TAPHONOMY OF ARBOREAL NESTING IN GREAT BLUE HERONS

by

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ABSTRACT

This research supports the growing number of modern bird taphonomic studies and furthers our understanding of the taphonomy of birds and non-avian dinosaurs. The purpose was to broaden modern taphonomic models available for the interpretation of fossil localities of both dinosaurs and birds through examination of the taphonomy of great blue heron (*Ardea herodias*) nesting materials found below their arboreal nests. Investigations took place during the 2012 and 2013 breeding season where heron generated materials were described within the colony and compared to Controls outside of the colony. The Cascade Heron Colony located along the Missouri River in central Montana produced heron eggshells, heron nests, heron prey, and heron bones. The heron diet greatly consisted of fish, small mammals, and crayfish. Of the 1,788 elements discovered, great blue herons made up 52% (*N*=934), of which at least 83% (*N*=776) were considered juvenile. Broken, disarticulated juvenile heron bones dominated the heron skeletal assemblage. The heron bone assemblage exhibited a strong and statistically significant bias for hindlimb elements (74.09%) in comparison to wing elements (25.91%). Of the bone assemblage, nearly 40% (*N*=702) of the materials were found in the subsurface survey. I compared the surface sample versus subsurface sample and found herons largely dominated both samples, but more mammal remains and fish remains made up the taxon-specific subsurface sample. All data were compiled for taphonomic interpretation, reporting and testing for significance. Using a 2x2 Fisher's exact test significant difference between the abundance of materials between surface and subsurface was found. Using a χ^2 for independence there was difference between plot types (sparsely vegetated, densely vegetated and controls). In the heron eggshell assemblage, ample eggshell was found (*N*= 947), but little was buried in the subsurface (*N*=31). Eggshells were described as small eggshell fragments (>1cm but <1/4 of an egg) and large eggshells (>1/4 of an egg). For small and large eggshells, a χ^2 test was used to compare against the null 1:1 'concave up'(CU): concave down'(CD) (CU: CD), and further against the alternative hypotheses for hatched (60:40) and predated eggs (70:30) (Hayward et al, 2011). Outside of plots the large eggshells were found in CU (77:23) positions and small eggshell fragments were found in CD (30:70) orientations. Inside plots small eggshells were found in CU (58:42) orientations. Eggshell orientations significantly differed from the null prediction and for large hatched eggshells (*N*=106) favored CU at 77.40%. Tree-based nesting relative to ground nesting localities had similar nesting material inputs as studied in ground-nesting birds (Hypothesis 1). Controls outside the colony provided the materials described her were generated by heron nesting activities. Hatched large eggshells preferred CU orientations above the hatched 60:40 expected ratio (Hypothesis 2). This work showed burial features of heron materials through the subsurface survey (Hypothesis 4). Tree-based nesting relative to ground nesting showed herons had a higher representations of leg elements than forelimb elements (Hypothesis 5), and the findings from this study showed that vegetation and pH did not influence the density of biological materials below heron nests (Hypothesis 6). Future work into tree-based nesting should examine fallen nest orientation trends and quantify the spatial patterns of juvenile carcasses in proximity to tree bases, tree-based nesting (Hypothesis 3). This works supports great blue herons as plausible models for past-life nesting locale reconstructions.

TAPHONOMY OF THE MODERN TREE-BASED NESTING OF GREAT BLUE HERONS

INTRODUCTION

Modern taphonomic studies provide a lens to understand and interpret fossil assemblages. In order for modern bird nesting sites to serve as proxies for ancient bird and non-avian dinosaur nesting locales, research should examine nesting behavior, developmental strategies, parental care strategies, nest and site usage as well as pre- and postmortem life histories and how these influence the generation of modern skeletal assemblages. Without a detailed understanding of modern bird taphonomy, it is impossible to make comprehensive past life reconstructions for animals of the theropod-bird evolution spectrum. The present study broadens our understanding of the taphonomy of birds and non-avian dinosaurs. No previous research has investigated the preservation potentials and biases of arboreal, semialtricial colonial nesters. Research on modern analogs such as nest sites of great blue herons (*Ardea herodias*) may help with the reconstruction of avifauna fossil localities (Hayward et al., 2000; Clayburn et al., 2004) and may guide the recognition of fossil nesting localities.

Increasing numbers of studies have focused on the taphonomy of ground-based nesting birds (Hayward references therein; Cruz references therein; Prassack, 2011; Wang et al., 2013) but taphonomic research on arboreal nesting colonies is novel. Modern colonial avian nesting sites provide a rich abundance of bones and eggshell remains valuable for paleontological interpretations (Horner, 1994; Hayward et al., 2000; Hayward et al., 2011). Great blue herons share a number of reproductive and behavioral traits found in other modern birds that have been studied taphonomically (Hayward et al., 1989; Cruz, 2007; Cruz, 2008; Hayward et al., 2000; Hayward et al., 2011; Wang et al., 2013) but their arboreal nesting is an important difference. In this study I tested hypotheses concerning the impact of air fall on the taphonomy of biological material below arboreal nests. I also describe the taphonomy of eggshells, bones and pellets below such nests.

THEORETICAL FRAMEWORK

Modern Colonial, Ground-Nesting Birds as Proxies for Ancient Eggs and Nesting Localities

Before describing the outcomes of this project and its limitations as a comparative model for dinosaur nesting sites, I present some parallel research and context. Research conducted by Hayward et al. (1989, 1991, 2000, 2011) and Wang et al. (2013) provided information on modern bird eggshell taphonomy and ground-nesting taphonomy. Studies on modern avian bird bones by Horner (1994), Behrensmeyer et al. (2003), Cruz (2005, 2007, 2008) and Prassack (2011) provided bone survivorship and anatomical representation expectations. Great blue heron research by Butler (1993, 1995, 1999) provided nesting site expectations and highlighted biological processes specific to herons with taphonomic importance. All of these works inspired the present research.

Hayward et al. (1989, 2000) studied ring-billed gulls (*Larus delawarnesis)* and California gulls (*L. californicus)* following rapid burial by volcanic ash following the 1980 eruption of Mount St. Helens. Hayward et al. (1989) reported on the biological material of ground-nesting gulls such as eggs, nests, rodent bones and teeth, bird bones, beetle carapaces and vegetation preferences (see Table 1). Hayward et al. (2000) detailed patterns of eggshell weathering, fragmentation as a consequence of hatched or depredated gull eggs, and eggshell orientation trends. Hayward et al. (2000) also described dispersion patterns of bones and provided distinct patterns of eggshell orientation, ‘concave up’ versus ‘concave down’.

Biotic and abiotic processes affecting the orientation of eggshells included hatching and transport through predation, wind and water. Specifically a ‘concave up’-‘concave down’ ratio of approximately 60:40 was witnessed for unhatched glaucous-winged gull (*L. glaucescens*) eggshell fragments. These results compared favorably to results from dinosaur eggshell sites which exhibited ‘concave up’ orientations at an approximate ratio of 60:40 (Hayward et al., 2000; Hayward et al., 2011). In contrast, glaucous-winged gull eggs depredated by bald eagles (*Haliaeetus leucocephalus*) and cannibalized by other glaucous-winged gulls exhibited a roughly 70:30 ratio (Hayward et al., 2011). Additionally, wind transport of fragments resulted in a predominance of ‘concave down’ orientations at approximately 20:80, while orientations of flume and natural stream transported fragments were predominately ‘concave down’. Stream transport of fragments resulted in a nearly 10:90 ratio, with a strong preference for ‘concave down’ (Hayward et al., 2011).

Colonial, ground-nesting locales contain biological material such as pellets, crustaceans, eggs, nests, etc., and illustrate inter-intra specific differences of nesting species (Hayward et al., 1989). Although they did not quantify the extent of bone weathering, Hayward et al. (2000) did mention the percent of fragmentary bones, and provide weathering features affecting the elements such as desiccation fractures and worn epiphyses. Their observations of the impact of vegetation (Hayward et al., 1989) and impact of acidity on eggshell abundances (Hayward et al, 1991; Hayward et al, 2000; Clayburn et al., 2004) illustrate the importance of environmental conditions in the role of transport, burial, and preservation of eggshells. Hayward et al. (2000) described how mildly acidic soils may effect eggshell preservation and posited that substrates with low moisture and high pH allow biological material to accumulate over time. This topic was examined in greater detail by Clayburn et al. (2004), who found eggshells absent in modern nesting colonies with acidic soils.

Similarly, Behrensmeyer (1978) found that for bone weathering, microhabitat conditions are more influential than the overall characteristics of the habitat. Acidic environments with lower pH dissolved eggshells at a much faster rate than higher pH areas (Hayward et al., 1991; Hayward et al., 2000; Clayburn et al., 2004). Even mildy acidic (pH= 6.4) environments rapidly increased dissolution whereas alkaline soils led to higher potentials of eggshell preservation (Hayward et al., 1991). Carpenter (1982), inferred that non-preservation of eggshell may be attributable to (low-Eh) depositional environments such as water logged and acidic soils.

Research by Wang et al. (2013) on colonial, ground nesting in common terns (*Sterna hirundo*) at Poplar Island in Chesapeake Bay, Talbot County, Maryland supported the 60:40 eggshell distributions from hatched sites reported by Hayward et al. (2000, 2011). Wang et al. (2013) evaluated common tern sand-scrape nests as well as the effects of egg predation in nesting locations placed in different vegetative areas (Table 1). Three common tern colonies were observed and 79 tern nests were assessed for eggshell orientation (hatched, predated, unknown). Of the 193 eggs described, 79 eggshell fragments were incorporated into the shallow (5 cm) subsurface with 33 fragments in ‘concave up’ position and 46 fragments in ‘concave down’ positions. No eggshell fragments were encountered below 4 cm from either nest type (vegetative or sand-scrape). Of the surface and subsurface eggshell fragments reported in their study (*N*=153), ‘concave-up’ was preferred at 54% (*N*=82), ‘concave-down’ orientations at 45% (*N*=69) and vertical positions at 1% (*N*=2). Wang et al. (2013) further reported biological material (e.g., eggs, hatchlings, invertebrate shells) within 21 of the nests and found some evidence of adult skeletal remains at two of the colonies.

Modern Bird Bone Taphonomy

Avian remains undergo pre-burial and taphonomic processes similar to those influencing mammal bones (Behrensmeyer et al., 2003; Cruz, 2007; Cruz, 2008), but avian remains exhibit weathering profiles biased towards the lower weathering stage (WS) (0–2) (Behrensmeyer et al., 2003; Cruz, 2008). Unlike mammals, birds exhibit bone pneumatization which varies among species (Higgins, 1999). This anatomical characteristic may explain weathering biases towards the lower end of the spectrum, the diversity of bone conditions in birds and the surface modification disparities between birds and mammals. Mammalian remains represent all stages of weathering and resist weathering longer than avian bones in the same environment (Behrensmeyer et al., 2003; Cruz, 2008). Avian skeletal representations differ from those of mammal sites possibly due to varying means of locomotion (flying, walking, or swimming) (Cruz, 2005), the fragile nature of avian bones, and/or the growth/ossification of avian bones (Higgins, 1999). Cruz (2008) found that, due to the fragility and internal structure of avian bones, the taphonomic histories of birds are shorter than mammals.

Livingston (1989) suggested differences in the anterior and posterior representations of skeletal elements, and thus preservation biases may exist. These skeletal representation biases may further be influenced by the respective features of avian bones (i.e.., size and density) and related locomotion strategies of the bird. The lightweight and fragile features (Higgins, 1999; Cruz, 2007) of avian bones may expedite pre-burial transport and destruction (Cruz, 2005). Compared with wading birds, strong flying birds may have more wing-dominated assemblages due to the more robust features of the forelimb (Behrensmeyer et al., 2003). Therefore, the ratios of anterior to posterior limb elements may describe the locomotion strategies of preserved animals thus influencing paleoecological interpretations. Cruz (2005) showed that hindlimb or forelimb representation biases may similarly be attributable to avian size and the means of locomotion. Distinct disarticulation patterns have been found for bird groups based on locomotive and ecological preferences (i.e., aquatic, semiaquatic, flying, etc.) (Behrensmeyer et al., 2003; Cruz, 2008).

In north central Montana, Horner (1994) observed the nesting grounds of American white pelicans (*Pelecanus erythrorhynchos*), double-crested cormorants (*Phalacrocorax auritus*) and herring gulls (*Larus argentatus*) on islands in Lake Bowdoin (Table 1). These modern birds were examined as modern analogs of Montana hypsilophodontid, hadrosaurid and lambeasaurid nesting assemblages in relation to the distribution and size ranges of skeletal remains. Horner described numerous juvenile carcasses and subsurface evidence for juvenile remains. Behrensmeyer et al. (2003) studied the taphonomy of a modern avian bone assemblage in Amboseli, Africa in comparison to a fossil assemblage of 54 modern avian skeletal remains in Amboseli Park, Kenya. Twenty-five of the remains were from ostriches (*Struthio camelus*), along with six eggshells and one nest (Table 1). To provide paleontological context, these modern remains were compared to a Pliocene (4-5 Ma) Langebaanweg assemblage and a late Eocene-early Oligocene Fayum assemblage in South Africa. Postmortem taphonomic processes such as weathering, bone surface modification, breakage, survival of differing elements, and time averaging were assessed. Fifty-six percent (*N*=126) of modern Amboseli bones were compared to 70% (*N*=4350) and 77% (*N*=32) of fossil bones at Langebaanweg and Fayum, respectively. The Amboseli modern assemblage exhibited a higher (54%) anterior element representation compared to 39% at the Langebaanweg fossil locale and 30% at the Fayum fossil site. Thus, the fossil remains suggest greater damage and selective sorting than observed in modern avian assemblages. Behrensmeyer et al. (2003) suggested that deviations from an anterior/posterior 50/50 ratio may be indicative of hydraulic sorting (Rich, 1980) or destructive processes that degrade lighter elements (Livingston, 1989). Overrepresentation of modern and fossil larger bones in these assemblages suggest an elemental size bias (Behrensmeyer et al., 1979; Behrensmeyer et al. 2003).

Cruz (1999) described skeletal representations in the Cabo Virgenes and Punta Dungeness magellanic penguin (*Spheniscus magellanicus*) colonies of Santa Cruz, Argentina. Forelimb bones were represented by humerii (15.33%), radii and ulna (10.06%), carpometacarpi (3.55%) and phalanges (1.88%); hindlimbs were represented by femora (12.59%), tibiotarsi (8.45%), tarsometatarsi (5.86%) and phalanges (4.35%) for a total of 1859 elements. Elsewhere, Cruz (2005) reported that ‘flying birds’ were dominated by wing bones (34–54% compared to leg elements at 13–38%) in Perito Moreno National Park, Gallegos River Valley, Cabo Virgenes, and Punta Medanosa. The birds consisted of a wide range of body sizes and anatomical variation, including members of families Phalacrocoracidae, Anatidae, and Laridae. By contrast, assemblages of ‘Ground birds’ such as the flightless lesser rhea (*Pterocnemia pennata*) were dominated by leg assemblages (48–100% occurrence). This evidence suggests pre-burial preservation bias for skeletal parts based on locomotion.

Cruz (2007) found that a prevalence of all limb bones (e.g., mainly humerus, tibiotarsus, femur, and the pectoral girdle, especially coracoids) dominated at the two modern ground nesting magellanic penguin (*Spheniscus magellanicus*) colonies (Cabo Virgenes and Punta Medanosa) (Table 1). Notably bones of the axial skeleton (cranium, mandible, vertebrae, ribs and sternum) and pelvic girdle (pelvis and sacrum) were under represented. Cruz (2008) also studied how nest locations differed due to landscape and vegetation (i.e., under bushes and dug out burrows) in four colonies of southern Patagonia (i.e., Perito Moreno, Gallegos River, Cabo Virgenes, Punta Medanosa) and how taphonomic processes affected the retention of avian remains versus mammalian remains. She found that bone density per spatial unit varied due to nest location and vegetation differences (e.g., wetlands, steppe habitats, marine coast). She further described the taphonomic processes acting on avian remains by habitat (e.g., weathering destruction and predator-prey interactions). Overall, she found greater destruction of avian rather than mammalian bones due to taphonomic processes (e.g., weathering and carnivorous action) (Cruz, 2008).

Prassack (2011) studied the bird bone survivorship of the modern lesser flamingo (*Phoeniconaias minor*) on the shoreline of Lake Emakat in northern Tanzania. In this assemblage, she described the effect of weathering on bird elements in the large nesting colony (Table 1). Here variation in depositional environments such as the saline-alkaline waters, corrosive soils, and increased solar radiation resulted in a decreased element survivorship. She reported that wing bones dominated over leg bones. The survivorship differences were thought to be the result of denser bone being more resistant to taphonomic processes. These biases provided support for specific proximal/distal weather-resistant features. The overall bone quality of this assemblage showed histological evidence of wet and dry cracking through deep, wide and longitudinal cracks from repeated submersion followed by drying. The local conditions of this colony would likely impact the preservation potentials of the lesser flamingo bones.

Large great blue heron colonies have been studied extensively by Robert Butler in British Columbia. His observations from 1986 to 1995 provided detailed behavioral and biological accounts important for understanding which provided specifics for this study. Although Butler never engaged in taphonomic research, his work indirectly measured many taphonomic processes. Butler's research documented heron nest 'housecleaning' behavior involves such as discarding eggshells from nests, thus making them candidates for fossil preservation. Moreover, corvids preyed on eggs leaving signature puncture marks on the eggs. These findings describe pre-burial processes and signatures that influence the preservation potentials of heron generated materials.

Butler (1999) estimated that 6,044 eggs were laid in the Point Roberts colony from 1987–1991; of these, 47.67% were lost as either eggs or chicks, assuming each female laid an average clutch of four eggs. The number of eggs was determined by the average clutch, and the number of chicks lost was figured by the difference between eggs laid and fledged herons (Butler, 1999, p. 115). He speculated that nearly half of all heron eggs laid became fledglings but of these only a third became yearlings. These high chick mortality events show how rich skeletal deposits may be at nesting site.

An analysis in 1995 investigated the causes of mortality in heron chicks. A veterinarian performed a postmortem necropsy on 43 chicks to determine the cause of death. Siblicide was suspected as a major cause of death given that 23 chicks died from falls and, of those, nine had broken bones in the healing stages prior to death. Only four of these chicks died of starvation. Observations such as the 1995 analysis provide behavioral insights that help accurately reconstruct possibilities of juvenile heron mortality. From several studies, Butler described the role of eagle predation on herons and heron colonies. Herons are known to nest near predators such as bald eagles if foraging is good (Butler, 1991; Butler, 1995; Butler, 1999). These observed predator-prey interactions provided heron depredated remain expectations and highlight the role eagles may play on heron colonies (Butler, 1991).

Another understudied area of taphonomy gaining more attention is on locale prey representations through pellet analysis. Modern pellet taphonomy (i.e., regurgitated, oblong masses of undigested bird food) may explain predation behaviors because pellet morphology is distinct and may be used as a signature of taxon-specific predation (Dodson & Wexlar, 1979; Fergus, 2013). Philopatric birds may yield enough accumulation to allow for reconstruction of geohistorical information about a site and the small vertebrate community compositions at a location (Terry, 2004).

Prey items often contain signatures reflecting the predator's ability to alter bones. One such signature egyptian vuluture (*Neophron percnopterus*) was beak/claw alterations (Serra, et al., 2013). Bone modifications by predatory birds consist of damages due to beak and claw use, including: notching, punctures, crushing, pits and crenulated edges (Serra, et al., 2013). Raptor predation leaves notches, semicircular, triangular or rectangular concave indentitations. Predation puncturing leaves oval, circular perforations of bone, while crushing leaves inward perforations into the cortical bone. Predation related pitting consists of circular or triangular superficial modifications and creulated edges??. Pits are typically found in bones of the anterior and posterior limbs (Serra, et al., 2013).

Table 1. Commonalities of modern avian taphonomy**.**
Modern bird colonial, taphonomic studies and species characteristics. For all information not available by author, the information was supplemented via an online source: http://animaldiversity.ummz.unich.edu

Author	**Development Mode**	**Order (Family)**	***Studied Spp.***	**Common name**	**Prey**	**Nest location**	**Nest type**	**Habitat**	**Predators**
McGrath 2014	Semi-altricial	Pelecaniformes (Ardedaie)	*Ardea herodias*	Great blue heron	Piscivorous: opportunistic omnivores	Trees	Simple elevated shallow, saucer shaped nests assembled with twigs	Large Cottonwood grove	Eagles and mesopredators
Hayward et al. 1989, 2000, 2011	Semi-precocial	Charadriiformes (Laridae)	*Larus delawarensis*	Ring-billed gulls	Omnivores	Ground	Platform scrape lined with twigs, sticks, grasses, leaves, lichens, or mosses	Harper Island in Sprague Lake, Adams County, Washington	California gulls, and herring gulls
	Precocial	Charadriiformes (Laridae)	*Larus californicus*	California gulls	Omnivores	Ground	Ground scrape in sand or dirt, lined with vegetation.	colony on Violet Point, Protection Island National Wildlife Refuge, Jefferson County, Washington	Eagles and other gulls
	Precocial	Charadriiformes (Laridae)	*Larus glaucescens*	Glaucous-winged gull	Omnivores	Ground	Platform mound of dried plants built amongst ground cover of low islands or rocky ledges	colony on Violet Point, Protection Island National Wildlife Refuge, Jefferson County, Washington	Bald eagles
Wang et al., 2013	Semi-precocial	Charadriiformes (Sternidae)	*Sterna hirundo*	Common terns	Primarily piscivorous	Ground	Platform pile of dead vegetation	Poplar Island in Chesapeake with scattered vegetation and the substrate consists of sand	Owls and gulls
Horner 1994	Semi-altricial	Pelecaniformes (Pelecanidae)	*Pelecanus erythrorhynchos*	American white pelican	Primarily piscivorous	Ground	Ground shallow nests made of soil	Lake Bowdoin within Bowdoin National Wildlife Refuge in north central Montana. Alkaline lake.	Gulls
	Altricial	Suliformes (Phalacrocoracidae)	*Phalacrocorax auritus*	double crested cormorant	Primarily piscivorous	Ground	Sophisticated platform pillar-like nests from twigs		
	Precocial	Charadriiformes (Laridae)	*Larus argentatus*	Herring Gull	Omnivores	Ground	Platform weeds and bushes; prefer to nest on rock/sand		

Behrensmeyer et al. 2003	Precocial	Struthioniformes (Struthionidae)	*Struthio camelus*	Ostrich	Primarily herbivorous	Ground	Simple scrape	Amboseli Park, Kenya,	Scavenging birds and mammals; raptorial species
Cruz 2005, 2007, 2008	Semi-altricial	Sphenisciformes (Sphenisciforms)	*Spheniscus magellanicus*	Magellanic penguin	Primarily piscivorous	Ground	Burrows and ‘‘mata verde’’shrubs	Substrate: Shingle and silt Sand and shingle, Vegetation: Almost continuous with shrub cover	American grey fox; little hairy armadillo; skuas and Kelp gull
Prassack 2011	Semi-precocial	Phoenicopteriformes (Phoenicopteriforms)	*Phoeniconaias minor*	Lesser flamingo	Primarily herbivorous	Ground	Ground soft muddy material	Lake Emakat, a saline-alkaline lake in northern Tanzania.	Predatory birds, leopard, sotted hyena, village doges, and several mongoose species

Fossil Nesting Localities

Morphological evidence from basal avian taxa strongly supports the theory that birds evolved from theropod dinosaurs (Sereno, 1999). Nevertheless, there still exists a lack of information on life-history, ecological and behavioral traits within non-avian theropods and ancient bird lineages (e.g. enantiornithines). Non-avian theropod dinosaurs are thought to have shared a number of reproductive and behavioral traits with modern birds (Horner, 1994; Varricchio, 2011). The North American theropod dinosaur, *Troodon formosus,* has been described as exhibiting colonial nesting, partially exposed nests, parental care of eggs and precocial young (Horner, 1982; Horner, 1984b; Varricchio, 1999; Horner, 2000). One shared feature between Troodontids and modern birds was the nidifugal ('nest-fleeing') nesting strategy (Horner et al., 2001). Evidence to support nidifugal nesting strategies can be found in well ossified fossil remains of juveniles (Horner, 1982; Horner, 2000; Horner et al., 2001). Another shared feature was the brittle calcitic eggs (Varricchio et al. 1997; Hayward et al, 2000).

