	38.9	**18**	45.5	54.5
Total		**25**	**33.8**	**21**	**28.4**	**28**	**37.8**	**74**	**54.3**	**45.7**
Mean		**1**	**45.3**	**0.9**	**33.1**	**1**	**21.5**	**2.96**	**56.2**	**43.8**

APPENDIX I

ELEMENT COMPLETENESS PER TAXON

Gull Nests

	C	MC	P	F	TOTAL	Mean
Actinopterygii	16	19	2	5	42	23.1
UNID Aves	28	13	12	9	62	34.1
Larus	36	14	5	0	55	30.2
P. erythrorhyncos	1	0	1	0	2	1.1
UNID Mammalia	0	0	2	0	2	1.1
Rodentia	6	7	4	0	17	9.3
Reptilia	1	0	0	0	1	0.5
Malacostraca	1	0	0	0	1	0.5
TOTAL	89	53	26	14	182	

Pelican Nests

	C	MC	P	F	TOTAL	Mean
Actinopterygii	128	163	193	71	555	49.0
UNID Aves	23	16	20	94	153	13.5
Larus	8	6	4	0	18	1.6
P. auritus	0	1	0	0	1	0.1
P. erythrorhyncos	16	13	14	2	45	4.0
UNID Mammalia	2	0	0	0	2	0.2
Rodentia	65	109	89	27	290	25.6
Amphibia	25	15	1	0	41	3.6
Reptilia	2	0	0	0	2	0.2
Malacostraca	7	6	11	2	26	2.3
TOTAL	276	329	332	196	1133	

Cormorant Nests

	C	MC	P	F	TOTAL	Mean
Actinopterygii	305	369	156	71	901	61.4
UNID Aves	9	8	4	40	61	4.2
Larus	26	10	1	0	37	2.5
P. auritus	154	50	23	1	228	15.5
P. erythrorhyncos	28	23	11	6	68	4.6
UNID Mammalia	1	2	0	0	3	0.2
Rodentia	2	2	3	1	8	0.5
Amphibia	15	2	1	0	18	1.2
Malacostraca	56	50	19	19	144	9.8
TOTAL	596	516	218	138	1468	

APPENDIX J

EGGSHELL TAXONOMY PER NEST

Date	Locality	Nest	NP	% Pelican	% Gull	% Cormorant	% Other
9/4/2015	L. Is.	NG13	ON	100%	0%	0	0
9/4/2015	L. Is.	NG13	IN	100%	0%	0	0
9/4/2015	L. Is.	NG13	EX	100%	0%	0	0
9/4/2015	L. Is.	NG14	N/A				
9/4/2015	L. Is.	NG15	IN	95%	5%	0	0
9/4/2015	L. Is.	NG15	EX	95%	4%	0%	1%
9/4/2015	L. Is.	NG16	N/A				
9/4/2015	L. Is.	NG17	N/A				
9/4/2015	L. Is.	NG18	IN	100%	0%	0	0
9/4/2015	L. Is.	NG18	EX	100%	0%	0	0
9/4/2015	L. Is.	NG19	IN	0%	100%	0	0
9/4/2015	L. Is.	NG19	EX	25%	75%	0	0
9/4/2015	L. Is.	NG20	IN	100%	0%	0	0
9/4/2015	L. Is.	NG20	ON	100%	0%	0	0
9/4/2015	L. Is.	NG20	EX	90%	10%	0	0
9/4/2015	L. Is.	NG21	IN	50%	50%	0	0
9/4/2015	L. Is.	NG21	EX	90%	10%	0	0
9/4/2015	L. Is.	NG22	IN	100%	0%	0	0
9/4/2015	L. Is.	NG22	ON	100%	0%	0	0
9/4/2015	L. Is.	NG22	EX	100%	0%	0	0
9/4/2015	L. Is.	NG23	ON	100%	0%	0	0
9/4/2015	L. Is.	NG23	EX	90%	10%	0	0
9/4/2015	L. Is.	NG24	N/A				
9/4/2015	L. Is.	NG25	N/A				
9/4/2015	L. Is.	NG26	IN	100%	0%	0	0
9/4/2015	L. Is.	NG26	EX	100%	0%	0	0
Mean				**87%**	**13%**	**0%**	**0%**

Date	Locality	Nest	NP	% Pelican	% Gull	% Cormorant	% Other
9/3/2015	W. Is.	G1	Grid	95%	5%	0	0
9/3/2015	W. Is.	G2	Grid	100%	0	0	0
9/3/2015	W. Is.	G3	N/A				
9/3/2015	W. Is.	G4	Grid	100%	0	0	0
9/3/2015	W. Is.	G5	Grid	100%	0	0	0
9/3/2015	W. Is.	G6	Grid	100%	0	0	0
9/3/2015	W. Is.	G7	Grid	100%	0	0	0
9/3/2015	W. Is.	NP1	IN	100%	0	0	0
9/3/2015	W. Is.	NP1	ON	97%	3%	0	0
9/3/2015	W. Is.	NP2	IN	100%	0	0	0
9/3/2015	W. Is.	NP2	ON	95%	5%	0	0
9/18/2015	W. Is.	NP3	IN	95%	5%	0	0
9/18/2015	W. Is.	NP3	EX	90%	10%	0	0
9/18/2015	W. Is.	NP3	ON	100%	0	0	0
9/18/2015	W. Is.	NP4	IN	95%	5%	0	0
9/18/2015	W. Is.	NP4	ON	95%	5%	0	0
9/18/2015	W. Is.	NP4	EX	100%	0%	0	0
9/18/2015	W. Is.	NP5	IN	100%	0%	0	0
9/18/2015	W. Is.	NP5	ON	100%	0%	0	0
9/18/2015	W. Is.	NP5	EX	100%	0%	0	0
9/18/2015	W. Is.	NP6	IN	100%	0%	0	0
9/18/2015	W. Is.	NP6	ON	100%	0%	0	0
9/18/2015	W. Is.	NP6	EX	100%	0%	0	0
9/18/2015	W. Is.	NP7	IN	100%	0%	0	0
9/18/2015	W. Is.	NP7	ON	100%	0%	0	0
9/18/2015	W. Is.	NP7	EX	100%	0%	0	0
9/18/2015	W. Is.	NP8	IN	100%	0%	0	0