Recent fossil egg discoveries such as the Transylvania assemblage (Dyke et al., 2012) and the Patagonia Comahue assemblage (Fernandez et al., 2013) provided evidence for colonial nesting in Cretaceous enantiornithines. The materials described in both assemblages included: juvenile bones, eggs and eggshells. In the Transylvania assemblage, the juvenile bones, eggs and eggshells exhibited uniformity and great abundance of all of these elements suggesting these enantiornithines were synchronous breeders with colonial nesting (Dyke et al., 2012). The nearly complete Transylvania eggs (*N*=7) were asymmetric and pointed as described in modern ground-nesting birds with precocial or semi-precocial young (Table 1). The Comahue locale described 65 eggs with some in semi-buried states and with embryonic remains near the eggs.

The spatial patterns of the eggs were non-random and eggs occurred in close proximity to one another suggesting gregarious behaviors found in colonial organisms (Fernandez et al., 2013).

The Eocene Green River Formation (Biaggi & Buchheim, 1999) in Fossil Lake, Wyoming revealed a large duck-like shorebird *Presbyornis* (Order: Anseriformes). The Fossil Lake *Presbyornis* accummulation not only details the characteristics of an ancient avian nesting locality, but also Leggitt provides one of the most complete and exhaustive taphonomic analyses of a fossil avian site. Leggitt (1996) recorded evidence of eggshell, avian bone, wing-to-leg ratios, MNE, and minimum number of individuals (MNI) in the assemblage. His taphonomic, biological and pathological investigation of the site supported a mass avian death via botulism poisoning. This work supports the preservation potentials for animals that have an ecological niche requiring water and the availability for such environments to provide rapid burial of organic remains.

Five eggs found within an aquatic avian twig-nest provide the first evidence into the potential preservation of non-scrape avian nest structure in the fossil record (Grellet-Tinner, et al., 2012). This *in situ* plant material of the early Miocene Tudela Formation in Spain illustrates a transition from mud ground scrapes to vegetative lined nests. This Podicipediformes-Phoenicopteriformes sister group avian twig-nest is significant because it illustrates the potential for all nest structures to potentially have preservable features. For example, behavioral characteristics of ground nesting animals and sedimentological evidence supported the interpretation of open shallow rimmed scrapes in the Two Medicine Formation of western Montana locale. Nests described as shallow bowl-shaped depressions with distinct rims and the tight arranged clutch of 24 eggs allowed for the inference of brooding in adult *Troodon* (Varricchio et al., 1997; Varricchio et al., 1999).

Arboreal-Cursorial Debate

Since the introduction of the theory of evolution scientists have engaged in debates about the origin of flight (Heers & Dial, 2012; Dyke et al., 2013). The arboreal-cursorial dichotomy (Dial, 2003) poses an interesting paleontological and evolutionary question. Some scientists believe avian flight was likely the response of predator-escape behavior in favor of the 'ground up' theory (Dial, 2003a, b). Others believe dinosaurs were able to climb trees and subsequently flight may have evolved from the 'tree down' (Naish, 2000a, b).

Dial (2003a) supports the 'ground up' theory on the basis of his wing-assisted incline running experiments and five parameter approach. Dial (2003b) describes five parameters of particular interest to the arboreal-cursorial debate with two parameters directly related to reproductive biology. These parameters include: (1) locomotor modules (e.g., forelimbs, forelimb/hindlimb/tail, hindlimb/forelimb, hind limb), (2) development spectrum (e.g., superprecocial, three categories of precocial species, two semialtricial, superaltricial) and parental care (nest attendance, etc.), (3) nest biology (e.g., simple ground, platform, simple elevated, excavated, complex elevated), (4) body size (~5-150 kg) and (5) flight styles (e.g., nonvolant/weak flight , narrow, versatile, aerobatic and coursers). Primitive features of extant birds include: dominant hindlimbs, typically nonvolant or weak flight styles, simple parental involvement, minimal nest attendance, and simple nest structures (Dial, 2003b).

In Dial's (2003a) incline running experiments, he placed chukar partridges (*Alectoris chukar*) on various inclines (50–105^{o} slopes) throughout their maturity and various textured slopes. He further investigated flight by trimming and removing flight feathers. His study supported the predator-escape model in which ground birds exhibit rudimentary aerial lift to avoid predation. His assisted incline running model demonstrated the locomotor advantage likely shared by extant birds and protobirds while also testing incipient feathered forelimbs of which are interpreted for small, bipedial protobirds.

It is the opinion of Padian and Dial (2005) that there is no evidence that non-avian theropods flew. Support for arboreality comes from research on pedal claw morphology which suggests *Archaeopteryx* likely climbed (Naish, 2000a, b; Naish, 2012, Naish, 2013). Additionally, *Microrapter,* a small, long-winged dromaeosaurid theropod from the Lower Cretaceous, had claw morphology supporting the ‘climbing’ hypothesis (Birn-Jeffery et al., 2012). Further experiments with wind tunnels on a *Microraptor* model depict its potential ability to glide on occasion and exhibit some form of flight. Modern research on arboreal nesters may impact this arboreal-cursorial debate by providing testable hypotheses for taphonomic signatures unique to arboreal nesters. The Cascade heronry assists the debate by describing arboreal heron generated materials, reproductive biases, skeletal representation frequencies and subsurface expectations for tree-based nesters.

Impetus for this Great Blue Heron Study

The Cascade Heron Colony may provide paleontologists with a clearer perspective on avian reproduction, nesting behaviors, life histories (Hayward et al., 2011; Janssen et al., 2011) and the ecological and the taphonomic histories of a tree-based nesting site. Hayward et al. (1989, 2000, 2011) documented taphonomic features of gull colonies. Gulls are colonial, ground-nesting semi-precocial birds with several taphonomic characteristics relevant to the Cascade heronry. These characteristics were also highlighted by Wang’s et al. (2013) tern study. Cruz’s (2005, 2007, 2008) looked at the colonial, ground-nesting of semi-altricial penguins. Her work, along with that of Behrensmeyer et al. (2003), provided avifauna skeletal representation expectations. Prassack (2011) characterized a large colony of ground-nesting flamingos and described taphonomic processes relevant to wet shoreline environments. Behrensmeyer et al. (2003), Cruz (2008), and Prassack (2011) further provided modern comparisons to fossilized avifauna locales. Horner (1994) described colonial, ground-nesting in three avian species and the materials found within the assemblage. No previous research has investigated the preservation potentials and biases of arboreal, semialtricial, colonial nesters as presented here.

Once great blue heron chicks have hatched, the adults discard eggshells from the nest (Species Profile: Great Blue Heron (*Ardea herodias*), 2013; Butler, 1999). Consequently, ample amounts of biological material may accumulate on the ground below, reflecting the productivity of nests above. Preservation of this material may be influenced by rates of sediment deposition, flooding potential, shear abundance of material from site fidelity and high nest densities within colonies. Great blue herons provide data for testing the following hypotheses about the potential preservation of arboreal nesting events.

Hypothesis 1: *Tree-based nesting will leave biological material (e.g., eggshells, pellets and bones) on the ground that could potentially be incorporated into the fossil record.* Tree-based nesters should share depositional production on par with ground nesting colonies (Hayward et al., 1989), the only difference being the arboreal origin of the deposited materials.

Hypothesis 2: *Due to air fall, hatched heron eggshells will prefer 'concave up' orientations that exceed the 62%–72% observed in a gull colony (Hayward's et al., 2011.* Due to extensive taphonomic research on eggshells (Hayward et al., 1989; 2000; 2011; Wang et al., 2013), it is believed gravity will positively influence eggshell fragments to assume stable 'concave up' orientations (Hayward et al., 2011).

Hypothesis 3: *Discernible distribution patterns for fallen biological material will exist due to nest location and the influence of gravity.* Visual ground inspections may reveal distribution biases. In Cruz's (2008) study, the spatial distributions of juvenile carcasses reflected environmental features related to the organisms' use of space. Juvenile herons may similarly have associations with certain environmental features of the colony. These preferences may lead to preservation and/or destruction characteristics unique to the location of nests.

Hypothesis 4: *Surface material will be incorporated into the subsurface with proportions reflecting the surface material input.* **Hypothesis 4a:** *Surface material will be incorporated into the subsurface and exhibit the same taxonomic representations as the surface.* **Hypothesis 4b:** *Surface material will be incorporated in the subsurface and exhibit the same skeletal representations as the surface.* Herons nest in proximity to high depositional environments with periodic flooding which may increase the potential for burial and long term preservation. Nesting in close proximity to water (Short & Cooper, 1985), having large geographic breeding ranges from Canada to Mexico (Fig. 1) (Quinn & Milner (n.d.); Short & Cooper, 1985; Butler, 1999), and colonies with upwards of 500 nests (Species Profile: Great Blue Heron, 2013) may contribute to high deposition and burial potentials.. It is believed that heron elements and biological material from the herons will be incorporated into the subsurface to at most a depth of 10 cm. As described in Horner's (1994) and Wang's et al. (2013) study it is anticipated that organic remains will be incorporated into the subsurface.

Hypothesis 5: *Skeletal elements found at the Cascade Heron Colony will be equally distributed across wing and leg elements.* Modern avian remains show similar pre-burial, taphonomic processes acting similar to processes influencing fossil assemblages (Behrensmeyer et al., 2003; Cruz, 2008) this means that any proximal and distal limb distribution biases may be potentially relevant for paleoreconstructions. Mass mortality events as reported by Leggitt (1996) should experience equal distributions across the wing and leg elements in a 1:1 wing-to-leg ratio. Rich (1980) hypothesized that differences in skeletal representation may reflect fluvial action where elements with higher density (e.g., tibiotarsi and tarsometatarsi) are more represented than lighter bones (e.g., elongated bones).

Hypothesis 6: *A low pH environment, created by decaying vegetation, may influence the density of biological material retention.* Research indicates that species have spatial preferences and these preferences may lead to biased biological material representations based on vegetation characteristics (Hayward, et al., 1989; Cruz 2007; Wang et al., 2013). Research on great blue herons shows how influential heron excrement is to the vegetation below nests. Excrement contributes to a low pH environment that kills understory and tree stands of large heron colonies (Butler, 1999).

Biology of the Great Blue Heron

Some characteristics of great blue heron relevant for paleoreconstructions include site preference, life histories, behavior, nest preference, nest location, and reproductive strategies. Dial (2003) provided a framework with five attributes and for comparison to other birds, great blue herons were classified with these qualities. The locomotor modules were presented by the order in which each bird species belonged (Dial, 2003b). Great blue herons belong to the order Pelecaniformes. The flight styles of Pelecaniformes are considered narrow and non-aerobatic with a fair mix of hind and forelimb locomotor capabilities (Dial, 2003) as adult wingspans range from 167–201 cm in length (Species Profile: Great Blue Heron, 2013).

The nesting biology for herons is considered semi-primitive in that the nest structures are simple, elevated saucer-like nests made out of twigs typically found in the upper reaches of the trees (Bock, 1956; Pratt, 1970; Butler, 1999, p. 111). The nests vary in size from approximately 50 cm across to more complete structures from multiple years of construction (Vennesland & Butler, 2011; Species Profile: Great Blue Heron, 2013). Nearest neighbor nest distances average 3.8 m (Butler, 1999; p.77).

Figure 1. Breeding, nonbreeding, and year-round ranges of the Great Blue Heron. Taken from: http://bna.birds.cornell.edu/bna/species/025/articles/introduction

Great blue herons are the largest North American herons with body masses twice that of any other heron species (Butler, 1999, p.7). Its size is considered primitive because it is relatively large in comparison to that of other flying birds (Dial, 2003, Figure 4, p.10). Great blue herons vary in size with males being slightly larger than females. Typically, their weights range from 2.1 to 2.5 kg and lengths from 97 to 137 cm (Vennesland, & Butler, 2011). In Dyke & Kaiser's (2010) study, great blue heron female mass was measured at 2110 g with an egg mass of 50.7 g and a mean femur length of 99.4 mm (Butler, 1999; Dyke & Kaiser, 2010).

Research suggests that the earlier in the season great blue herons breed, the more successful they are at raising young to fledgling age (Butler, 1999, p.130). The parents produce one clutch per year and are monogamous for that year but may re-mate with another partner in subsequent years (Butler, 1999). Great blue herons exhibit site fidelity (Butler, 1999, p.89; Vennesland, & Butler, 2011) and lay clutches of 1–8 eggs. Great blue herons lay relatively small eggs that are roughly 3% of the female’s mass. The eggs are pale blue and tend to fade with age. The egg length is 6.1–7.6 cm and egg width is 4.5–5 cm (Butler, 1999; Vennesland & Butler, 2011; Species Profile: Great Blue Heron, 2013). Within the colony (amongst other nests) the hatching events are closely synchronized (Butler, 1999, p.89; Vennesland, & Butler, 2011). Parents raise about two young per year with a mean clutch size of roughly (2.9) (Bennett et al., 1995; Butler 1999). Great blue herons exhibit biparental incubation which typically lasts 27–29 days. Using Starck’s (1993) and Starck and Ricklef’s (1998) definitions the great blue heron is described as “semi-altricial”.

Hatchlings remain in the nest and are not considered mobile. The great blue heron parents exhibit extensive parental care and feed the young until they fledge. Unlike colony hatching events, individual clutches exhibit asynchronous hatching. Asynchronous hatching contributes to the first hatched chick being larger and typically more successful than its younger siblings (Butler, 1999, p.92). The first laid chick tends to have more testosterone which may contribute to chick aggression and siblicide behavior (Butler, 1999, p. 93). Sources of mortality for chicks typically include starvation but sibling competition may be another reason (Bennett, 1993; Butler, 1999). Some chicks may die from falls from the nest (both accidental and sibling-caused) (Bennett et al., 1995; Species Profile: Great Blue Heron, 2013).

METHODS

Great Blue Heron Site

The Cascade Heron Colony (GPS: 47°14’ N; 111°43' W) located near Cascade, Montana was chosen for this taphonomy project due to its dense heron population and site fidelity (Fig. 2). The colony is approximately 85 m away from the large, slow moving Missouri River. Its proximity to the river provides a desirable location for herons due to its sustainable prey base. It is also near to other small bodies of freshwater which provide ample resources. The size of the colony is 110 m x 68 m.

Figure 2. Satellite imagery of Cascade Heron Colony. Image was taken from GoogleEarth in August 2011.

The colony landscape is easily traversable, and largely removed from human disturbance. Occupied trees were identified by locating nests using binoculars and inspecting the ground below for excrement and feathers. Ground inspections were preferred for determining active nests, as nest height generally exceeded 22 m and dense leaf coverage made identification difficult. The colony contained 54 cottonwoods trees with 136 nests in 2012. Research conducted at this colony took place from April 2012 to August 2013, including two breeding seasons. In 2012, the site was visited April 20, May 4, 11 and 23, June 1, August 3–4, September 22, and October 27 for a total of nine visits. In 2013, the site was visited January 27, April 27, May 12 and 25, June 10 and 22, July 7 and 20, August 10 and 24 for a total of ten visits. Visits in 2012 included documenting when birds returned to the colony, when nest building took place, when eggs hatched, when herons fledged and when herons abandoned the colony for the season. Reproductive materials were considered eggs, eggshells, heron nests, and pre-fledgling nest-bound juveniles. Non-heron vertebrate and invertebrate remains were also described. These observations provided focus for the comprehensive 2013 investigation.

In April 2012, initial colony observations included identifying trees containing nests via visual counts and flagging trees with markers for future collections. Observations continued throughout the season and involved documenting nesting behaviors such as hatch dates. Preliminary counts were recorded for eggshell orientations (i.e., ‘concave up’ or ‘concave down’) in 2012. Evidence for chick mortality and predation was photographed throughout the breeding season. These observations provided site expectations and information on where to place plots. The 2012 plots were created to determine the present and past characteristics of the ground below the nests. These plots were reused as prepared areas for the 2013 collection.

2012 Data Collections

Active Nests and Trees

Determining numbers of nests per tree and their locations were conducted in fall 2012, after trees had defoliated. Coordinates were obtained for trees, nests and plots using Real Time Kinematic (RTK) mapping methodology. The RTK was also used for the plot locations in 2012

(A, C, E, G, H and I) and 2013 (A-L) (Table 3; Table 4). Coordinates were used to create 2-D images of the colony (Fig. 3). Maps were used to facilitate data collection inventories and interpretations.

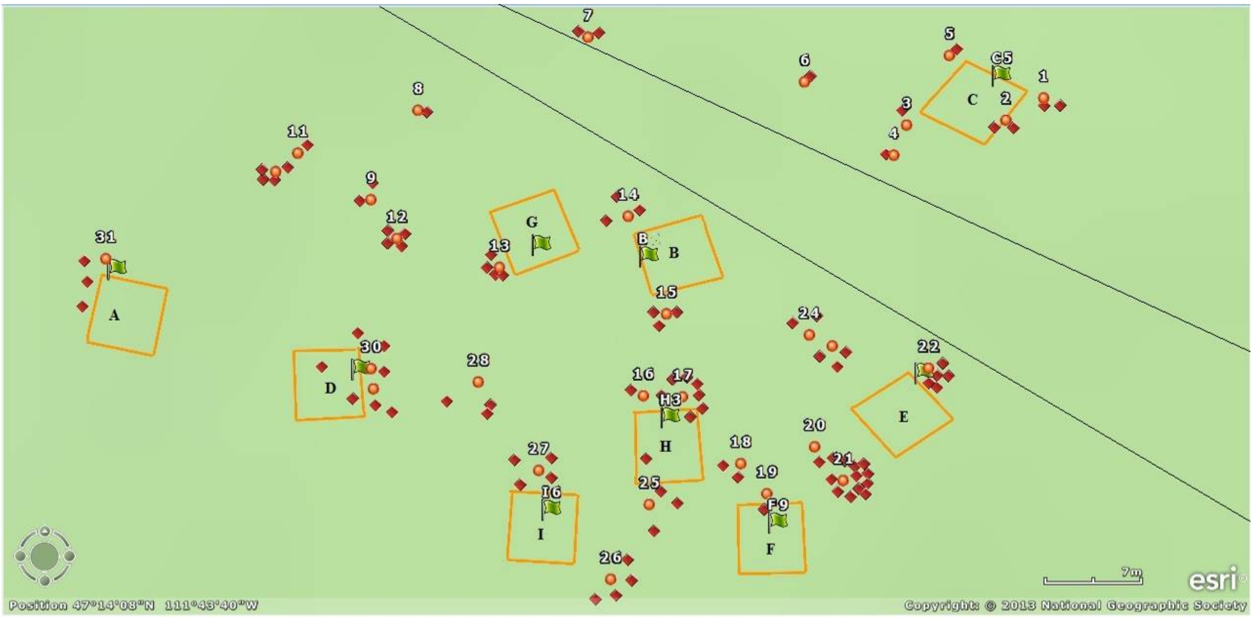


Figure 3. 2-D image of Cascade Heron Colony. This 2-D image of the Cascade Heron Colony is based on the October 27, 2012 data. This image shows 31 trees (circles), 91 nests (diamonds) and nine plots (flags) as outlined with boxes (A-I). The long parallel lines indicate a channel separating the northeast trees (1-7), nests (1-10) and plot C from the rest of the colony.

Once the total nest population was determined, the area of interest for this study was narrowed down to an area of 71 m x 40 m containing 31 cottonwoods trees supporting 91 nests. Based on the large area and care necessary to avoid disturbing the nesting herons, surveying the entire colony was considered too vast for the scope of the project. For the area of interest, occupied trees were marked with flagging tape and assigned an identification number. Marked trees were also used to reference ground plots and to orient researchers within the colony. Diameter at breast height (DBH), distance to nearest occupied tree and nests in the vicinity of ground plots to support RTK observations were recorded for each tree. RTK observations were only as accurate as tree coverage would allow and determinations had to account for tree nest fluctuations as trees experience nest fluctuations year to year. At least 30 nests were considered 'active' based on ground inspections and visual counts. Intraplot investigations involved surveys that sampled materials within the colony (A–I) plots. Extraplot investigations involved any investigation that sampled material outside of plots (A–I) but within the 71 m x 40 m colony.

Extraplot 2012 Eggshell Survey

Multiple surveys (April through September) in 2012 provided total counts for the 2012 Extraplot data. To seek future potentials of biological material for the 2013 breeding season, these preliminary investigations served to identify trees and provide the area of interest for future study. Hereafter, eggshells will be referred to by the survey type (i.e., Extraplot or Intraplot) and the eggshell size (i.e., small or large). For the purposes of this study, large eggshell fragments (>1/4 the size of an egg) were reported separately from small eggshell fragments (>1cm but <1/4 egg). Lage eggshells were designated as hatched or depredated (criteria provided below) and photographed (Fig. 5). Any identified dead chicks below the nests and active nests were also photographed. These observations allowed for determination of colony behavioral characteristics and site expectations. During four visits to the colony in 2012 (May 4, 11 and 23, and June 1, 2012), eggshells were mapped. On June 1, 2012 'concave up' and 'concave down' orientation were determined for the Extraplot.

Plots

Plots were established and sampling was carried out after herons had abandoned the colony. Six plots were created in 2012 with three additional in-colony plots and three out-of-colony control plots added in 2013 (Table 3; Table 4). These six 2012 plots ranged in size from 10 m^2 to 36 m^2 and were created based upon the presence and abundance of biological material (i.e., surface bones, crustacean remains, eggshell fragments and pellets). The researchers examined taphonomic characteristics (presence of eggshell, vertebrate remains, invertebrate remains, regurgitated pellets, droppings, etc.) of the plots using a meter-square grid system (Wang et al., 2013). Locations of biological material were plotted on a survey map.

Subsurface Excavations

Subsurface excavations were carried to depths not exceeding 10 cm. The size of excavated areas within plots varied from 1 m^2 to 2 m^2 but all plots were sampled. Excavation methods were considered preliminary. Initial excavation methods were rudimentary and information obtained was used to improve later subsurface excavation techniques. All subsurface biological material was collected for lab analysis.

Plot Collection Criteria

Data collected from bones and carcasses on plot surfaces included taxon, ontogenetic stage (immature, mature), element, condition (broken, unbroken, weathering stage (0–5), bite marks, beak/claw alterations, etc.), plunge (e.g., vertical to substrate), state of articulation including the number of articulated bones, and carcass completeness. For subsurface avian elements, the above criteria were used as well as depth and element plunge for *in situ* elements. Element identifications were based on comparisons with skeletons of a complete immature (~1–2 week old chick, a nearly complete fledgling, and two partial mature adult great blue heron skeletons.

The weathering scheme (WS) (0–5) used was based on Behrensmeyer (1978) five-stage scheme adapted for birds of heron size (Table 2).

Table 2. Weathering stages (0–5) for bird bones.

Stage	Exfoliation	Cracking
0	No visible signs	No visible signs
1	Mosaic or isolated linear striations; superficial cracks that do not penetrate through the cortical bone	Superficial with signs of fine cracks
2	Present and associated with linear striations which lead to flaking especially along the ends of long bone shafts	Present; thin, longitudinal cracks
3	Patches of rough exfoliation covering up to 50% of the shaft where some of the outermost layer of bone has flaked off	Longitudinal cracks begin to widen
4	Texture, large and small splinters covers more than 50% of shaft	Cracks open especially at breaks
5	Greater than 75% of bone is exfoliated falling apart *in situ* where unlikely to preserve in any identifiable state	Highly cracked and fragmented; bone falling apart *in situ*

Pellets

Three regurgitated heron pellets were collected in the 2012 Survey near plot G to ascertain Cascade heron prey abundance and prey compositions within the colony. During 2012 site preparation activities an additional 16 pellets were collected and used to assess prey distribution and representations at the colony. Pellets were analyzed for taphonomic interpretations and pellet dispersal (intact, partially intact or dispersed) (Dodson & Wexlar, 1979; Terry, 2004). An additional 14 pellets were collected during the 2013 breeding season and were used to determine predation behavior of Cascade herons. For the 2013 collection, all intact and partially dispersed pellets were collected on the day of identification for future lab analysis. Of the 33 pellets collected, three collected pellets had to be discarded due to bacterial and fungal growth from heavy moisture content due to precipitation.

2012 Site and Vegetation Classifications

In 2012, vegetation characteristics were measured within the colony. These designations resulted in ‘dense’ vegetation areas (DV) being described as no soil visible, in contrast, the prominent feature in ‘sparse’ vegetation areas (SV) was soil followed by some fallen debris and minimal vegetation (Fig. 4; Table 3; Table 4). In the 2012 survey, plots (A, C, E, G, H and I) were further prepared for the 2013 survey by the removal of vegetation and other debris after herons had abandoned the nesting area for the 2012 breeding season. Table 3 and 4 show the vegetation regrowth in 2013.

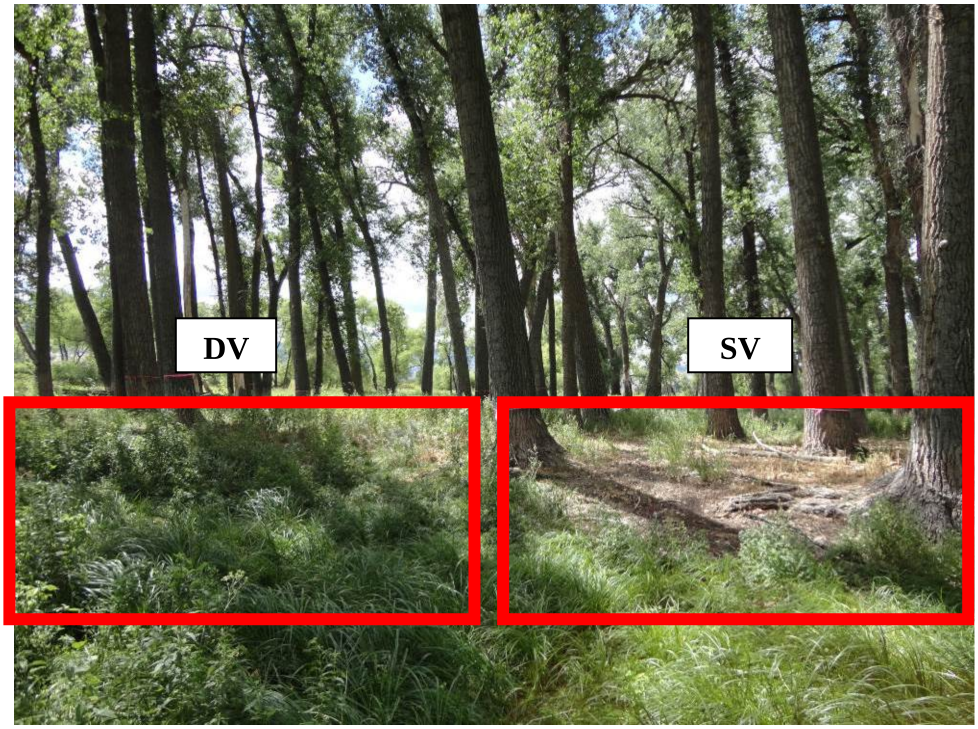


Figure 4. Cascade Heron Colony vegetation characteristics. This photo was taken August 4, 2012. This shows a difference in the vegetation densities in close proximity. Dense vegetation (DV) signifies dense vegetation and sparse vegetation (SV) indicates sparse vegetation.

2013 Collections

Plots

Three additional plots (B, D, F) were added to the original six 2012 plots (A, C, E, G, H, and I) within the colony giving a total of nine 2013 in-colony plots (Table 4). The (A–I) plots took into consideration the 2012 vegetation characteristics and nest densities (Table 3; Table 4). All plots (A–I) were prepared equally by removing vegetation and surface material and leveling the substrate to maintain surface uniformity prior to 2013 collections. This preparation before the 2013 breeding season was necessary to ensure no prior biological materials or vegetation impacted the collections. These nine plots each measured 5 x 5 m and included four plots (A, B, C, H) in sparse vegetation areas, three plots (E, F, I) in dense vegetation, and two in-colony control plots (D & G). Plots (D & G) each 5 x 5 m were covered with plastic tarp and garden fabric to eliminate vegetation growth and thus its effects on the sampling design. All plots were placed below active heron nests and in close proximity to the tree base. Stakes were used to mark the borders of the plots (Table 3).

In addition, three 2 x 2 m, randomly selected plots (J, K, L) were established as Out-of-Colony controls 51 m away from the farthest periphery nest on the western edge of the colony upstream of the Missouri River in an area with no nests. These plots were selected as a control site, as the location was similar to the colony area in supporting a cottonwood grove near the Missouri River. The control location had trees of similar maturity, density and likely experienced high animal traffic and scavenging as documented in the colony. The control was established to discern background bone and eggshell accumulation from that associated with the heronry. These plots were selected without considering their vegetation characteristics.

Table 3. Plot Characteristics for those within the colony. This figure depicts the 2012 and 2013 plots and defines their site collection history, vegetation characteristics, excavation status, nests in the vicinity of the plot, the visibility of sample surface, visibility of soil and the pH of the plot. Any plot not sampled or attribute not sampled was coded (NS). Sparsely vegetated plots were coded (SV), densely vegetated plots were coded (DV) and plots serving as in-colony controls were coded (IC). All vegetation characteristics were defined in 2012 and these A–I pictures show the 2013 regrowth.

Plot	A	B	C	D	E	F	G	H	I
Location (Coordinates)	111°43'42"W 47°14'08"N	111°43'40"W 47°14'08"N	111°43'39"W 47°14'08"N	111°43'41"W 47°14'08"N	111°43'39"W 47°14'08"N	111°43'40"W 47°14'07"N	111°43'41"W 47°14'08"N	111°43'40"W 47°14'07"N	111°43'41"W 47°14'07"N
Vegetation	SV	SV	SV	IC: DV	DV	DV	IC: SV	SV	DV
In-Colony 2012 Plots	A	NS	C	NS	E	NS	G	H	I
Size of plot 2012 Plots	5m x 5m	NS	6m x 6m	NS	8m x4m	NS	5m x 2m	5m x 2m	5m x 2m
Distance to tree	0.71m – Tree 31	0.89m – Tree 15	2.74m – Tree 1	1.63m – Tree 29	2.03m – Tree 22	0.74m – Tree 19	1.50m – Tree 13	1.06m – Tree 17	1.88m – Tree 27
Size of excavation 2012 Plots	1-1m^2	NS	2-1m^2	NS	NS	NS	1-1m^2	1-1m^2	1-1m^2
Size of excavation 2013 Plots	NS	2-2m^2	NS	NS	2-2m^2	NS	2-2m^2	NS	NS
2013 nests in vicinity of plot	9	<5	6	12	7	8	11	12	5
2013 visibility of sampled surface	100%	100%	100%	100%	50%	50%	100%	100%	50%
2013 Visibility of soil	80% 	80% 	70% 	50% 	50% 	0% 	100% 	80% 	40% 
2013 pH of soil	7.0	7.0	6.6	7.0	6.5	6.7	6.7	6.5	6.6

Table 4. Control Plot Characteristics. This figure depicts the three 2013 plots located outside of colony control plots as controls and defines their soil characteristics, vegetation characteristics, excavation status, nests in the vicinity of the plot, the visibility of sample surface, visibility of soil and the pH of the plot. A code of NA indicated that the attribute was not applicable. All vegetation characteristics were defined in 2012 and these J–L pictures show the 2013 regrowth.

2013 Out of Colony Control Plots	J	K	L
Substrate	Soil texture coarser than colony	Soil texture coarser than colony	Soil texture coarser than colony
Vegetation	Low	Low	Low
Nests in vicinity of plot	No heron nests	No heron nests	No heron nests
2013 visibility of sampled surface	100	100	100
2013 pH of soil	NA	NA	7.3
2013 excavation status	NA	NA	Excavated
2013 visibility of soil	90%  DSC01220	50%  DSC01222	75%  DSC01223

Colony Survey 2013

Beginning April 27, 2013, a two person crew surveyed the 12 plots (A–L) using a meter-by-meter grid system recording any surface biological material, including bones, eggs, eggshells, invertebrate remains, and regurgitate pellets. This procedure was repeated every two weeks for a total of nine times through August 2013. None of the biological material was collected during the bi-weekly visits. Care was taken to avoid disturbing the area, biological material and brooding herons. Due to nesting and brooding activities, survey time was limited to approximately one hour while herons occupied the colony. In the August final survey, all biological material was collected for analysis.

Eggs, Eggshells, Bones and Pellets

Data recorded for each eggshell fragment (i.e., small or large) included: orientation (‘concave up’ or ‘concave down’). Hatched large eggshells were differentiated from predated eggshells by examining fracture, puncture marks, condition of membrane and presence/absence of blood (Fig. 5). Criteria used for recognizing depredated eggshells included: attached, transparent eggshell membranes, puncture/fracture marks and the presence of blood (Fig. 5) (Butler, 1989; Mabee, 1997; Butler, 1999, p. 114; Hayward et al., 2000; Kandel, 2004; Wang et al., 2013). I used depredated eggshell criteria to classify depredated eggshells, but due to shell sizes puncture/fracture marks were more indicative of eggshell fate (Hayward et al., 2000). Large eggshells were marked and numbered to assess future transport (e.g., wind, water, predation, tramping, etc.). All eggshells greater than 1 cm were mapped and photographed every visit during the field period as in previous studies of Hayward et al. (2000) and Wang et al. (2013).

Depredated egg: Blood present, fractures inward and transparent membrane	**Hatched:** Membrane white and separated from eggshell	**Fragmentation:** Separation from membrane; breaking into smaller fragments
		

Figure 5. Depredated, Hatched and Fragmented Eggs**.** 2012 Extraplot photographs of great blue heron eggs.

Identified heron regurgitated pellets were mapped, photographed and then collected for subsequent dissection. Each pellet was photographed and assigned a degree of intactness (i.e., partially dispersed, dispersed or intact) (Fig. 6). Only intact and partially dispersed pellets were collected for this study as fully dispersed pellets were too spread out and difficult to identify in the time allotted in the field.

Any surface bone present was mapped and photographed during each visit. All biological material located during the 2013 survey had the same taphonomic data recorded as performed in the 2012 Survey. All elements were identified, photographed and all taphonomic modifications were recorded. The final site collection in August re-inspected the field taphonomic interpretations.

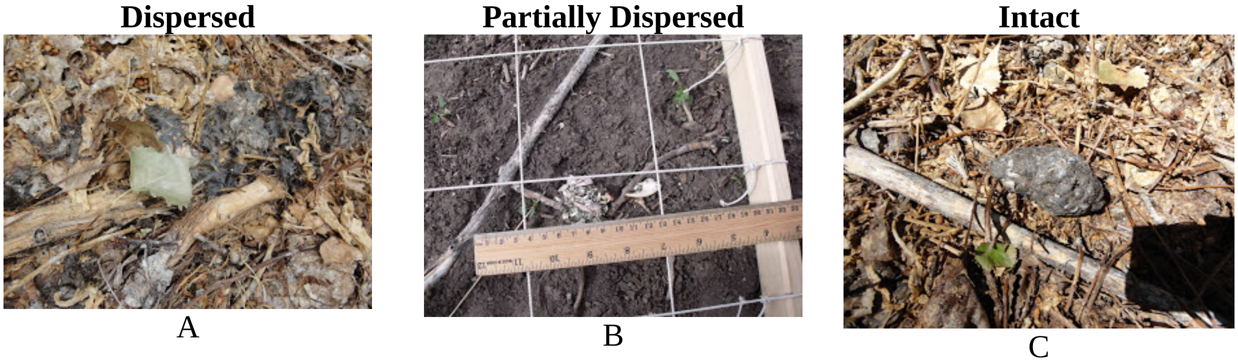


Figure 6. Degree of Pellet Intactness. Image A is a picture of fully dispersed pellet. Image B shows a partially dispersed image with mostly crayfish makeup. Image C shows an intact pellet with mostly mammalian makeup.

Extraplot 2013 Eggshell Survey

On June 10, 2013, I conducted an additional one time survey of eggs and eggshell from outside of the (A–I) plots. Eggs and eggshells greater than 1 cm were counted and their orientations ‘concave up’ versus ‘concave down’ were recorded. This additional survey was performed because plots (A–I) were only capturing a small sample of the colony’s eggshell. Eggshells were initially documented during the May 12 visit with an increase in abundance noted in the May 25 visit. June 10 was chosen as the survey date since all chicks were believed to have hatched at this point consequently leading to the highest potential for eggshell. In some areas, vegetation exceeded 137 cm and obscured identification efforts, but care was taken to identify eggs and eggshells in areas with tall and dense vegetation.

Excavations

Two-by-two meter excavations were carried out on four plots (B, G, E and L) post-fledging to a depth not exceeding 10 cm. There was no overlap between the 2013 excavations 2012 excavations. Care was taken to map the locations of the 2012 excavations as well as considerable efforts were made during plot preparations prior to the 2013 excavations to ensure no overlap of assessments. Excavations were made to determine if any biological material was incorporated into the subsurface and to detect changes in biological composition. Depths were recorded wherever possible for these *in situ* elements; all other unearthed material was lumped together as subsurface material. All *in situ* elements were measured from length to width along the vertical axis of the element.

Final Site Collection

During the final inventory on August 24, 2013, all biological material was photographed and mapped. Skeletal remains and regurgitate pellets were collected for analysis. For plots G and D, tarps were removed for subsurface excavations and site cleanup. Any biological material found below the tarps also was photographed, mapped, recorded and collected for analysis. In August 2013, 10 soil pH tests were performed at the colony using a Rapid test soil pH meter on Plots A–I and L.

Laboratory Analysis

All collected bones were identified by taxon, counted, photographed, and examined for surface modifications. Bones were measured from the proximal end to the distal end, or where this was not applicable along its longest axis. Poor quality of most juvenile elements prohibited identification as to right and left. Consequently, the MNI was calculated by taking the greatest number of limb elements and dividing that number by half. These counts were rounded up to the nearest whole number. All bones were considered broken if any part of the element was missing. All surface modifications and characteristics were recorded.

Great blue heron bones were identified following a modified version of Cruz's anatomical units (Cruz, 2005; Cruz, 2007; Cruz, 2008). The reporting categories used were mandible (i.e., maxilla and dentary), braincase (i.e., all cranium elements and quadrates), vertebrae (i.e., cervical, dorsal, caudal and sacral), ribs, scapular girdle (i.e., scapula, sternum, coracoid and furcula), forelimb (i.e., humerus, ulna and radius), pelvic girdle (i.e., ilium, ischium and pubis), hindlimb (i.e., femur, tibiotarsus, fibula, patella, and tarsometatarsus) and digits (metacarpal (I, II, III), manual phalanges, pedal phalanges pes and pedal ungal). The forelimb category did not include radiale or ulnare as these elements were not identified in the assemblage. In the modified analysis, the carpometacarpus was not treated as a forelimb element but placed within the digit category due to the unfused and unfinished nature of great blue heron juvenile elements. The addition of digits was added as the juvenile quality of most of the elements made differentiating between phalanges difficult and time prohibitive (Table 5).

Table 5. Heron expected elements. Vertebral counts were derived from the works of Shufeldt, R.W., (1889), Selby et al, (1860) and Sclater, P.L., (1862). The digits category was analyzed to calculate expected values but was included here to demonstrate the elements of a complete heron skeleton. The total expected elements with digits included was 126 and without was 92. For my chi-square analyses, I expected 92 elements per skeleton. Considerations of the expected versus observed elements included bones of the skull which were not considered individually but as representation of an adult fused skull denoted with an (a). The synasacrum was not reported individually in order to not duplicate reporting counts. Instead the synsacrum elements were counted individually: the ischium, ilium, pubis, and all sacral vertebrae. These qualifications were denoted with a (b). For the tarsometatarsus, the elements were referred to as the fused assemblage of all of the bones, therefore, the count was considered one per extremity as opposed to counting each individual bone; this reference was denoted with a (c). Due to the nature of the manus in juvenile herons, the digit category was treated separately. For instance, all distal elements including the ungals were lumped into this category. Acknowledgement of fused versus unfused nature of the carpometacarpal were given; therefore, digits were not tested for significance compared to observed frequencies. This qualification was represented with a (d).Tibiotarsus had no association with tarsals in the observed assemblage; therefore, the count is reflective of only the tibia which was noted with an (e).

Expected Category	Expected element	Count	Grouping	Expected number
Mandible	Maxilla	1	Mandible	2
	Mandible (dentary)	1		
Quadrate	Quadrate	2	Quadrate	3
Braincase	Parietal[a]	1	Braincase	
	Occipital[a]	1		
	Squamosal[a]	1		
	Frontal[a]	1		
	Lacrimal[a]	1		
Vertebrae	Cervical vertebrae	16	Vertebrae	44
	Dorsal vertebrae	7		
	Caudal vertebrae	7		
	Sacral vertebrae[b]	14		
Ribs	Cervical ribs	4	Ribs	14
	Vertebral rib	10		
Scapula	Scapula	2	Scapular girdle	7
Sternum	Sternum	1		
Coracoid	Coracoid	2		
Furcula	Furcula	2		
Humerus	Humerus	2	Forelimb	6

Ulna	Ulna	2		
Radius	Radius	2		
Pelvic Girdle	Ilium	2	Pelvic girdle	6
	Pubis	2		
	Ischium	2		
Femur	Femur	2	Hindlimb	10
Tibiotarsus	Tibiotarsus[e]	2		
Fibula	Fibula	2		
Patella	Patella	2		
Tarsometatarsus	Tarsometatarsus[c]	2		
	TOTAL	**96**		**92**
Manus	Metacarpal I[d]	2	Digits	34
	Metacarpal II[d]	2		
	Metacarpal III[d]	2		
	Phalanges – manus	8		
Metatarsal I	Metatarsal I	2		
Phalanges	Phalanges pes[d]	10		
Ungals	Ungal pes	8		
	TOTAL	**130**		**126**

Bones were reported for mammals and fish separately from those of great blue heron. In these analyses, the axial skeleton was reported. The axial skeleton for mammals constituted cranial bones, jaws, teeth, vertebral bones, sternum, and ribs. For fish, the axial skeleton was comprised of vertebrae, ribs, jaws, skull, opercular, and clavicle.

In the lab, pellets were measured, hydrated overnight and picked apart with forceps (Dodson & Wexlar, 1979; Terry, 2004). All discovered elements were identified by taxa, counted, photographed, examined for any surface modifications and measured. For pellet skeletal representations, the anatomical units followed the great blue heron anatomical reporting categories above with the addition of the following elements: appendicular skeleton (i.e., pectoral girdle), thoracic cage (i.e., ribs, sternum, and furcula), skull (i.e., maxilla, mandible, teeth, hyoid) and invertebrate (head, wing, thorax, abdomen, cephalothorax, pincer, and shell).