9/18/2015	W. Is.	NP8	ON	90%	10%	0	0
9/18/2015	W. Is.	NP8	EX	100%	0	0	0
9/18/2015	W. Is.	NP9	IN	100%	0	0	0
9/18/2015	W. Is.	NP9	ON	100%	0	0	0
9/18/2015	W. Is.	NP9	EX	90%	0%	0	10%
9/18/2015	W. Is.	NP10	ON	100%	0%	0	0
9/18/2015	W. Is.	NP10	EX	100%	0%	0	0
9/18/2015	W. Is.	NP10	IN	100%	0%	0	0
9/18/2015	W. Is.	NP11	EX	100%	0%	0	0
9/18/2015	W. Is.	NP11	IN	100%	0%	0	0
9/18/2015	W. Is.	NP11	ON	100%	0%	0	0
9/18/2015	W. Is.	NP12	EX	100%	0%	0	0
9/18/2015	W. Is.	NP12	IN	100%	0%	0	0
9/18/2015	W. Is.	NP12	ON	100%	0%	0	0
9/18/2015	W. Is.	NP13	IN	93%	5%	0	2%
9/18/2015	W. Is.	NP13	ON	99%	0	0	1%
9/18/2015	W. Is.	NP13	EX	100%	0	0	0%
9/18/2015	W. Is.	NP14	IN	100%	0	0	0%
9/18/2015	W. Is.	NP14	ON	100%	0	0	0%
9/18/2015	W. Is.	NP14	EX	100%	0	0	0%
9/18/2015	W. Is.	NP15	ON	100%	0	0	0%
9/18/2015	W. Is.	NP15	EX	100%	0	0	0%
9/18/2015	W. Is.	NP15	IN	100%	0	0	0%
9/18/2015	W. Is.	NP16	ON	100%	0	0	0%
9/18/2015	W. Is.	NP16	IN	100%	0	0	0%
9/18/2015	W. Is.	NP16	EX	85%	15%	0	0%
9/18/2015	W. Is.	NP17	IN	100%	0	0	0%
9/18/2015	W. Is.	NP17	ON	100%	0	0	0%

9/18/2015	W. Is.	NP17	EX	100%	0	0	0%
9/18/2015	W. Is.	NP18	IN	100%	0	0	0%
9/18/2015	W. Is.	NP18	ON	100%	0	0	0%
9/18/2015	W. Is.	NP18	EX	100%	0	0	0%
9/18/2015	W. Is.	NP19	IN	100%	0	0	0%
9/18/2015	W. Is.	NP19	ON	100%	0	0	0%
9/18/2015	W. Is.	NP19	EX	100%	0	0	0%
9/18/2015	W. Is.	NP20	IN	100%	0	0	0%
9/18/2015	W. Is.	NP20	ON	100%	0	0	0%
Mean				**99%**	**1%**	**0%**	**0%**

Date	**Locality**	**Nest**	**NP**	**% Pelican**	**% Gull**	**% Cormorant**	**% Other**
9/5/2015	P. Is. N.	NC1	EX	0%	0%	100%	0%
9/5/2015	P. Is. N.	NC2	IN	0%	0%	100%	0%
9/5/2015	P. Is. N.	NC3	IN	0%	0%	100%	0%
9/5/2015	P. Is. N.	NC4	N/A				
9/5/2015	P. Is. N.	NC5	IN	0%	0%	100%	0%
9/5/2015	P. Is. N.	NC6	EX	0%	0%	100%	0%
9/5/2015	P. Is. N.	NC7	IN	0%	0%	100%	0%
9/5/2015	P. Is. N.	NC8	IN	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC9	N/A				
9/6/2015	P. Is. N.	NC10	IN	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC10	EX	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC11	IN	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC11	EX	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC12	N/A				
9/6/2015	P. Is. N.	NC13	EX	0%	0%	100%	0%

9/6/2015	P. Is. N.	NC14	N/A				
9/6/2015	P. Is. N.	NC15	IN	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC15	EX	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC16	IN	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC16	EX	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC17	EX	0%	0%	100%	0%
9/6/2015	P. Is. N.	NC18	IN	0%	0%	100%	0%
9/17/2015	P. Is. N.	NC19	EX	0%	0%	100%	0%
9/17/2015	P. Is. N.	NC20	IN	0%	0%	100%	0%
9/17/2015	P. Is. N.	NC21	IN	0%	0%	100%	0%
9/17/2015	P. Is. N.	NC22	IN	0%	0%	100%	0%
9/17/2015	P. Is. N.	NC22	EX	0%	0%	100%	0%
9/17/2015	P. Is. N.	NC23	IN	0%	0%	100%	0%
9/17/2015	P. Is. N.	NC24	N/A				
9/17/2015	P. Is. N.	NC25	IN	0%	0%	100%	0%
9/17/2015	P. Is. N.	NC25	EX	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC1	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC2	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC3	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC4	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC5	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC6	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC7	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC8	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC9	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC10	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC11	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC12	Grid	0%	0%	100%	0%

9/5/2015	P. Is. N.	GC13	Grid	0%	0%	100%	0%
9/5/2015	P. Is. N.	GC14	Grid	0%	0%	100%	0%
Mean				**0**	**0**	**100%**	