Weather Data

Throughout the study weather was recorded from an online weather source from Fall 2012 to Fall 2013. Using http://weathersource.com from the Great Falls International Airport Weather Station the following data was collected: temperature, precipitation and wind. Weather parameters for Cascade were recorded to assist in taphonomic interpretations of bones, eggshells and invertebrate specimens.

Statistical Analyses

For reporting purposes, several different surveys were performed from 2012 to 2013. Each survey type was described separately to provide more detail on the biological materials encountered during that investigation. The biological materials were described disaggregated to indicate the survey used to collect the materials. These reporting methods resulted in separate surveys representing eggshell materials (i.e., Intraplot versus Extraplot eggshell surveys), prey materials (bi-weekly observations, dissected pellets and final site collection), heron behavior materials (e.g., fallen nests), and heron remains (i.e., final site collection). All of the 2012 and 2013 data were compiled for statistical analysis. For all statistical analyses, GraphPad InStat 3 was used to calculate significance.

In each Intraplot and Extraplot surveys, the eggshell orientations were determined and compared against the null prediction 1:1 and against the alternative hypothesis of 60:40 for hatched sites and 70:30 for predation sites (Hayward et al., 2011). These orientations were represented by ‘concave up’ (CU) and ‘concave down’ (CD). For avian skeletal representations, a comparison of the observed counts to the expected counts was made using a χ^2 test. Expected values were derived from expectations of an entire heron skeleton, and the total sample size following Varricchio (1995). *P*-values defined whether or not individual anatomical categories were over or underrepresented in relation to expected ratios. Additionally, a χ^2 test was performed against the null 1:1 ratio for wing-to-leg ratios. No statistical testing was performed for the pellet skeletal representation due to mammalian remains making up over 80% of the assemblage.

An χ^2 test for independence was used to determine if there was any difference between the abundance of biological materials between the different plot types: control plots (G and D), sparsely vegetated plots (A, B, C, and H) and densely vegetated plots (E, F and I). Further testing was done to determine if excavation types (surface vs. subsurface) varied between the two samples. A 2x2 Fisher's exact test was used to determine if there was any difference between subsurface and surface values.

RESULTS

The Cascade Heron Colony with all surveys combined as a total aggregate value from 2012 to 2013 produced 2,931 biological materials (Appendix D). The biological materials from combining the Intraplot and Extraplot eggshell surveys produced 947 eggshell fragments (>1 cm to nearly whole eggshells). Below these data are shown in disaggregate form by fragment size per survey type and tests for significance against the null and alternative hypothesis in Figs. 9–14; Tables 6-9. The great blue heron prey materials from bi-weekly observations (Fig. 7; Fig. 17), dissected pellets (Fig. 16; Table 13), and the final site collection (Table 13; Appendix C) yielded 980 prey items. All avian remains (i.e., final site collection) were totaled using the 2012 and 2013 final site collection materials where 996 elements were found and 934 were identified as great blue heron bones (Table 13; Appendix C). The heron behavior materials (e.g., fallen nests) (Fig. 15) and other activities (Fig. 7) that may have attributed to gains and losses of the heron generated colony materials are detailed below.

This area experiences extreme weather events so that any high wind, rain, flooding or other atypical weather was considered relevant for fall 2013 taphonomic interpretations. Some weather was extreme and may have influenced the data and taphonomic interpretations summarized here. Additionally, during 2013 breeding season, the site was visited in bi-weekly intervals beginning April 27 and concluding on August 24, 2013. During this time the colony was observed by a local birder who documented the Cascade Heron Colony behavior. These bi-weekly visitations assessed the colony's gains and losses through qualitative observations. Weather record, biweekly visits, and birder observations provided a history of the 2013 breeding season.

On April 27, 2013 the first site visit occurred. During this visit there was no atypical weather. Very few birds were present but there was evidence of crayfish predation, pellets, eggshells, and several bones not from this breeding season. Wind speed in excess of 121 km kilometers per hour (kph) may have been a possible factor for transport and abiotic processes affecting the biological material of the colony. Fewer adult herons appeared present during April 27, 2013 than counted in April, 2012.

On May 12, more herons were present at the site and more eggshell was present on the forest floor than witnessed on April 27, 2013. On May 12, 2013 more heron bones were visible on the surface than during April 27. During this two week time frame 1.14

cm of precipitation occurred and five days with wind in excess of 48 kph. On May 12, 2013 there were 54 kph winds. Between the second visit to the colony (May 12) and the third visit (May 25) 2.14 cm of precipitation occurred at the site. Also during this time period there were six days with wind speeds upwards of 48 kph. Shortly following the May 12 visit an eye witness account from the local birder observed a golden eagle (*Aquila chrysaetos*) attack on an adult heron and later observed it feeding on the heron carcass (Hartman, personal interview). Outside of the plots, on May 12, the adult heron carcass was collected and an approximately one-week-old chick for skeletal element comparisons.

Between the April 27 visit and the May 12 visit there was wind in excess of 75 kph and 1.14 cm of precipitation. These high winds and precipitation may have positively influenced erosion and other abiotic processes making elements (not produced by the 2013 breeding season) more identifiable for surface identifications. Heavy precipitation from May 30 to June 19, 2013 may have been responsible for the dense vegetation in some areas exceeding 1.6 m. A highly decomposed complete body of small mammal (rodent) was identified during bi-weekly observations in plot D and by July 7, 2013 all remains had disappeared. Transport potentially in the form of precipitation such as minor short-lasting flash flood may have been responsible for displacing the carcass. Scavenging may have been another transport possibility but unlikely due to the extreme decomposition of the carcass. Using literature on incubation and breeding behavior the time Cascade herons laid eggs was estimated to be early April and incubated eggs (27–29 days) until early May (Butler, 1993; Great Blue Heron (n.d.); Vennesland & Butler, 2011). These dates were derived from counting back from the time the herons were known to have fledged.

During the second week of May hatching was observed in the bi-weekly visit. During the May 25, 2013 visit a golden eagle was observed threatening and harassing the adult herons who were protecting their nests. Also, noted on May 25, 2013 was the greatest count of adult herons in the nests with roughly 30 individuals. May 11, 2012 over 50 adults were counted compared to this 2013 count. Lots of eggshell was found on the forest floor but no orientation counts were taken outside of the plots on this visit. Outside of the plot B, a predated chick with its intestines strewn about was photographed as documentation of predation.

On May 30 through June 10, 2013 there was a total of 7.77 cm of precipitation. On the June 10 observation, the vegetation was recorded due to densely vegetated state. This visit included the Extraplot eggshell survey where concavity orientation counts were taken and eggs photographed. On June 12, a severe thunderstorm occurred with hail and high winds. After the storm passed, an eye witness documented the golden eagle attacking a nest, grabbing and killing a chick from a heron nest. It later dropped the uneaten body to the forest floor (Hartman, personal interview). Plot observations revealed more evidence of eggshell, fish predation, and surface heron bones. In addition, a small mammal (rodent) found in plot D and a dead chick was discovered just outside of plot B.

On June 12, 2013 there was a severe thunderstorm with hail, high winds and lightning. On June 19, 2013 a total of 0.91 cm of precipitation and 77 + kph winds hit the colony. Over the 14-day time span a total of 2.08 cm of precipitation fell at the colony along with two days with winds over 48 kph. During the June 22, 2013 visit there was very dense vegetation especially in plot F making it difficult to find any surface biological material. More fish predation, pellets, and heron bones were discovered during this observation. A 2013 immature wing with tissue and feathers attached was found in plot H along with more eggshell. In plot E, some of the vegetation was beginning to recede.

The heron nestlings remained in the nest until late July which from this observation the heron nestlings adhered to a narrower nestling period (i.e., 49–81 days) (Butler, 1993; Great Blue Heron (n.d.); Vennesland & Butler, 2011). On the July 7, 2013 the heron colony was very quiet with few herons present. A golden eagle was observed flying overhead and remaining close to the heronry. As result of heavy precipitation during the preceding weeks, the vegetation reached its peak and was measured during this visit. In some areas, the vegetation exceeded 1.6 m. Vegetation of this extent was not reported to this degree in the 2012 breeding season. During site observations for plot A more pellets, and fish predation were present. Several meters from the plot A half of an adult heron was found. Near plot C and plot G there was evidence of decomposition via fly action, abundance of feathers and the smell of rotting flesh. In plot D, a nest had fallen next to the tree base as well as the small (rodent remains) were missing from the plot. On July 8, 2013 there were 80+ kph winds followed by 0.36 cm of precipitation and 64+ kph winds on July 17.

Five days between the July 7 visit and the July 20, 2013 visit had winds at 48 + kph. During this visit most of the eggshells within the plots were highly fragmented. Also, during this visit more surface bones were found with some partially buried in plot A. Three suspected fledglings were found just outside of plots C, D, E and G. On July 20, no herons were present in the colony and there was no evidence of a golden eagle. All herons were assumed to have abandoned the colony by this visit.

It was suspected that the juvenile herons fledged (by the end of July) as no herons were present in August (Butler, 1993; Great Blue Heron (n.d.); Vennesland & Butler, 2011). From July 20 to August 10, there was 2.77 cm of precipitation. August 16 the maximum temperature reached 38.33^{o} Celsius (C). Moreover, during this time period three days had winds upwards of 48 kph with a gust of 157.43 kph on July 30, 2013. On August 10, 2013, in plot A all of the identified surface bones were not recovered. In plot G, there was a fresh wing and in plot H, more surface bones were observed. On the August 10 visit, a suspected heron fledgling was found likely predated, outside of plot C and another outside of D. The remains were disarticulated with feathers and body parts covering an area over 5 m^2.

August 24, 2013 was the last visit to the colony and served as the final site collection. Three days of winds upwards of 48 kph had occurred since the last visit and 0.076 cm of precipitation had fallen at the site. A brief summary of the 2013 weather phenomenon as well as golden eagle predation, vegetation characteristics, and biological material gains and losses are shown in Fig. 7. A more detailed record of the weather over 120 days from April 27 to August 24 can be found in the Appendix (Appendix A).

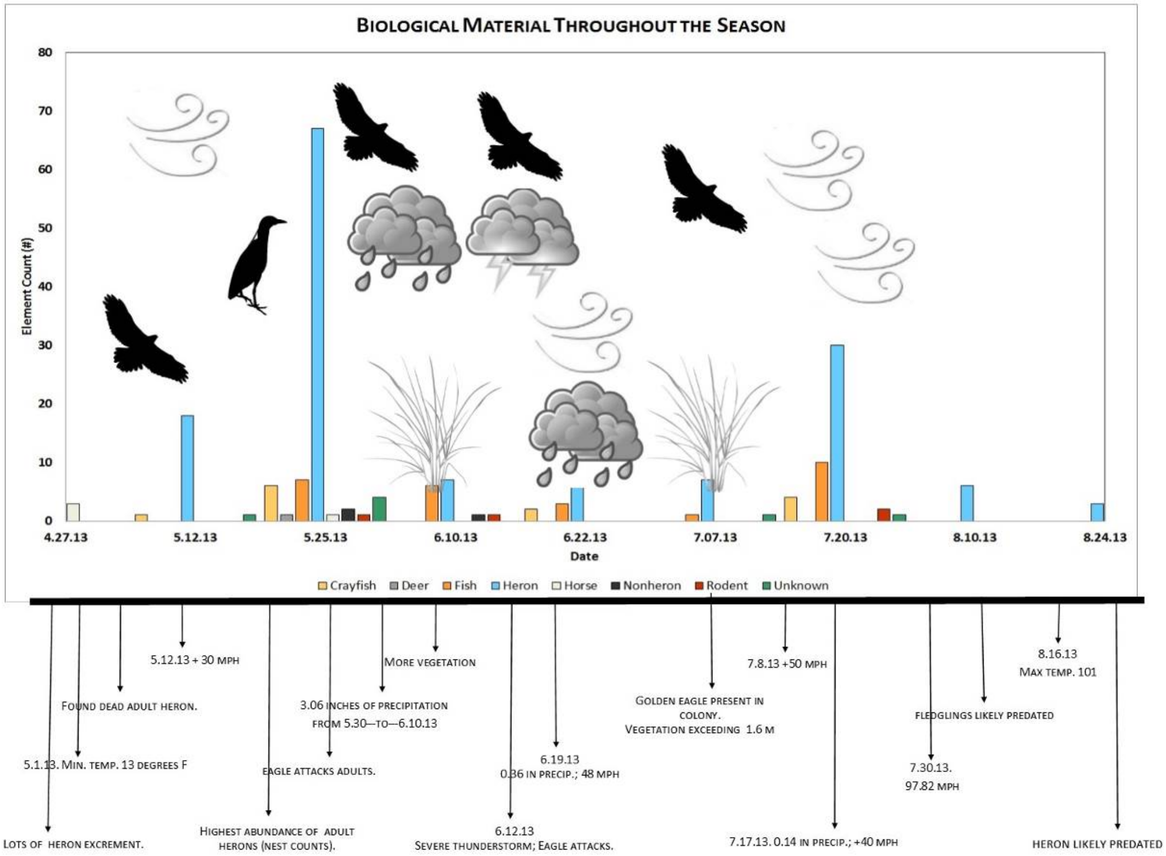


Figure 7. Heron Colony Bi-weekly events. During the bi-weekly visitations gains and losses were experienced within the 2013 (A–I) plots. None of the biological material was collected during these visitations only observations are shown in this figure. Elements found versus time and qualitative observations are depicted in this graphic. No egg or eggshell was considered for this figure. Nonheron referred to any avian element not great blue heron. The eye witnessed golden eagle interactions are plotted. The extreme weather phenomena including precipitation (above 0.00 cm), wind (48 + kph) and temperature (>32 (^{o}C) along with vegetation are shown in relation to the x-axis (time).

Figure 8. Juveniles at tree bases. Image A show a juvenile great blue heron (complete) next to a tree base. Image B shows a fledgling near plot D completely disarticulated with feathers and remains next to a tree base.

Bi-weekly Intraplot investigations allowed for the reporting of gains, losses and histories of the biological material within the plots. The outside of colony Controls (plots J, K and L) yielded no biological material during the study. Out of colony control plot L was excavated to a depth not exceeding 10 cm and no biological material was found within the subsurface. Table 13 summarizes the 2012 and 2013 bone and invertebrate counts. Not included in Table 13 were any unrecoverable but bi-weekly identified Intraplot investigation biological materials such as crayfish remains, fish remains, and animal excrement.

From the bi-weekly collection of fish remains, crayfish remains, rodent remains, heron remains, Nonheron bird remains, unknown and animal excrement, there were 303 heron elements, 27 fish elements, 21 crayfish elements, seven unknown, four rodent elements, and five droppings (Fig. 7). These aforementioned crayfish, fish and animal excrement were not included in the final site collection count as they were not recoverable (Table 13; Appendix C).

No strict analyses were performed to assess spatial and distribution biological material patterns, however, the plot maps captured some of the spatial contexts of the biological material within them. For plot A and C, an accumulation of biological material was witnessed in close proximity to the tree base (Appendix B). For other plots some materials had spatial preference within the plots, others had no distinguishable patterns, and some preferred areas farthest away from tree bases.

Eggs and Eggshells

Intraplot Eggshells (2012 and 2013)

The Intraplot survey yielded 297 eggshell fragments and 46 eggshell fragments with indeterminable orientations (Appendix D). No indeterminable eggshell were used to represent the total identified eggshell counts as their orientation trend was unknown. In the 2012 survey, I found 190 small eggshells in plots; of these 103 were in the ‘concave up’ orientation, 85 were in the ‘concave down’ orientation, and two were vertical and 26 were indeterminable. Many additional eggshell fragments not meeting the size criteria were encountered but not counted. These 190 eggshells were found within the 2012 plots spanning an area of 123 m^2 of the colony or a density of 1.5 eggshell fragments/m^2.

In the 2013 survey, I found a total of 107 small eggshells with 55 in the ‘concave up’ orientation, 32 eggshell fragments in the ‘concave down’, and 20 were indeterminable. As seen in 2012, many eggshell fragments smaller than 1 cm were present in the plots but not counted. These 107 eggshells were found within the 2013 plots spanning an area of 225 m^2 of the colony or a density of 0.48 eggshell fragments/m^2. Once again, no taphonomic attributes (i.e., hatched or depredated) were assigned to these samples due to the inability to use the criteria from Fig. 5, however, it was speculated that all of the fragments were from hatched eggs.

The CU: CD ratios for 2012 and 2013 were respectively, 55:45 (*N*=188) in 2012 and in 2013, 64:36 (*N*=87) (Fig. 10; Table 7). These results were tested for significance against the null and alternative prediction (Table 7). For the Intraplot small eggshell survey, the eggshell densities of each plot were described (Table 6) as ranging from 0.08 to 3.56 with most distributed around 0.8–1.56 eggshell fragments/m^2. In total, plots (A–I) eggshells were found within the 5x5 m plots at a rate of 1.32 eggshell fragments/m^2 (Table 6).

The bi-weekly observations yielded evidence of reproduction (large and small eggshells) starting in April. These reproductive inputs peaked by the June 10 Extraplot survey. The most fallen eggshells were observed on the May 25 visit. Another pattern revealed during the bi-weekly observations was fragmentation (Fig. 9). These fragmentation trends were specific to larger eggshell pieces. Through the course of the biweekly observations weathering played a role in the fragmentation history of the large eggshells. For example, from bi-weekly visitations over time originally ‘concave up’ large eggshells experienced abiotic and biotic processes. These once ‘concave up’ large eggshells fragmented into smaller eggshells with ‘concave down’ positions.

From the Intraplot survey, all fallen large eggshells were eventually considered small eggshells. The final eggshells counts were derived from the July 20 visit as any identified pieces on the final site collection day were too small to count (Fig. 9). These counts reflected the fragmentation history and less represented the original orientation preference of the large eggshell. No large eggshell pieces that were marked for transport were recovered after their initial identification. All eggshell inside the plots were considered hatched as the depredated criteria especially puncture/fracture marks were not observed.

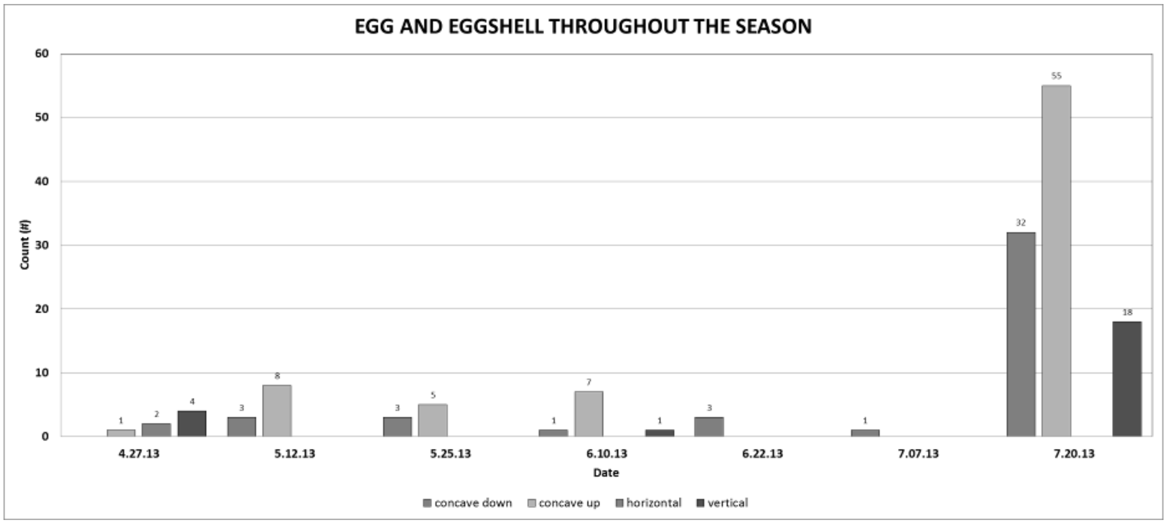


Figure 9. Bi-weekly observations of identified small and large eggshells. This figure illustrates large and small eggshells. Large eggshells were identified early in the season and through the course of the season became considerably more fragmented into smaller eggshell pieces. A fragment total was taken from the July 20 visit. The reproductive productivity peaked before June 10 and the subsequent observations illustrate the fragmentation history of the eggshell and the unique orientations trends of these small eggshell fragments.

Table 6. 2012–2013 Survey for CU: CD in Large and Small Eggshell Fragments. The vegetation of the plots was described as sparse vegetation (SV), dense vegetation (DV) and in colony control (IC). For large and small eggshells where the orientation was determinable for 'concave up' it was coded as CU, and 'concave down' coded as CD.

Plot	A	B	C	D	E	F	G	H	I	Plot totals
Vegetation	SV	SV	SV	IC: DV	DV	DV	IC: SV	SV	DV	Na
Nests in vicinity of plot	9	<5	6	12	7	8	11	12	5	75
Visibility of soil	80%	80%	70%	50%	50%	0%	100%	80%	40%	Na
pH of soil	7	7	6.6	7	6.5	6.7	6.7	6.5	6.6	Na
2012 CU	16		16				29	29	13	103
2012 CD	12		16				8	26	23	85
2012 vertical	2									2
2013 CU	36	4				15				55

2013 CD	14	10	3			5				32
2013 vertical	9	9	2							20
CU Total	52	4	16			15	29	29	13	158
CD Total	26	10	19			5	8	26	23	117
Vertical Total	11	9	2							22
Plot size	5x5 m	5x5 m	5x5 m	5x5 m	5x5 m	5x5 m	5x5 m	5x5 m	5x5 m	225 m^2
Egg frag total	89	23	37			20	37	55	36	297
Eggs or eggshells / m^2	3.56/m^2	0.92/m^2	1.48/m^2	0/m^2	0/m^2	0.8/m^2	1.48/m^2	2.2/m^2	1.44/m^2	1.32/m^2

A χ^2 test was used to test the null prediction 1:1 and the alternative hypothesis for hatched eggshells (60:40) (Hayward et al., 2011) for each year and overall. These eggshells were believed to be evidence of hatching as there was no evidence of inward puncture marks, blood, or attached membranes. The observation of ‘concave up’ was found to occur 57.45% of the time and 42.54% ‘concave down’ (Fig. 10). The χ^2 test showed no significance against the null prediction for 2012, but the χ^2 test found significance for the 2013 null prediction. Overall there was no significance found for the overall totals (N=275). The χ^2 test further did not find any statistically significant difference when the counts were compared to the 60:40 expected ratio (Table 7).

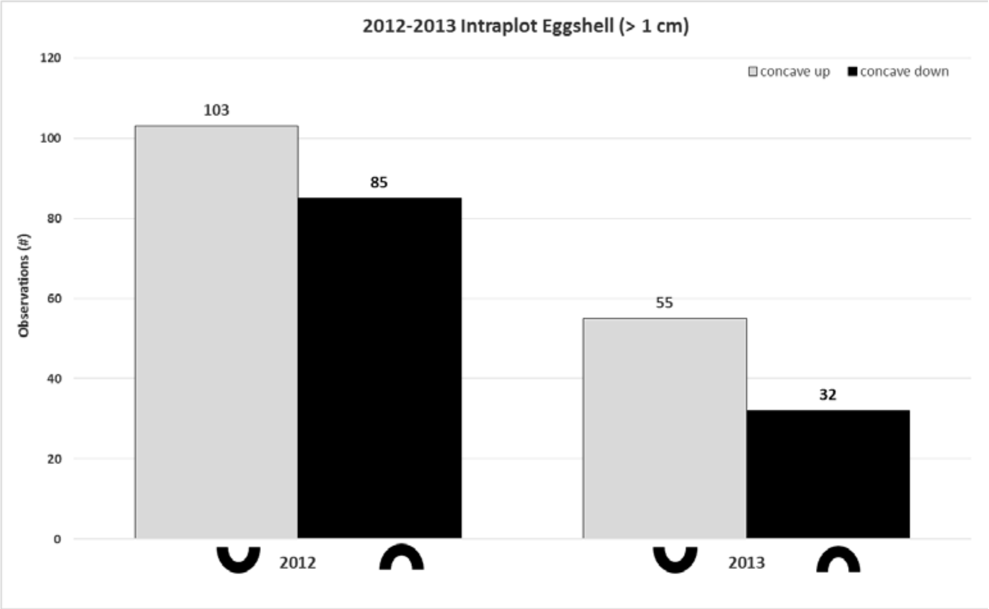


Figure 10. 2012-2013 Intraplot Eggshell Small Fragments. Here the counts for ‘concave up’ and ‘concave down’ are reported for the 2012 and 2013 breeding season. In 2012, 54.79% were found in the ‘concave up’ orientation and 45.21% were found in the ‘concave down’ orientation out of 188 fragments. In 2013, 63.22% were found in the ‘concave up’ orientation and 36.78% were found in the ‘concave down’ orientation out of 87 fragments.

Table 7. Intraplot Small Eggshell Fragments Significance. A χ^2 test was used to test against the expected null 1:1 for 2012, 2013 and both years combined (all). These observed counts were further compared to the expected hatched ratio of 60:40 (Hayward et al., 2011).

A. Ho= Small Eggshell will occur with equal proportions (50:50).			
	Concave Up	Concave Down	Total
2012	103	85	188
2012 Orientation (%)	54.79%	45.21%	
X^2 = 1.723, 1 d.f., p = 0.1893			
2013	55	32	87
2013 Orientation (%)	63.22%	36.78%	
X^2 = 6.080, 1 d.f., p = 0.0137			
All Orientation Total	158	117	275
All Orientation (%)	57.45%	42.54%	
X^2 = 6.113, 1 d.f., p = 0.0134			
H_1= Small Eggshell will occur ‘concave up’ with proportions greater than 60%.			
X^2 = 0.742, 1 d.f., p = 0.3889			

Extraplot Eggs and Eggshells (2012 and 2013)

Here eggshell counts of small and large eggshells are reported based on their taphonomic attribute (hatched or predated), and year surveyed. In the small fragment surveys, a total 552 eggshell fragments were found. Without considering hatched or predated taphonomic attributes in the 552 small eggshells, 27.71% of the eggshells were ‘concave up’ (*N*=153) and 69.20% were ‘concave down’ (*N*= 382). Of the large eggshell assemblage, 115 large eggshells were found. Excluding the taphonomic attribute (i.e., hatched or predated) an overall orientation trend was calculated. In total (*N*=115), 76.52% were found in ‘concave up’ orientation (*N*=88) and 23.48% were found in ‘concave down’ orientations (*N*=27) (Table 12). Below the taphonomic attribute was considered for each eggshell survey by year.

In the 2012 hatched small eggshell survey, nearly 30% of the fragments were in ‘concave up’ orientations. Of these 273 identified CU: CD fragments, three fragments were indeterminable (Fig. 11; Table 8). The 2013 hatched small eggshell survey observed 227 fragments, where 32% were in the ‘concave up’ position and 14 were considered indeterminable (Fig. 11; Table 8). The 2012 and 2013 hatched large eggshell survey found nearly 77% or higher of the eggshell fragments in ‘concave up’ positions and none were considered indeterminable (Fig. 13; Table 10).

The 2012 predated small eggshell survey found 33% of the fragments were in ‘concave up’ positions and in 2013 10% in ‘concave up’ positions. From 2012, two fragments considered indeterminable and in 2013, one fragment was indeterminable (Fig. 12; Table 9). The predated large eggshell survey found 83% were in ‘concave up’ orientations and in 2013, only 30% were in ‘concave up’ orientations (Fig. 14; Table 11).

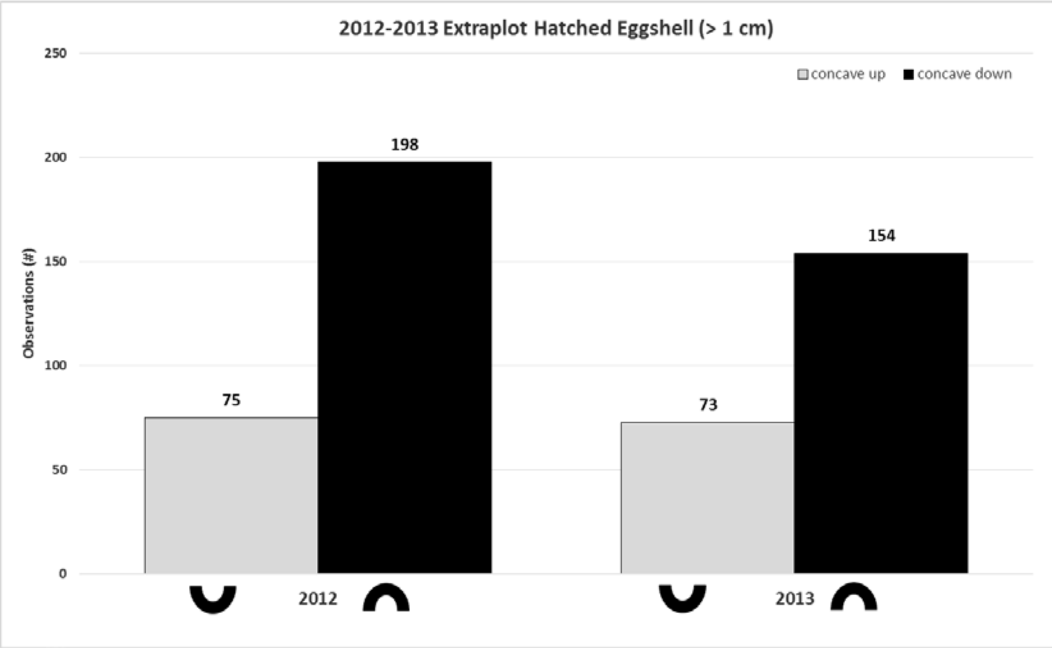


Figure 11. 2012–2013 Extraplot Hatched Small Eggshell. From the 2012 collection and the 2013 collection, 514 eggshell fragments of which 148 were in the ‘concave up’ orientation (29.60%), 352 were in the ‘concave down’ orientation (70.40%), and 17 were indeterminable.

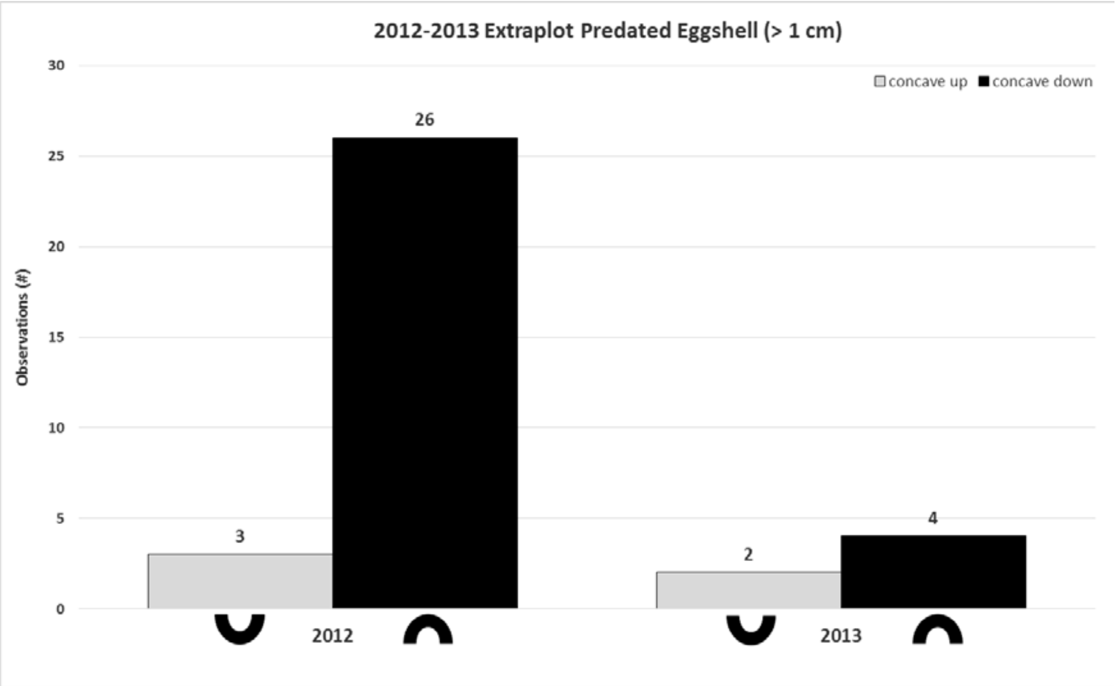


Figure 12. 2012–2013 Extraplot Predated Small Eggshell. From the 2012 collection and the 2013 collection, 38 eggshell fragments of which five were in the ‘concave up’ orientation (14.30%), 30 were in the ‘concave down’ orientation (85.70%), and three were indeterminable.

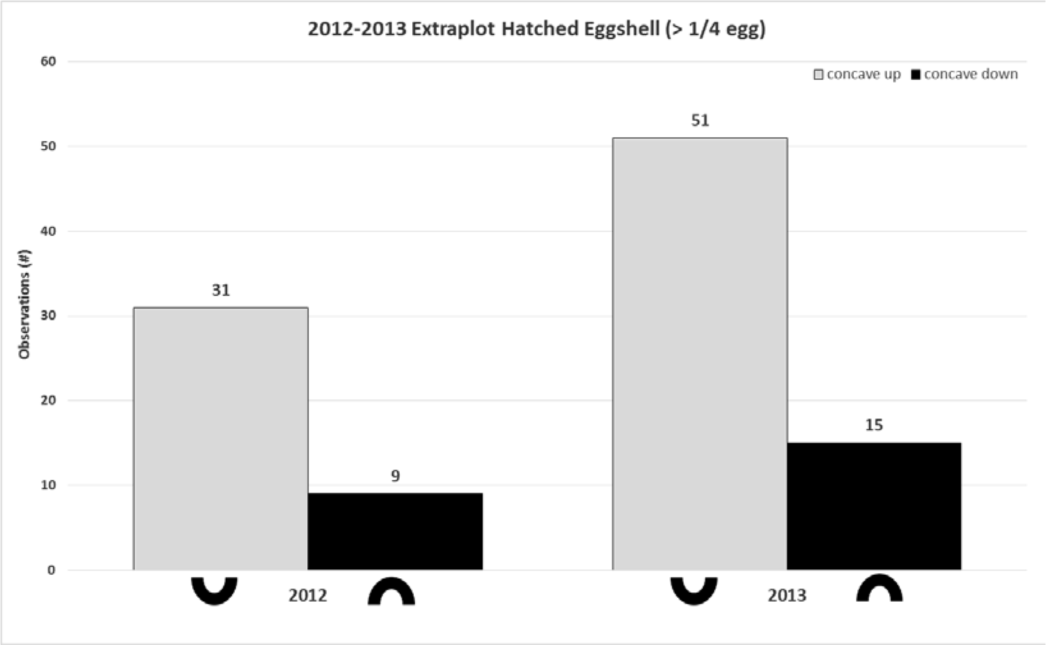


Figure 13. 2012-2013 Extraplot Hatched Large Eggshell. From the 2012 collection and the 2013 collection, a total of 106 eggs with 82 eggshell fragments in ‘concave up’ orientations (77.40%), 24 fragments in ‘concave down’ orientations (22.60%).

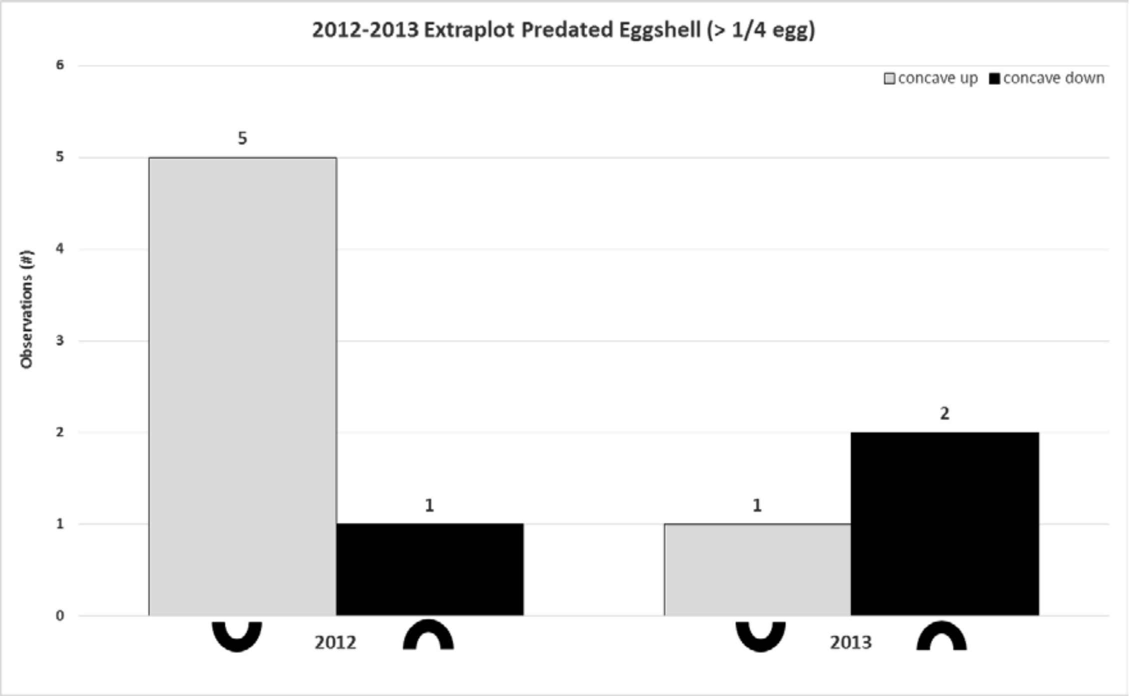


Figure 14. 2012-2013 Extraplot Predated Large Eggshell. From the 2012 collection and the 2013 collection, a total nine eggs, of which six eggshell fragments were in the ‘concave up’ orientation (66.70%), and three fragments were in the down’ orientation (33.30%).

Extraplot Significance

In Tables 8–11, a χ^2 test was used to test the significance for hatched and predated small eggshell, and hatched and predated large eggshell. All eggshells were tested against the null prediction 1:1 and further compared to Hayward's et al., (2011) ratios. For hatched eggshells, they were tested according to 60:40 expectations for 'concave up' and predated eggshells were tested against 70:30 expectations for 'concave up' (Hayward et al., 2011). The small eggshell fragment findings are presented initially (Table 8; Table 9) followed by the large eggshell (Table 10; Table 11).

Table 8. Extraplot Small Fragments with hatched significance. A χ^2 test was used to test against the expected null 1:1 for 2012, 2013 and both years combined (all). These observed counts were further compared to the expected hatched ratio of 60:40 (Hayward et al., 2011). Test A shows these results were statistically significant in favor of 'concave down'.

A. Ho= Hatched small eggshell will occur with equal proportions (50:50).			
	Concave Up	Concave Down	Total
2012	75	198	273
2012 Orientation (%)	27.47%	72.53%	
$X^2 = 55.418$, 1 d.f., $p < 0.0001$			
2013	73	154	227
2013 Orientation (%)	32.16%	67.84%	
$X^2 = 28.903$, 1 d.f., $p < 0.0001$			
All Total	148	352	500
All Orientation (%)	29.60%	70.40%	
$X^2 = 83.232$, 1 d.f., $p < 0.0001$			
H_1= Hatched small eggshell will occur above the 60% expectation (Hayward et al., 2011).			
$X^2 = 192.533$, 1 d.f., $p < 0.0001$			

Table 9. Extraplot Small Fragments with predated significance. A χ^2 test was used to test against the expected null 1:1 for 2012, 2013 and both years combined (all). These observed counts were further compared to the expected predated ratio of 70:30 (Hayward et al., 2011). For the 2012 category, no χ^2 test performed as the test was not applicable for samples less than five. Test B shows these results were statistically significant for 2013,

combined years (all), and for the alternative predated hypothesis in favor of ‘concave down’.

B. Ho= Predated small eggshell will occur with equal proportions (50:50).			
	Concave Up	Concave Down	Total
2012	2	4	6
2012 Orientation (%)	33.33%	66.67%	
X^2 not applicable			
2013	3	26	29
2013 Orientation (%)	11.54%	89.66%	
X^2 *=18.241,* 1 d.f., *$p < 0.0001$*			
All Total	5	30	35
All Orientation (%)	14.30%	85.70%	
X^2 = 17.857, 1 d.f., $p < 0.0001$			
H_1= Predated small eggshell will occur above the 70% expectation (Hayward et al., 2011).			
X^2 = 51.735, 1 d.f., $p < 0.0001$			

Table 10. Extraplot Large Eggshells with hatched significance. A χ^2 test was used to test against the expected null 1:1 for 2012, 2013 and both years combined (all). These observed counts were further compared to the expected predated ratio of 60:40 (Hayward et al., 2011). Test C shows that for all categories these results were statistically significant in favor of ‘concave up’.

C. Ho= Hatched large eggshells will occur with equal proportions (50:50).			
	Concave Up	Concave Down	Total
2012	31	9	40
2012 Orientation (%)	77.5%	22.5%	
X^2 =12.100, 1 d.f., $p < 0.0005$			
2013	51	15	66
2013 Orientation (%)	77.27%	22.73%	
X^2 =19.636, 1 d.f., $p < 0.0001$			
All Total	82	24	106
All Orientation (%)	77.40%	22.60%	
X^2 = 31.736, 1 d.f., $p < 0.0001$			
H_1= Hatched large eggshell will occur above the 60% expectation (Hayward et al., 2011).			
X^2 =13.308, 1 d.f., $p < 0.0003$			

Table 11. Extraplot Large Eggshells with predated significance. A χ^2 test was used to test against the expected null 1:1 for 2012, 2013 and both years combined (all). These observed counts were further compared to the expected predated ratio of 70:30 (Hayward

et al., 2011). Test B shows these results were statistically significant for 2013, combined years (all), and for the alternative predated hypothesis in favor of ‘concave down’. Test D had no χ^2 test performed as the test was not applicable for samples less than five.

D. Ho= Predated large eggshell will occur with equal proportions (50:50).			
	Concave Up	Concave Down	Total
2012	5	1	6
2012 Orientation (%)	83.33%	16.67%	
X^2 not applicable			
2013	1	2	3
2012 Orientation (%)	33.33%	66.67%	
X^2 not applicable			
All Total	6	3	9
All Orientation (%)	66.70%	33.30%	
X^2 not applicable			
Ho= Predated large eggshell will occur above the 70% expectation (Hayward et al., 2011).			
X^2 not applicable			

For the Extraplot small eggshell fragments, the χ^2 test used for hypothesis A, which suggests significance for all categories tested, but the results favor ‘concave down’. The comparison to Hayward et al. (2011) does not support the expected hatched ‘concave up’ distribution of 60:40 (Table 8). For hypothesis B, the results were significant for all categories except the 2012 counts as they were unreportable using χ^2 test. In comparison to Hayward et al. (2011), these counts were tested against the 70:30 ratio and showed favor inverse of the expected, that is, preferring a ‘concave down’ orientation (Table 9).

For the Extraplot large eggshell, a χ^2 test was used to calculate significance and found significance for all categories tested in favor of the ‘concave up’ orientation. For hypothesis C, significance outside of the 60:40 expectation (Hayward et al., 2011) suggests these results are significant. These results provide support for the alternative hypothesis in favor of ‘concave up’ with a CU: CD ratio of 77:23 (Table 10). For hypothesis D, no significance testing was performed as the sample size was less than 10. Therefore, the data had no support to reject the null hypothesis (Table 11).

By removing the taphonomic attribute (i.e., hatched or predated) a more direct comparison between the Extraplot and Intraplot surveys was allowable as no large eggshells were totaled for Intraplot investigation counts and due to the eggshell size, the pieces were not interpreted for their taphonomic attribute. It was speculated that all Intraplot eggshells were hatched but little fracture pattern evidence allowed for a definitive taphonomic placement. The Extraplot analysis found an abundance of eggshell evidence with 650 eggshell fragments (Appendix D). For small eggshell fragments with identifiable orientations, 500 eggshell fragments were found for the hatched survey and 35 for the predated survey. In total, 552 small eggshell fragments were found of those 535 fragments had known orientations. A total of 115 large eggshell fragments were discovered. Nearly 30% of small eggshell fragments were in 'concave up' positions (i.e., 25.59%) and for large eggshell fragments roughly 77% favored 'concave up' (i.e., 76.52%). For the 297 Intraplot small eggshell fragments, 53% favored ‘concave up’ positions. Disregard of the eggshells’ size (i.e., small or large) the predated eggshells favored ‘concave up’ at 25% and for hatched eggs favored ‘concave up’ at 44% (Table 12; Appendix D).

Table 12. Taphonomic Interpretations of Heron 2012 & 2013 Eggshell. This table illustrates the hatched and predated eggshell interpretations by their size, and orientation (i.e., 'concave up', 'concave down' or 'indeterminable'). The 'concave up' and 'concave down' totals are derived from the 2012 and 2013 combined results to indicate how many of each taphonomic attribute were found throughout the study. For the Intraplot study, it was suspected that all fragments were of hatched eggshell but not all criteria was applicable for ascertaining the taphonomic attribute of the eggshell.

Survey (12' & 13')	**Taphonomic Attribute**		**concave up**	**concave down**	**Indeterminable**	**Total**
Small Eggshell Fragments						
Extraplot	Predated		5	30	3	38
Extraplot	Hatched		148	352	14	514
		Total	153	382	17	552
Large Eggshell Fragments						
Extraplot	Predated		6	3		9
Extraplot	Hatched		82	24		106
		Total	88	27		115
Small Eggshell Fragments						
Intraplot	Hatched		158	117	46	297

2012-2013 Skeletal Plot Representations

This study attempted to assess weathering using Behrensmeyer's (2003) 0–5 scale but due to the ossification/growth of the juveniles in this project it was difficult to differentiate the degree of ossification from weathering. Hence, I did not attempt to report weathering stages due to this reason. None of the avian WS biases found with Cruz (references therein), Behrensmeyer et al. (2003) and Prassack (2011), that is, the affinity for avian bones to have WS biased towards the lower stages were documented as the application of WS were considered unsuitable due to the juvenile nature of the vast majority of great blue heron bones.

The entire colony was measured to be 2480 m^2 and 123 m^2 were sampled in the 2012 survey and 225 m^2 were sample in the 2013 survey. From both the 2012 and 2013 years, without consideration of sampling type (i.e., pellet survey, bi-weekly survey, surface survey and subsurface survey) the Cascade Heronry contained 1,876 vertebrate remains and 100 invertebrate remains (Appendix D). Exclusive to the 2012 and 2013 surface and subsurface surveys, the Cascade Heron Colony yielded a total of 1,788 elements, of which 93.96% were identifiable by taxa (NISP, N=1,680) and 6.04% were unidentifiable to taxa (*N*=108). Of the identifiable elements, 55.60% (*N*=934) were great blue heron (Table 13). For both years, the MNI was 72 based on the highest number of elements per reporting category (i.e., heron, nonheron, mammal and rodents) divided by half.

MNI by taxa was determined by taking the highest number of taxon elements found in Appendix C. For the great blue herons, the tibia was found with the highest frequency subsequently the MNE were totaled as 69. This number divided by half indicating at least 35 individuals were present in the assemblage (Table 13). Heron generated invertebrate prey items were 14 snails (order: Stylommatophora) represented by the shell abundance and 16 crayfish (family: Astacidae) represented by taking the highest number of chelipeds (i.e., pincer) and dividing by half (Table 13).

Of the colony's total area (2480 m^2), the 2012 Survey plots represented 4.95 % of the colony's area and 54.95% of the nests present in the area of interest (*N*=91). The 2013 Survey plots represented 9.07 % of the colony's area and 82.42% of the nests within the area of interest (*N*=75) (Appendix B). In the 2012 Survey, a total of 6 m^2 were excavated to a depth not exceeding 10 cm and in 2013, 3 m^2 excavated to a depth not exceeding 10 cm. From the surface and subsurface 2012 Survey, a total of 850 elements were collected and in 2013, 938 surface and subsurface elements were collected. From these surveys, most represented taxa were herons and fish (Table 13). The table below depicts the most represented taxa by year and plot type (Table 13; Appendix C).

Table 13. Colony 2012 & 2013 Biological Material Plot Representations. Element count total of the biological material found below the great blue heron nest from the 2012 to 2013 surface and subsurface surveys. The question marks following taxa were suspected to be this taxon.

Plots	**A**		**C**		**E**		**G**		**H**		**I**		**B**	**D**	**F**				
Year	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013	2013			2012 NISP Total	2013 NISP Total	Total	Pct of Total (%)
HERON	121	49	76	2	76	75	48	202	61	30	23	12	154	5	0	405	529	934	52.24%
HERON?						1		34					17			0	52	52	2.91%
NONHERON BIRD		3				5		2								0	10	10	0.56%
MAMMAL						2		3								0	5	5	0.28%
RODENT	5	26				14	4	4	13				5	2		22	51	73	4.08%
RODENT?		3														0	3	3	0.17%
FISH	5	9	37	2	2	43	32	69	105		128	1	44	7		309	175	484	27.07%
FISH?								11								0	11	11	0.62%
SNAKE							34				21					55	0	55	3.08%
CRAYFISH	8	10			4	2	1	5	2		1	1	3	1	2	15	24	39	2.24%
GASTROPOD	2	2			2		6		2							12	2	14	0.78%
UNIDENTIFABLE		22				49	2		25		5	1		4		32	76	108	6.04%
Element by Plot Total	**141**	**124**	**113**	**4**	**84**	**191**	**127**	**330**	**208**	**30**	**177**	**15**	**223**	**19**	**2**	**850**	**938**	**1788**	**Overall Total**
Plot Total	265		117		275		457		238		192		223	19	2	1788			
Plot	A		C		E		G		H		I		B	D	F				

Based on the 1, 788 identified elements heron only remains were grouped into eight anatomical groups and only bones that were identifiable to an element were used. The digit category (*N*=80) which included: phalanges above, phalanges subsequent, ungals pes, carpometacarpus but was not included in significance testing due to the problems surrounding fusion and the juvenile quality of the bones. This omission resulted in 744 reportable great blue heron elements (Table 5). A summary of these data can be found in Table 14 and Table 15 below.

A χ^2 test was used to calculate significance for each individual heron anatomical category against the expected null percentages. The vertebrae and ribs were underrepresented for an entire skeleton in this sample. The most represented identifiable surface and subsurface heron anatomical unit was the vertebrae group at 43.28%. However, the vertebrae were still underrepresented for what was expected. These distributions were non-random and are considered to be extremely statistically significant. The abundance calculation takes into account the observed difference compared to the expected (Table 14).

In Table 15, the wing-to-leg ratios were tested for significance using a χ^2 test against the null hypothesis 1:1. For the Heron Group in both years, the wing-to-leg ratios were 26:74. The wing elements occurred at a significantly lower abundance than the wing expected elements and the leg elements occurred at a higher abundance than the leg expected values. The wing and leg elements were enriched compared to the entire skeleton.

Table 14. Heron Anatomical Category Representation. This analysis reflected 744 great blue heron elements. Not included in this analysis was the 105 elements which were unidentifiable to a reporting category (i.e., 14 suspected long bones, 10 shaft frags and 81 completely unidentifiable). Another 3 were suspected as braincase elements and 1 possible rib. Due to the lack of confidence in these classifications of ‘unidentifiable elements’ and ‘suspected elements’ they were not reported in this analysis (N=109).The (+) indicates this observed category

occurred at a higher ratio than the expected. The (-) indicates the observed category was at a lower ratio than the expected.

Grouping	**Expected number**	**Observed Count**	**Expected %**	**Observed %**	**Abundance**
Mandible	16	30	2.15	4.03	+
Braincase & Quadrate	24	23	3.23	3.09	-
Vertebrae	356	322	47.85	43.28	-
Ribs	113	38	15.19	5.11	-
Scapular girdle	57	66	7.66	8.87	+
Forelimb	48.5	57	6.52	7.66	+
Pelvic girdle	48.5	45	6.52	6.05	-
Hindlimb	81	163	10.89	21.91	+
Total	744	744	100	100	
$X^2 = 151.493$, *7 d.f., p< 0.0001*					

Table 15. Wing-to-Leg Ratios. The (+) indicates this observed category occurred at a higher ratio than the expected. The sample size for this statistic was 220. The (-) indicates the observed category was at a lower ratio than the expected.

Grouping	**Expected number**	**Expected Projected**	**Observed Count**	**Expected %**	**Observed %**	**Abundance**
Forelimb	6	83	57	37.50%	25.91%	-
Hindlimb	10	138	163	62.50%	74.09%	+
Total	16	220	220	100.00%	100.00%	
$X^2 = 12.611$, *1 d.f., p< 0.0004*						

Nests

A quantitative evaluation for nest orientation shows that 5 out of 8 nests had ‘concave down’ (i.e. upside down) orientations. Qualitatively, it was noted that nests may prefer ‘concave down’ orientations but due to small sample sizes no significance could be reported. These heron nests ranged in sizes from 70-84 cm in width which indicates multiple years of construction (Butler, 1999). One of the nests in Fig. 15 was a not a heron nest and was much smaller in size. In plot G, one of observed fallen nests was dissected in the Primary 2012 survey. In the nest dissection, no biological material was found except for heron excrement.

A
‘concave down’

B
‘concave up’

C
Nonheron ‘concave up’ nest

Figure 15. Fallen Nests. All fallen nests were photographed, concavity orientation recorded, mapped, and measured. Image A shows a ‘concave down’ nest and Image B shows a ‘concave up’ heron nest. Image C shows the difference in nest type compared to another bird species nesting within the heron colony.

Pellet Skeletal Representations

In the 2012 Survey, three pellets were dissected. In 2012, 14 were collected and in 2013 16 were collected. Three of the pellets were discarded due to microorganism growth. In total 30 pellets, revealed a total of 136 NISP. Of the 136 identifiable elements, <1% were fish, 19.12% were invertebrate and 80.15% were mammal (Table 16; Fig. 16). A bias of mammal remains was represented in the pellet dissection survey as illustrated in Table 16. Of the pellets dissected in the lab, 24% were of the axial skeleton, 24% were mammalian teeth, and 22% were hindlimb elements. These percentages show a bias for certain elements such as 7% of the sample was crayfish chelipeds. Not contained in this figure were the 71 elements considered unidentifiable mammal bones. Furthermore, four were considered unidentifiable elements and unidentifiable taxon.

Qualitatively, Fig. 17 illustrates heron predation on fish and crayfish (Table 13 and Fig. 25) which was not sufficiently recognized in the pellet analysis. Discarded fish as shown in Fig. 17 Image A present how unlikely these fish remains were to solidify into pellet form. No articulated vertebral columns or fish tails made up any of the pellet parts.

Anatomical Unit	FISH	INVERTEBRATE	MAMMAL	NISP
Abdomen		5		5
Appendicular Skeleton	0		32	32
Axial Skeleton	1		0	1
Cephalothorax		0		0
Forelimbs			7	7
Head		0		0
Hindlimbs			30	30
Leg		9		9
Mandible			6	6
Maxilla			0	0
Pincer		10		10
Shell		0		0
Skull			1	1
Teeth			33	33
Thorax		0		0
Wing		2		2
Total	**1**	**26**	**109**	**136**

Table 16. Pellet Skeletal Representations by taxa. Each major reporting category for each taxa was present with a total Number of Identified Specimens (NISP) for the major reporting category.

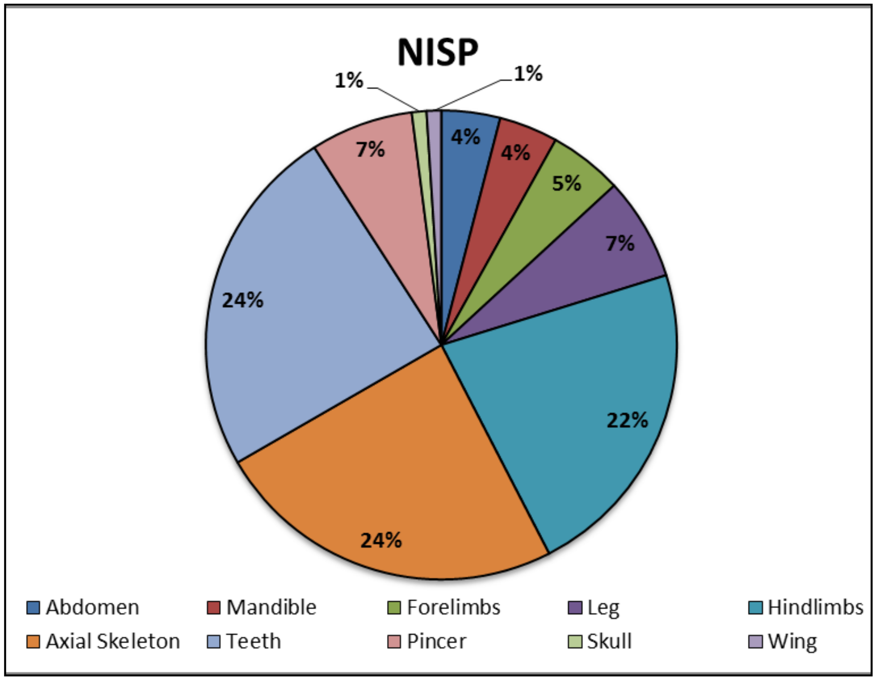


Figure 16. Pellet Anatomical Representation. The taxa represented this graph include fish (0.74%), invertebrates (19.12%) and mammals (80.15%). The most represented elements were teeth (24.26%) and the axial skeleton (24.26%).

Figure 17. Heron Prey Evidence. Image A shows evidence of heron fish predation and image B shows evidence of heron crayfish predation.

Additional Predatory Signatures Found on Broken Heron Bones

Mechanical alterations from avian predators are suspected on some of the modified heron bones. Some predatory alterations (Fig.18) are the result of beak/claw alterations and pits (Serra et al., 2013). Other conditions described in this assemblage were broken and/or fragmentary bones. Of the 1,788 elements (surface and subsurface), 1,555 bones were considered broken. Of the broken elements, there were 1,494 that were identifiable to taxa. Of these 31.39% (*N*=469), were unidentifiable fragmentary elements. For the identifiable taxa and elements (*N*=1025), vertebral elements made up 42.73% (*N*=438). For great blue heron bones, there were 485 broken elements and 87 were unidentifiable. For all broken bones, identifications were made using the comparison skeletons. These great blue heron broken bones were grouped by identifiable elements (*N*=398) to show the 5% or more altered bones. The broken states greatly ranged by element. For example, the great blue heron vertebrae group had 48.99% (*N*=195) broken bones followed by the tibiotarsus at 6.28% (*N*=25) (Appendix E).

Non-great blue heron bones were considered as other taxa. Of the surface and subsurface sample, other identifiable taxa made up 630 of the broken bones. Of the 630 broken bones, 47.78% were unidentifiable fish bones (*N*=301), 18.41% were fish vertebrae (*N*=116), and 8.73% were snake vertebrae (*N*=55). No avian elements were considered for this analysis (i.e., Heron (*N*=805), Heron? (*N*=52), or Nonheron bird (*N*=7)) and further excluded from this figure was unidentifiable to taxon elements (*N*=61).


A B C

Figure 18. Depredated great blue heron bones. Here great blue heron bones were assigned an interpretation of predation. An unidentifiable long bone is depicted in Image A with likely beak/claw alterations on an unidentifiable long bone. In Image B, there is evidence for claw/beak alterations on the humerus. In Image C, a humerus is shown with a possible pit.

Surface and Subsurface Findings

A complete review of the subsurface findings for 2012 and 2013 compared to surface elements show the difference between the surface and subsurface samples are statistically significant (Table 18). Using a 2x2 Fisher's exact test to compare the two samples (i.e., surface (*N*=1086) versus subsurface (*N*=702)) the result showed these samples were significantly different from one another. The 2012 surface sample was 33% of the entire sample (*N*=850) and the 2013 surface sample was 38% of the sample (*N*=938). Of the 1,788 elements, 61% were surface (*N*=1086) and 39% was subsurface (*N*=702). A total of 702 elements were found within the subsurface of this assemblage. Of these elements 238 were fish, 381 were heron bones, 34 were rodent bones, 30 unidentifiable, four bird, one small mammal, one crayfish and one gastropod. Heron bones (*N*=381) were found within the subsurface at 40.79% (Appendix E).

In 2012, all plots were excavated but only plots B, E and G were excavated in 2013. From the 2012 collection, a total of 263 elements were found within the subsurface and in 2013, there were 439 elements were found within the subsurface (Table 18; Table 18). In 2012, researchers found 31 eggshell fragments in the subsurface from plots H and I and all other plots were lacking subsurface eggshell evidence. The subsurface assemblage was dominated by heron and fish as measured by MNE (Table 18; Fig. 19; Fig. 20).

Great blue heron bone condition, including completeness, discoloration, maturation, and articulation differed between the surface and subsurface assemblages. The great blue heron juvenile remains were more represented in the surface survey than within the subsurface survey. Of the entire assemblage (*N*=934), 40.79% were surface (*N*=381) and 59.21% were subsurface (*N*=553). Of the known bone maturity bones (*N*=580), 514 bones were considered broken immature heron bones and 66 were considered fledglings and/or adults. Of the immature heron elements, 168 were found on the surface and 346 were found in the subsurface. Of the mature bone sample (fledglings and/or adults), 29 were found on the surface and 37 within the subsurface. Of the subsurface great blue heron elements recovered, 56.06% were mature and 32.24% were immature.

Another burial feature identified in this study was the frequency of upright bones. From these excavations, several *in situ* elements were unearthed at depths ranging from 4.2–10 cm. The *in situ* elements are shown with the depth of discovery and element position (Fig. 21).

Through the plot B and E excavations several vertically positioned upright bones were unearthed. In comparison to the total subsurface sample, plot G and excavations from other plots in 2012 did not identify vertically oriented elements at the same frequency as reported in plots B and E. Plot B and E were located near the northeast periphery of the colony near the channel (Fig. 21).

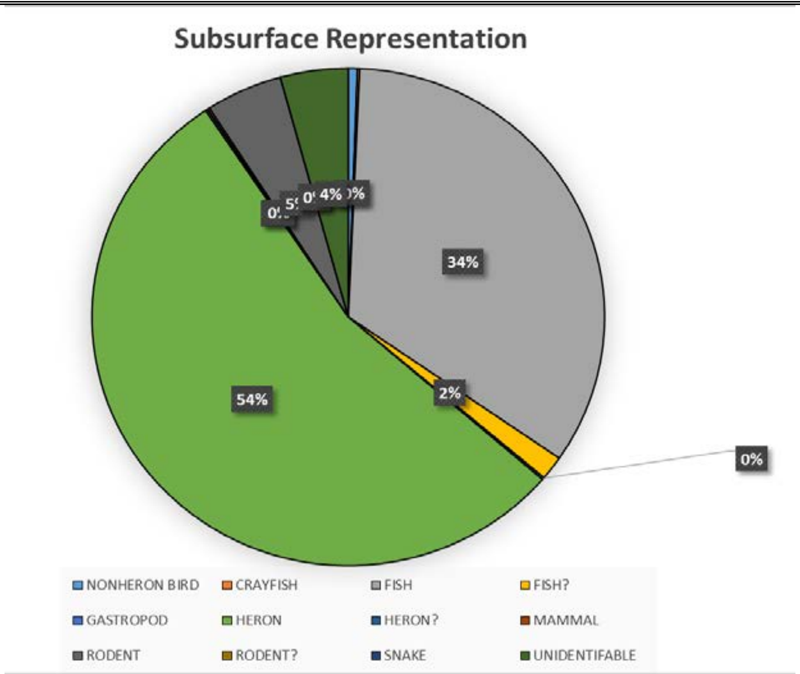
Further differences in the condition of the bone are described based on broken fragile and robust elements. Of the known taxa representing this sample, 1,494 elements were classified as broken. These elements were in some form altered and in a non-complete state; therefore, 83.56% of the elements found in this study were classified as broken. Of the broken bones, 702 were surface and subsurface elements, and 36.18% of these were recovered in the subsurface survey. Similar sized elements such as the scapula and the coracoid had similar subsurface representations at 45–50%. The fragile and robust reporting groups contained nine elements per each category which are described in Appendix E. For the robust category, eight of the elements were found within the subsurface at 20% or higher compared to only four elements of the fragile group at 20% or higher. In general, these data suggest a tendency for the more robust elements to makeup the subsurface sample (Appendix E). Of the broken bones, many robust elements were reported at a higher percentage than the fragile elements (Appendix E).

Table 17. Surface and Subsurface Elements by Plots (A–I). This table shows the surface and subsurface elements by plot type, vegetation characteristics, year excavated and excavated status. Sparsely vegetated plots were coded (SV), densely vegetated plots were coded (DV) and plots serving as in-colony controls were coded (IC). Only final site collection material was included in this analysis, therefore, no egg, eggshell, nests, etc. were represented in these counts. The totals also do not consider the spatial representation differences between the two collection types. The surface assemblage is taken over a much greater area, but at zero depth and the subsurface has a much smaller area, but with a depth of 10 cm.

Plot	A	B	C	D	E	F	G	H	I	Sampled Area
Vegetation	SV	SV	SV	IC: DV	DV	DV	IC: SV	SV	DV	
2012 excavation size	1-1m^2	NS	2-1m^2	NS	NS	NS	1-1m^2	1-1m^2	1-1m^2	6 m^{2}s
2013 excavation size	NS	2-2m^2	NS	NS	2-2m^2	NS	2-2m^2	NS	NS	12 m^{2}s
Surface Sample										
2012	141		113		84		95	51	103	587
2013	124	76	4	19	103	2	126	30	15	499
Surface Total	265	76	117	19	187	2	221	81	118	1086
Subsurface Excavations										
2012							32	157	74	263
2013		147			88		204			439
Subsurface Total	0	147	0	0	88	0	236	157	74	702

Table 18. Surface vs. Subsurface Comparison. These subsurface counts are reported by taxa, year and overall. Only final site collection material was included in this analysis, therefore, no eggshell is represented in these counts. Additionally, surface area was not considered. The surface assemblage is taken over a much greater area, but at zero depth. The subsurface has a much smaller area, but with a depth of 10 cm. Using a 2x2 Fisher's exact test for comparison the abundance of surface versus subsurface samples were significantly different.

Taxon	**Subsurface**			**Surface**		
	2012	**2013**	**Subsurface Total**	**2012**	**2013**	**Surface Total**
NONHERON BIRD		4	4		6	6
CRAYFISH		1	1	15	23	38
FISH	189	49	238	120	126	246
FISH?		11	11	0	0	0
GASTROPOD	1		1	11	2	13
HERON	34	347	381	371	182	553
HERON?		1	1		51	51
MAMMAL		1	1		4	4
RODENT	11	23	34	11	28	39
RODENT?	0	0	0		3	3
SNAKE	0	0	0	55		55
UNIDENTIFABLE	28	2	30	4	74	78
Grand Total	**263**	**439**	**702**	**587**	**499**	**1086**
p-value < 0.0001						



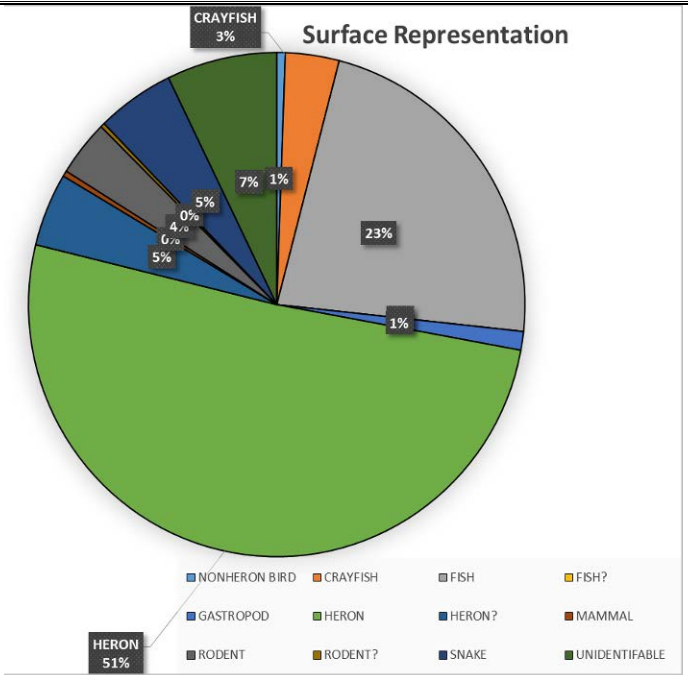


Figure 19. Subsurface skeletal representation by taxa percentage of MNE. Only final site collection material was included in this analysis, therefore, no eggshell is represented in these counts. The subsurface has a much smaller area, but with a depth of 10 cm.

Figure 20. Surface skeletal representations by taxa percentage of MNE. Only final site collection material was included in this analysis, therefore, no eggshell is represented in these counts. The surface assemblage is taken over a much greater area, but at zero depth.

A
Tibia

B
Unidentifiable long bone

C
Ulna

Figure 21. *In situ* Vertical Subsurface Elements. These images represent *in situ* 2013 vertically positioned elements. Depths of discovery were recorded for each element excavated in situ in plots (B, G, and E).

The outside of the colony Control plots, representing a total area of 12 m^2 did not produce any biological material (i.e., invertebrates, bones, eggshell or pellets) on the surface or within the subsurface. Plot L was excavated but nothing was encountered at depths up to 10 cm. There were no active nests in the vicinity of plots (J–L) and even with a comparable environment and animal traffic only horse droppings were observed. The soil texture of this area was slightly different than within the heron colony. It had larger grains of sand in its soil profile than was witnessed inside the colony where it had complex composed more of a silt matrix.

Vegetation

A χ^2 test for independence was used to determine if there was any difference between the vegetation of plots. The control plots (G and D) with an area of 50 m^2 were compared to densely vegetated plots (E, F and I) with an area of 75 m^2 and to sparsely vegetated plots (A, B, C, and H) with an area of 100 m^2. The control plots, the sparsely vegetated plots, and the densely vegetated plots were tested by their raw values from data found in Appendix C. This quantity of materials by plot type analysis using a χ^2 test for independence is presented in Table 19. No statistical test was used to compare the sample sizes per area counts, however, these raw values show sparsely vegetated areas with 8.43 elements/m^2 ranging from 117–265 elements. Densely vegetated areas had 6.25 elements/m^2 ranging from 2–275 elements. In-colony Controls had 9.52 elements/m^2 with elements ranging from 19– 457 elements (Table 17). Reproductive data devoid from this statistic were eggshells and nests. From this test, the difference between the samples was significant (Table 19).

Before the pH analysis the sparsely vegetated areas were considered as potential indicators of acidic environments created by decaying vegetation. The pH of the sparsely vegetated plots varied from 6.5–7.0. Densely vegetated areas exhibited pH values of 6.5–6.7. The in-colony controls had a pH of 7.0 for plot D and for plot G a pH of 6.7. The outside of colony control had a slightly alkaline pH of 7.3 (Table 3; Table 4). The χ^2 test for independence used for testing the vegetative plot type differences and the 2x2 Fisher's exact test used for determining the difference between surface and subsurface revealed significance. The control plots (G and D) had 476 elements making up 26.62% of the total sample. The sparse vegetation plots (A, B, C, and H) with 843 elements made up 47.15% of the total sample. The dense vegetation plots (E, F and I) with 469 elements made up 26.23% of the total sample. Below a table shows the overall counts per these treatments (Table 19) where small differences between the samples were apparent.

Table 19. Excavation Plot Type Significance Differences. This table calculates the 1,788 sample by plot type and excavation type. It further shows a two-sample assuming unequal variances Fisher's Exact Test 2x3 contingency table used to test the difference between surface and subsurface treatments by plot type (i.e., the control plots, the sparsely vegetated plots, and the densely vegetated plots). Significance was found between the rows and columns with a p-value < 0.0001.

Plot Type	Control		Sparse Vegetation		Dense Vegetation	
Excavation status	Subsurface	Surface	Subsurface	Surface	Subsurface	Surface
Plot Element Total by Excavation Type	236	240	304	539	162	307
Expected Counts by Element Total and Excavation Type	186	289	330	512	184	284
Total Elements by Plot	476		843		469	
$X^2 = 29.253$, 2 d.f., $p < 0.0001$						

DISCUSSION

Hypothesis 1: Tree-based nesting will leave biological material that could potentially be incorporated into the fossil record

As reported in Hayward et al., 1989, depositional products generated from colonial nesting may be presented as eggs, eggshells, pellets, insect exoskeletons, bones and other biological materials. This taphonomic investigation described several biotic and abiotic processes which acted on the organic materials produced by this heron colony and that were not reported within the Controls outside of the colony. All materials discovered within the Cascade heronry were interpreted as heron generated materials as the Controls outside of the colony were relatively undisturbed with the exception of animal excrement. Bi-weekly accounts further served to identify heron nesting materials such as heron prey, heron eggshells, fallen heron nests and fallen immature herons. Through surface surveys, the most encountered remains were immature great blue heron bones. These remains were found frequently and typically with broken, partially ossified bones.

From the bi-weekly accounts, the breeding season influenced the abundance of the materials encountered below the nests as well as the types of materials observed. The 2013 fully prepped plots (A–I) showed weather related phenomenon acting on the heron generated organic materials. During bi-weekly visits heron bones were unearthed from prior breeding seasons. These uncovered bones found within the subsurface surveys had mainly broken, juvenile and disarticulated bones.

Through subsurface surveys, more heron remains and mature small vertebrate remains were identified. Little eggshell was found within the subsurface and for those 31 eggshells described the fragments were within the upper strata of the 10 cm excavation. Eggshells within the subsurface positively reflect the reproductive inputs from tree-based nests but the occurrence was rare and poorly indicative of the overall productivity of the colony. Unlike Wang et al. (2013), with 52% of the 153 eggshell fragments identified being found in a buried state, only 10% of the 297 intraplot small eggshells identified in this heronry were buried.

Few strong indicators of nesting behaviors such as buried eggs, eggshells or nests were presented in this study. I offer additional nesting evidence which I believe positively reflects heron nesting. For example, all pre-fledgling or other heron generated materials (e.g., prey items and juvenile bones) may additionally offer evidence of heron nesting. Of the heron assemblage, nearly 40% of the materials described were found in the subsurface survey. Burial of heron bones and heron prey items were typically broken, very disarticulated and comprised of more mature elements. The depositional environment of the heronry included features (e.g., potential flooding) that made burial of heron generated materials possible.

Due to the shear abundance of skeletal remains, it is possible these elements could become incorporated into the fossil record. Of the 1,788 elements discovered, great blue herons made up 52% (*N*=934), of which at least 83% (*N*=776) were considered juvenile. From the great blue heron tibia found in this study, at least 35 great blue heron individuals represented this assemblage (Appendix C). These heron tibia were comprised of 78% immature herons (*N*=54). The descriptions of heron bone were limited to completeness, discoloration, maturation and articulation as the heron bone condition was typically juvenile, therefore, ascertaining weathering stages was nearly impossible.

Of the 1,788 elements described, 1,555 were considered broken. The broken great blue heron bones represented 52% of the heron sample, that is, 485 of the 934 identified great blue heron elements. Due to the incomplete and fragmentary conditions that many of the bones were in, 58 elements were unable to be placed to taxon. For those that were non-heron, an additional 1,012 elements of this assemblage were described as broken. Most of these broken non-heron remains were unidentifiable elements at 38% (*N*=385) of which fish bones largely made up the sample at 47%.

Of the 934 heron bones, 76% were considered juvenile (*N*=714). Of the 485 broken juvenile elements, 86% (*N*=418) were juvenile, 6% (*N*=28) post-fledging elements, and 8% (*N*=39) had an unknown maturity designation. Of these broken juvenile bones, 13% (*N*=56) were found in the subsurface survey compared to 61% (*N*=17) of the mature great blue heron bones (Appendix E). Overall, fully ossified and larger elements (e.g., femur, humerus, radius, tibia, ulna and vertebrate) were found at a higher incidence than juvenile bones. The condition and quality of most of the great blue heron sample was immature and broken but for subsurface surveys large and mature bones dominated (Table 13; Appendix C; Appendix E).

Heron predation was a contributor to the organic inputs of this assemblage. Herons are opportunistic foragers and will consume small mammals, fish, amphibians, reptiles, invertebrates and birds (Krebs, 1974; Gibbs et al., 1988, Butler, 1991; Butler, 1992; Butler, 1993; Bennett et al., 1995; Vennesland, 2004; Fergus, 2013). From the pellets and non-pellet prey remains, fish, small mammals, crayfish and snakes were believed to be generated by great blue heron predation (Appendix C). These heron prey remains consisted of 980 elements and from bi-weekly observations, staple foods during the breeding season were considered small mammals, fish and crayfish. The Controls outside of colony provided further evidence that these observations were specific to the nesting area only. Only 51 m away from the farthest peripheral nest of the colony, in an area with similar characteristics, nothing was found on the surface or subsurface of the three plots (Table 4).

These prey-items suggest strong evidence for how taxon-specific predation can yield large small-vertebrate and invertebrate accumulations in a nesting locale (Fig. 6-7 and Fig. 16-17) (Terry, 2004). In both the pellet analysis and the bi-weekly surveys, the distal parts of these invertebrates were greatly represented (e.g., chelipeds, tails, and legs). For non-pellet analysis, the preyed on crayfish represented 2% of the entire surface and subsurface sample (*N*=39). Fish comprised < 1% of the pellet sample, but fish in the final site collection made up 27% (*N*=484). Qualitatively, fish were not discarded in pellet form; rather, they were regurgitated in complete articulated form (Fig.17). This observation coincides with how herons consume prey; that is, in whole form (Fergus, 2013; Jenni, 1969). Due to pellet concretion (i.e., typically regurgitated, oblong fur-matted undigested food) (Dodson & Wexlar, 1979; Terry, 2004), it appears the pellets with mammalian make-up have a higher tendency to remain in intact and partially intact pellet states. Therefore, any pellets on the dispersed end of the spectrum may have less representation in the pellet analysis and these pellets are typically biased with mammal remains.

Pellet analyses, such as those described in this study, give modern expectations for birds and may provide guidance for paleoreconstructions of the theropod-bird spectrum. For example, work in the Upper Cretaceous Two Medicine Formation of western Montana described remains of a smaller hypsilophodont species, *Orodromeus makelai*. *Orodromeus makelai* was found in the *Troodon formosus* nesting site and was inferred as *Troodon formosus* prey discarded near their nesting site (Varricchio et al., 2002). Understanding more and gaining a more complete picture of the nesting assemblages of modern-day birds may help provide better evidence and biases which can be used to describe and interpret these fossil assemblages.

Hypothesis 2: Due to air fall, hatched heron eggshells will prefer ‘concave up’ orientations that exceed the 62%–72% observed in a gull colony (Hayward’s et al., 2011)

Great blue heron eggs are gently tossed out of the nest upon chick hatching and tend to fall in nearly complete states with only the blunt end of the egg missing consequence of heron chicks hatching (Cornell Heron Cam, 2012). Large, nearly complete eggshells fallen from these tree-based nests were documented in the Extraplot study and these eggshells had different orientation histories than small eggshell fragments. Hayward et al. (2000, 2011) and Wang et al. (2013) provided a framework and focus for the eggshell taphonomy of this study. Specifically, the findings of these authors were used as expectations for hatched and predated eggshell orientations both within plots and outside of plots. Unlike in their ground-based studies, gravity was considered a factor. The nest cleaning behavior of great blue herons may provide a rich and potentially preservable reproductive input for the fossil record. One aspect of eggshell taphonomy relevant to nesting paleoreconstructions was on the orientation preference of eggshell and fracture patterns (Hayward et al., 2000).

Some characteristics of the Cascade heronry not reported elsewhere included ‘concave up’ preferences in 77% of the hatched large eggshell sample. A total of 106 hatched large eggshells were found in this Extraplot survey. The Extraplot analysis for large hatched eggshells revealed a ‘concave up’ preference above 77 % which falls slightly outside of Hayward et al.’s (2011) and Wang et al.’s (2013) expectations. These results were significantly outside the norms for other modern day colonial ground nesters (Hayward et al., 2000; Hayward et al., 2011; Wang et al., 2013). However, eggshell sampling and methodological differences presented here not reported by the authors make for unfair comparisons between the studied locales (Table 1).

Hayward et al. (2011) and Wang et al. (2013) did not report eggshell sizes for hatched and predated eggs as described in the Cascade Heron Colony. Hayward et al. (2011) quantified eggshell sizes for wind experiments and stream experiments where slightly different orientation preferences were shown. The Cascade Heron Colony found preference above 77% for hatched heron eggshells preferring ‘concave up’ orientations above 60%. This result (77:23) may indicate a tree-based specific signature as a preference above the 60:40 expectation may be attributable to the influence of air fall (Hayward et al., 2011) (Table 8; Fig. 11-15).

More reproductive data found supporting tree-based nesting included Intraplot eggshell and fallen tree-based nests. The Intraplot small eggshell survey contained all plots within the colony and produced a total of 275 fragments with 58% of the eggshells preferring ‘concave up’ (*N*=158) and 42% preferring ‘concave down’ (*N*=117). This difference was significant when compared to the null prediction but unexpected when compared to Hayward et al.’s work (2000, 2011) and Wang et al.’s (2013) findings. The strong ‘concave down’ trend for Intraplot small eggshells was unique to this study. Fragmentation histories of eggshells may explain this observation. For example, large eggshells may have weathered over the breeding season (i.e., April to August), as such, eggshells may exhibit ‘concave down’ preferences not seen in large eggshell pieces.

For the Intraplot survey with small eggshells, as the eggshells were studied, they fragmented over time into small eggshell fragments. A final assessment of the fragment orientations revealed very different results than found in the onetime observation for Extraplot large eggshell fragments. A possible explanation for this difference may be that the large eggshell surface most exposed to the elements (sun, wind, precipitation, etc.) experiences the first fragmentation. Because of the way fragmentation occurs with the membrane (Hayward et al., 2011) it seems logical that this may influence the fragments into ‘concave down’ orientations (Fig. 9).

A trend not supporting this hypothesis but potentially indicative of arboreal eggshells was the strong small eggshell ‘concave down’ preference. A total of 514 Extraplot hatched small eggshell were analyzed for significance against the null prediction 1:1 and the 60:40 alternative hypothesis. Against the null prediction, the small eggshell fragments significantly preferred ‘concave down’ at 70%. In comparison to the 60:40 alternative hypothesis, the results were also significantly different, but not in favor of the ‘concave up’ hypothesis, and as such, do not concur with Hayward et al. (2011) or Wang et al. (2013) for hatched sites. One reason for these dissimilarities may be due to the differences between arboreal and ground nesting assemblages. Hayward et al. (2011) and Wang et al. (2013) looked at the area within and adjacent to the ground nests. This study described material that had already fallen from the nest and dispersed over a much wider area. Further confounding the Extraplot eggshell materials was how far the eggshells had traveled since they were discarded from the nest. In the Cascade heronry, these eggshells may be transported great distances away due to the height of the cottonwoods and the strong winds in the area.

These data suggest not only the depositional inputs of the site but also have implications for how these eggshells may contribute to the fossil record and subsequently the orientations in which they may become incorporated into the subsurface. Large eggshell fragments with ‘concave up’ preferences above ground-based nesting locales (i.e., 60%) may be important for paleoreconstructions as these trends may indicate a tree-based nesting bias. Small eggshell fragments with principally ‘concave down’ preferences may reveal transport processes meaningful for nesting site reconstructions.

For a more standardized reporting of the orientation of eggshell fragments, it seems future assessments should place emphasis on the size of the fragments. Hayward’s et al. (2011) wind tunnel experiments designated eggshells as small and large fragments and these experiments showed slightly different orientation trajectories when considering eggshell size. Furthermore, Hayward's et al. (2011) wind tunnel CU: CD ratios provided similar 'concave down' preferences as shown in the Cascade small eggshell findings. Wind may have been a factor within the Cascade heronry that led to increased 'concave down' eggshell orientation preferences. In future studies, researchers should measure individual eggshells and place emphasis on the size of the eggshell for ascertaining concavity preference. It was apparent in this study that large eggshells greatly preferred 'concave up' orientations and as size decreased orientations were more on par with the null prediction.

Hypothesis 3: Discernible distribution patterns for fallen biological material will exist due to nest location and the influence of gravity

Due to the arboreal nature of the nests, several distinct findings occurred in the Cascade Heron Colony. All plots were placed near tree bases in order to represent the active heron nests above the tree. These plots were erected to capture the behaviors of the nests above them. No analyses were performed to assess the spatial and distribution organic remain patterns other than the positions of items on the plot maps. A qualitative review of the maps reveals some spatial and distribution tendencies. Plot A provides some evidence of biological material being near the base of the tree. The observation was repeated for plot C and plot B. No distribution pattern was evident for plots F, G, H, and I. For plot D and E, the material seemed equally dispersed between the trees near this plot.

A hypothesis was generated from these juvenile remains at tree bases. A qualitative observation of mention was the affinity for chicks and fledglings to perish at or near the base of trees (Fig. 8). It may be possible that these are non-lethal falls before the birds are ready to fledge. In this event, these juvenile birds may be attempting to reach their nests but for whatever reason they succumb to death (i.e., starvation, predation, injury, etc.). Extreme weather events such as high winds, unseasonable precipitation, extreme temperature fluctuations and flooding (even during winter months) (Cameron, 2012, personal interview) may influence the abundance of juvenile remains. The temperature fluctuations in Cascade, Montana may produce extreme weather events that influence heron survival and the biological material below the nests. For example, heron chicks are unable to regulate their body temperatures until they are approximately three weeks old (Bennett, Whitehead, & Hart, 1995) so any extreme heat or cold may lead to chick mortality due to their lack of thermoregulation until later in the breeding season. During this sensitive thermoregulation time period, there were 43 days of minimum temperatures at or below zero (^{o}C) during the course of this study (Appendix A). Another potential factor at the colony was high winds. Over the course of the study, there were 89 days where maximum wind speeds were at least 48 kph (Appendix A). Wind may cause nestlings to fall out of the nest and it may also influence whether the nest structures will remain secure in the tree's canopy (Fig. 7). Another disarticulation sequence qualitatively recognized in this study was fledging juvenile remains that were found disarticulated and in close proximity to tree bases.

Fallen tree-based nests may also provide discernible distribution patterns and orientation preferences reflecting the nest location and the influence of gravity. For example, during the study, entire nests fell from the tree and had some observable orientations (Fig. 15). Fallen nests may provide distinct 'concave up' or 'concave down' orientations. The design of this study did not facilitate more careful assessment of outside of plot material as these observations were not a part of the Intraplot surveys. Arboreal *in situ* nesting may be unlikely to make it into the fossil record, but based on evidence from this colony, it illustrates potential for tree-based nests to have an affinity to fall in distinct orientations. Due to the small sample presented here, future testing is suggested to further confirm this observation and test orientation trends for fallen tree-based nests.

For the studied colony, reports indicate this site has been active since at least 1972 (Peck, 2012, personal interview). Due to the philopatric nature of these birds, their tremendous depositional input at the locale and given the opportunity for rapid burial (e.g., flooding), these events may show spatial bias within the subsurface, especially near tree bases. Future work should try to document spatial preferences using quantitative data collection in order to discern whether any spatial bias may exist. If this behavior is common among other arboreal nesters, then finding locales with multiple horizons of accumulated juveniles in one location may suggest arboreal nesting in the fossil record.

Hypothesis 4: Surface material will be incorporated into the subsurface with proportions reflecting the surface material input

The Cascade Heron Colony yielded ample heron generated surface material and through subsurface surveys many of these surface identified elements were also revealed in the excavations. One surface material with relatively little representation within the subsurface was heron eggshell. Based on the pH of the soil in the colony it seems unlikely that eggshells would make it to the fossil record (Hayward, 1991; Clayburn et al., 2004). Generally, skeletal remains made up most of the subsurface sample. Of the 1,788 elements in this assemblage, 61% (*N*=1086) were found in the surface survey and

39% (*N*=702) were found within the subsurface survey. Over 39% of the assemblage being subsurface remains indicates the high burial potential at this colony and potentially alludes to the likelihood of heron generated materials being fossilized.

Testing whether the surface sample had similar proportions to the subsurface revealed that the most represented subsurface taxa were heron (*N*=381), fish (*N*=238), rodent (*N*=34) and Nonheron bird (*N*=4). In the surface sample, the most represented taxa were heron (*N*=553), and heron prey (e.g., fish (*N*=246), snake (*N*=55), rodent (*N*=39) and Nonheron bird (*N*=6)). Invertebrate remains were not found at proportional percentages to the surface sample (*N*=51). These invertebrate remains greatly constitute part of the heron diet, but crayfish only made up 2.6% (*N*=1) of the subsurface sample (*N*=38) and gastropods made up 7.6% (*N*=1) of the sample (*N*=13).

For the overall surface and subsurface sample, the 2x2 Fisher’s exact test revealed statistical difference between the abundance of surface versus subsurface materials. The samples were largely the same, but with some differences which are detailed below. The subsurface assemblage included fewer great blue heron remains (41%), but more fish (49%) and mammal remains (47%). The less represented great blue heron elements may be explained by the bone structure differences, such as, the pneumatization (hollow bones) of avian bones (Higgins, 1999). Therefore, great blue heron bones may exercise more pre-burial destructive forces (e.g., weathering and carnivorous action) which may explain their less represented state compared to fish and mammals. Based on the great blue herons’ preference to nest in close proximity to water, the high depositional inputs of the colony, and the frequent flooding of the area, the Cascade Heron Colony has a high potential for biological material to make it into the subsurface. Subsequently, these characteristics contribute to the potential for great blue heron biological material to make it into the fossil record.

Hypothesis 5: Skeletal elements found at the Cascade Heron Colony will be equally distributed across wing and leg elements

Proximal/distal disarticulation differences may be indicative of tree-based nesting, predation and/or other sorting processes. This study found distribution differences across wing and leg elements. Using avian limb reporting criteria similar to methods from Cruz (2005, 2007, 2008), I report similar nesting species bias as described in her ground nesting studies. However, the Cascade species did not have wing and leg distributions as reported in Cruz's (2005, 2007, 2008) studies. According to Cruz's (2005) work, 'flying birds' were reported to have higher wing representations. Since great blue heron is a 'flying bird', her work provides a site expectation of a wing dominated assemblage (i.e., 34–54% over four sampled areas).

One bias learned from the Cascade Heron Colony was the high proportion of leg elements in respect to the wing-to-leg ratio. Higher representation of leg elements at 74% compared to wing elements at 26% has not been reported in other modern bird taphonomic studies and needs further research to explain this occurrence (Table 11 and Table 12). Through statistical testing this observed great blue heron wing-to-leg difference was statistically significant. One explanation for this bias may be that chicks on the altricial side of the spectrum, like great blue herons, may have disproportionate limb maturation due to development mode with hindlimbs developing earlier in ontogeny than the forelimbs (Starck & Ricklefs, 1998; Dial et al., 2012). This altricial-based development mode may delay ossification of wing elements and lower skeletal survivorship of these elements in juveniles.

Another characteristic of this Cascade assemblage not detailed in Cruz's (2005) work was the high representation of juvenile remains in comparison to adult herons. This highly juvenile assemblage may present a locale difference making comparisons to Cruz (2005) impractical. Nevertheless, most nesting locales have high juvenile representation and low adult representation supported by Horner's (1994) study. Horner (1994) did not report remains using the wing-to-leg representation but he did describe a high prevalence of juvenile remains and no adults. Behrensmeyer et al. (2003), Prassack (2011), Cruz (2007) and Leggitt (1996) describe skeletal representation biases of avian nesting sites. Leggitt (1996) qualified his fossil locale findings as an undisturbed mass mortality event and archaeological studies show higher forelimb representation possibly due to human selection (Cruz references therein).

Some non-nest location related explanations for proximal/distal disarticulation differences may be explained by predation. For example, Bochenski et al. (2009) studied eagle predation and reported wing dominated elements with poorly represented leg elements. Eye witness accounts suggest the likely predatory birds of Cascade great blue herons are golden and bald eagles (Hartman, 2013, personal interview). For the broken Cascade assemblage, some of the surface modifications may be attributable to predation and subsequent scavenging by terrestrial carnivores. Upon element analysis, support for predation was described through avian typlogies such as beak/claw alterations. Predation may alter taxa representations, it may bias the frequencies of elements at the site, it may increase the percent of fragmented and broken bone and it may produce specific typologies (e.g., beak/claw alterations and pitting) (Bochenski et al., 2009; Serra, et al., 2013). Hartman's eye witness accounts (Hartman, 2013, personal interview) and the raptor signatures provided support for golden eagle predation on great blue herons (Fig. 9; Fig. 18). Unfortunately, predation typically leaves wing dominated assemblages which were not observed in the Cascade heronry. The great blue heron limb distribution was more on par with the limb representations of 'cursorial birds' (Cruz, 2005).

It is more likely that this leg dominated bias was attributable to ontogeny or locomotor modules rather than scavenging and/or predation. Locomotor module support for Pelecaniformes may result from the 'wading' terrestrial motion (Gatesy & Dial, 1996; Dial, 2003) herons use for feeding. Hindlimb locomotor modules used for terrestrial locomotion are considered primitive in extant aves. This locomotor module was also a shared characteristic with basal theropods (i.e., single hind and tail) (Gatesy & Dial, 1996). High percentages of leg elements may provide support for semi-altricial assemblages and potentially Pelecaniformes in the fossil record. I believe this representation may be the result of the heron development mode and/or hindlimb locomotion modules. More research is needed to describe these skeletal representation biases.

Hypothesis 6: A low pH environment, created by decaying vegetation, may influence the density of biological material retention

Hayward studied inter- and intra-specific nesting differences between gulls (Hayward et al., 1989) and gull biological material inputs (Hayward et al., 1989; Hayward et al, 2000). He also examined processes responsible for impacting eggshell retention (e.g., weathering, dissolution, corrosion, coloration, etc.) (Hayward et al, 2000; Smith & Hayward, 2010; Hayward et al., 2011; Janssen et al., 2011). Addtionally, these studies (Hayward et al, 2000; Wang et al. 2013) took into account the role vegetation played for ground-nesting birds. Unlike the ground-nesting studies, vegetation was not used to test predation risk by habitat type. This study examined vegetation as a potential indicator of a low pH environment. Before pH confirmation, sparsely vegetated areas were considered acidic in contrast to densely vegetated areas. It was expected that sparsely vegetated areas would have fewer eggshells and vertebrate material within them due to the acidic environment. This supposition came from research documenting herons producing vast amounts of excrement below their tree-based nests (Butler, 1999) which may lead to stunted vegetation and/or vegetation kill-off. Observations on vegetation, made during the 2012 breeding season, appeared to support this finding (Table 3).

From the pH in plots (A-I), mildly acidic environments were found. These mildly acidic soils may have impacted the retention of eggshells within the subsurface surveys (Hayward et al, 1991; Hayward et al, 2000; Clayburn et al., 2004). Unexpectedly, the pH analysis did not support sparsely vegetated areas as being more acidic. More abiotic processes could be confounding this pH result as no other tests were used to describe the soil chemistry of the area. No depositional measurements were taken, however, qualitative observations show that over the span of one year, much vegetation and leaf litter were found decaying on the forest floor in the colony (71 m x 40 m) (Table 3; Table 4).

Ignoring the pH results there were differences found between vegetated areas. These minor differences may be attributable to the area surveyed as opposed to actual vegetation differences. For example, the control plots (G and D) surveyed 50 m^2, the vegetated plots (E, F and I) surveyed 75 m^2 and the sparsely vegetated plots (A, B, C, and H) surveyed 100 m^2. These differences by vegetated plot status led to sparsely vegetated areas yielding the highest element counts at 47% (*N*=843), followed by densely vegetated areas at 26% (*N*=469) and in-colony Controls at 27% (*N*=476) (Table 3; Table 4; Table 17; Table 19). No statistical test was used to compare the significance of elements by area. Instead elements were found at 9.52 elements/m^2 for In-colony Controls followed by 8.43 elements/m^2 for sparsely vegetated areas and 6.25 elements/m^2 for densely vegetated areas (Table 17). These elemental and vegetative differences show not all plots produced similar heron materials.

The in-colony Controls had a surface devoid of vegetation that could be used to indicate any differences between a non-vegetated surface. The sparsely vegetated plots had much more identified elements possibly attributable to the visibility of elements in sparsely vegetated areas as opposed to the concealed nature elements were in for densely vegetated plots. Additionally, sparsely vegetated areas may experience more taphonomic processes (e.g., erosion) which could erode soils away and expose incorporated subsurface elements to the surface. Another reason for these differences could be the amount of active nests in the plots' vicinity (Table 3). The sparsely vegetated plots had 32 nests within their vicinity followed by 23 nests in the vicinity of the In-colony Controls, and 20 nests within the vicinity of the densely vegetated plots (Table 3; Table 17). Through the χ^2 test for significance comparing within-colony Control plots versus sparsely vegetated plots, and densely vegetated plots significant difference was found between them. This difference did not appear correlated with the pH levels (Table 3;

Table 4). The χ^2 test was limited in that causation was not established here and this reported difference could be due to many factors (e.g., elements/area, nests in vicinity, pH, vegetative differences, etc.). More testing is needed to discern if these observed plot type differences were truly significant for skeletal representations within different sampled areas.

The results from this great blue heron study provided evidence for taphonomic signatures unique to tree-based nesters and added to the work already performed on colonial, ground nesting locales. The research on great blue herons furthers our knowledge of extant birds and thus provides a more comprehensive understanding of the taphonomy of colonial nesters. It is unlikely arboreal nesting would be preserved *in situ* but this research helps support alternative ways to test the tree-down theory for the evolution of flight.

CONCLUSION

The work performed here presented the first investigation into an arboreal, semialtricial colony. From the studied eggshells, bones, pellets, and nests in this tree-based colony there was ample support for tree-based nesting birds to leave biological material that may be incorporated into the fossil record. My evidence suggests that philopatric birds such as great blue heron contribute vast amounts of organic material to their locale. Through the analyses performed in this study, great blue heron nesting locales could serve as models for fossil nesting localities. Due to the low incidence and preservation potentials of buried eggshell, and fallen nests large quantities of broken, juvenile heron bones followed by heron prey items (e.g., fish and small mammals) not only resemble the modern day nesting of great blue herons, but are more likely to be preserved. Arboreal nesting is unlikely to be preserved *in situ*, this research described other testable biases left by tree-based nesters.

Another feature of this study was providing direction into future arboreal nesting taphonomic research. Here juvenile carcasses qualitatively appeared to be in close proximity to tree bases and fallen tree-based nests may prefer a certain ‘concave up’ or ‘concave down’ positions. Based on the small sample size of these nests and lack of spatial analyses on the juvenile affinities towards tree bases the study cannot draw any conclusions from the observations. I believe future work should examine nest structure concavity biases as well as concentration of juveniles near tree bases as this observations may suggest juvenile spatial biases as well as fallen nest preferences.

Certain behaviors witnessed in the analyses of this arboreal colony may be useful for nesting site paleoreconstructions. Predation was examined as both heron generated predation and predation upon great blue herons. Eye witness accounts and raptor typologies found on several great blue heron bones gave support for eagles preying on great blue herons. Certain raptor typologies and surface modifications on prey materials were important for understanding taxon-specific diets. For instance, through pellet analysis, and bi-weekly site visitations it was apparent that great blue heron preyed upon crayfish, fish and small mammals. Through bi-weekly observations and beak/claw alterations it was plausible that golden and bald eagles likely consumed juvenile and adult great blue herons.

The eggshell taphonomy of this study revealed ‘concave down’ preferences for small eggshell fragments and ‘concave up’ preferences for large eggshell. For Extraplot hatched large eggshells, ‘concave up’ orientations above 77% were observed. This trend exceeds ground-based nesting expectations and was statistically different than the hatched 60:40 expectation. For Extraplot hatched small eggshell, trends of 70% in favor of ‘concave down’ orientations was observed. For Intraplot small eggshell survey, 58% were in preference of ‘concave up’. Intraplot small eggshell findings were more equivalent to the ground-based nesting expectations from Hayward et al., (2011) and Wang et al. (2013). The Extraplot hatched small fragments greatly differed from Hayward et al., (2011) and Wang et al. (2013) with 30:70 preference for ‘concave down’.

Many avian taphonomic research has assessed the skeletal distribution biases as they relate to the proximal and distal limb bones (Behrensmeyer et al., 2003; Cruz, 2005; Cruz, 2007, Cruz, 2008; Prassack, 2011). Behrensmeyer et al., (2003) and Cruz (2005) discuss disarticulation sequences determined by size and locomotion characteristics to influence the frequencies of wing and leg elements. In the Cascade Heron Colony, the higher representation of leg elements above 74% versus 26% wing elements reveals a bias for these remains. The bias may be attributable to the features of great blue heron ontogeny, it may be the wading predation style used by the herons, or it could be a signature of arboreal nesting. Due to the paucity of research in the taphonomy of arboreal nesting, more work is needed to explain this occurrence. Both eggshell orientation preferences CU:CD and skeletal disarticulation sequences of great blue herons may be signatures of tree-based nesting as no modern-day ground nesting locale has documented this.

The subsurface evidence of this study may provide paleontologists with a clearer perspective on the taphonomy of avian reproduction, nesting behaviors, ecological influences/ habitat use, and the life histories of a tree-based colony. Excavations documented what tree-based materials herons generate and through 40% of the assemblage being represented within the subsurface survey these results indicate how easily heron materials can become incorporated into the soil. With the high depositional features and potential for rapid burial via flooding with the Missouri River just meters from the colony this work illustrates the significance modern nesting locales have for site reconstructions. Comparisons to Controls outside of colony further substantiated the types of materials, abundance of materials, and the frequency of materials heron nesting produces. All of these surface and subsurface organic remains, provided support for the potential contributions great blue herons can make to the fossil record. This work provides paleontologists with a clearer understanding of the biotic and abiotic processes acting on the organic remains of the arboreal, semialtricial nesting in great blue herons.

REFERENCES

Behrensmeyer, A. K. (1978). Taphonomic and Ecologic Information from Bone Weathering. Paleobiology, 4(2), 150-162.

Behrensmeyer, A. K., Stayton, T. C., & Chapman, R. E. (2003). Taphonomy and Ecology of Modern Avifaunal Remains from Amboseli Park, Kenya. Paleobiology, 29(1), 52-70.

Bennett, D. C. (1993). Growth and energy requirements of captive Great Blue Herons (Ardea herodias). University of British Columbia: Master of science in the faculty of graduate studies (department of animal science).

Bennett, D. C., Whitehead, P. E., & Hart, L. E. (1995). Growth and Energy Requirements of Hand-Reared Great Blue Herons (Ardea herodias) Chicks. The Auk, 112(1), 201-209.

Biaggi, R., & Buchheim, H. P. (1999). Paleoecology and paleoenvironments during initial stages of eocene fossil lake, SW wyoming. National Park Service Paleontological Research, 4, 54-65.

Bickart, K. J. (1984). A Field Experiment in Avian Taphonomy. Journal of Vertebrate Paleontology, 4(4), 525-535.

Birn-Jeffery, A., Miller, C. E., Naish, D., Rayfield, E. J., & Hone, D. W. (2012). Pedal Claw Curvature in Birds, Lizards and Mesozoic Dinosaurs – Complicated Categories and Compensating for Mass-Specific and Phylogenetic Control. 7(12).

Bock, W. J. A Generic Review of the Family Ardeidae (Aves). (1956). American Museum Noviatates. 1779.

Bochenski, Z. M., & Tomek, T. (1997). Preservation of Bird Bones: Erosion Versus Digestion by Owls. International Journal of Osteoarchaeology, 7, 372-387.

Bochenski, Z. M., Tomek, T., Tornber, R., & Wertz, K. (2009). Distinguishing nonhuman predation on birds: pattern of damage done by the white-tailed eagle Haliaetus albicilla, with comments on the punctures made by the golden eagle *Aquila chrysaetos*. Journal Archeological Science, 36, 122-129.

Borella, F., & Cruz, I. (2012). Taphonomic evaluation of penguin (Spheniscidae) remains at a shell-midden on the northern coast of Patagonia (San Matías Gulf, Río Negro, Argentina). Quaternary International, 278, 45-50.

Butler, R.W. (1991). Habitat selection and time of breeding in the Great Blue Heron (Ardea herodias). Ph.D. dissertation. Univ. B.C., Vancouver, B.C.

Butler, R.W.(1992). Great Blue Heron. In The birds of North America No. 25. A. Poole, P. Stettenheim, and F. Gill (editors). Philadelphia: Acad. Nat. Sci., Philadelphi, Penn., and Am. Ornith. Union, Washington, D.C.

Butler, R.W. (1993). Time of breeding in relation to food availability of female Great Blue Herons (Ardea herodias). The Auk, 693-701.

Butler, R. W., Whitehead, P. E., Breault, A. M., & Moul, I. E. (1995). Colony Effects on Fledging Success of Great Blue Herons (Ardea herodias) in British Columbia. Colonial Waterbirds, 18(2), 159-165.

Butler, R.W. (1999). The Great Blue Heron. University of British Columbia Pr.

Cameron, D. (2012, May 08). Ranch owner. (A. McGrath, Interviewer).

Clayburn, J., Smith, D., & Hayward, J. (2004). Taphonomic Effects of pH Temperature on Extant Avian Dinosaur Eggshell. Palaios, 19, 170-177.

Cottrille, W. P., & Cottrille, B. D. (1958). Great Blue Heron: Behavior at the Nest. Museum of Zoology, University of Michigan, 1-15.

Cornell Lab of Ornithology.(2012). Great Blue Heron Nest at the Cornell Lab. Sapsucker Woods Pond, Ithaca, New York. http://www.livestream.com/cornellherons

Cruz, I. (1999). Pinguinos de cabo virgenes (prov. Santa cruz). Aspectos tafonomicos e implicaciones arqueológicas. Actas del XIII congreso Nacional de arqueológica Argentina, 95-108.

Cruz, I. (2005). La representación de partes esqueléticas de aves. Patrones naturales e interpretación arqueológica. Archaeofauna, 14, 69-81

Cruz, I. (2007). Avian taphonomy: observations at two Magellanic penguin (Spheniscus magellaniscus) breeding colonies and their implications for the fossil record, Journal of Archaeological Science, 34, 1252-1261.

Cruz, I. (2008). Avian and mammalian bone taphonomy in southern continental Patagonia: A comparative approach. Quaternary International, 180, 30-37.

Cruz, I. (2011). Tafonomia de huesos de aves. Estado de la cuestión y perspectivas desde el sur del Neotrópico. Antropologia Biológica e Zooarqueologia, 147-174.

Davis, P. G., & Briggs, D. E. (1998). The Impact of Decay and Distarticulation on the Preservation of Fossil Birds. Palaios, 13(1), 3-13.

Dial, K. (2003a). Wing-assisted Incline Running and the Evolution of Flight. Science, American Association for the Advancement of Science, 299(5605), 402-404.

Dial, K. (2003b). Evolution of avian locomotion: correlates of flight style, locomotor modules, nesting biology, body size, development, and the origin of flapping flight. The Auk, 120(4), 941-952.

Dial, T.R., Heers, A.M., & Tobalske, B.W. (2012). Ontogeny of aerodynamics in mallards: comparitive performance and developmental implications. The Journal of Experimental Biology, 215, 3693-3702.

Dodson, P., & Wexlar, D. (1979). Taphonomic Investigations of Owl Pellets. Paleontological Society, 5(3), 275-284.

Dyke, G., & Kaiser, G. (2010). Cracking a Development Constraint: Egg Size and Bird Evolution. Australian Museum, 62, 207-216.

Dyke, G., Kat, R. d., Palmer, C., Kindere, J. v., Naish, D., & Ganapathisubramani, B. (2013). Aerodynamic performance of the feathered dinosaur Microraptor and the evolution of feathered flight. Nature.

Dyke, G., Vremir, M., Kaiser, G., & Naish, D. (2012). A drowned Mesozoic bird breeding colony from the Late Cretaceous of Transylvania. Naturwissenschaften, 99(6), 435-442.

Fergus, C. (2013, April 21). Heron Family. Retrieved from Pennsylvania State of Independence: Commonwealth interpretise: www.portal.state.pa.us/portal/server.pt/document/.../herons_pd.

Fernández, M., Garcia, R., Fiorelli, L., Scolaro, A., Salvador, R., Cotaro, C... Dyke, G. (2013). A large accumulation of avian eggs from the Late Cretaceous of Patagonia (Argentina) reveals a novel nesting strategy in Mesozoic birds. PLoS ONE.

Gibbs, J. P., Woodward, S., Hunter, M. L., & Hutchinson, a. E. (1988). Determinants of Great Blue Heron Colony Distribution in Coastal Maine. Auk, 104, 38-47.

Great Blue Heron. (n.d.). Retrieved from All About Birds: The Cornell Lab of Ornithology: http://www.allaboutbirds.org/guide/Great_Blue_Heron/lifehistory

Grellet-Tinner, G., Fiorelli, L., & Salvador, R. (2012). Water vapor conductance of the Lower Cretaceous dinosaurian eggs from Sanagasta, La Rioja, Argentina –paleobiological and paleoecological implications for South American faveoloolithid and megaloolithid eggs. Palaios, 27, 35-47.

Grellet-Tinner, G., Murelaga, X., Larrasoan, J., Silveira, L., Olivares, M., Ortega, L., … Pascual, A. (2012). The First Occurrence in the Fossil Record of an Aquatic Avian Twig-Nest with Phoenicopteriformes Eggs: Evolutionary Implications. PLOS One, 7(10), 1-14.

Hartman, R. (2013, May). Amatuer birder. (A. McGrath, Interviewer)

Hayward, J. L., Amlander, C.J., & Young, K.A. (1989). Turning Eggs to Fossils: A Natural Experiment in Taphonomy. Journal of Vertebrate Paleontology, 9(2), 196-200.

Hayward, J. L., Folsom, S. D., Elmendorf, D. L., Tambrini, A. A., & Cowles, D. L. (1997). Experiments on the Taphonomy of Amniote Eggs in Marine Environments. Palaios, 12(5), 482-488.

Hayward, J. L., Hirsch, K. F., & Robertson, T. C. (1991). Rapid Dissolution of Avian Eggshells Buried by Mount St. Helens Ash. Palaios, 6(2), 174-178.

Hayward, J. L., Zelenitsky, D. K., Smith, D. L., Zaft, D. M., & Clayburn, J. K. (2000). Eggshell Taphonomy at Modern Gull Colonies and a Dinosaur Clutch Site. Palaios, 15, 343-355.

Hayward, J. L., & Smith, D. (2010). Bacterial Decomposition of Avian Eggs: A Taphonomic Experiment. Palaios, 25, 318-326.

Hayward, J., Janssen, J., & Mutch, W. (2011). Taphonomic Effects of High Temperature on Avian Eggshell. Palaios, 26, 658-664.

Hayward, J. L., Dickson, K. M., Gamble, S. R., Owen, A. W., & Owen, K. C. (2011). Eggshell taphonomy: environmental effects on fragment orientation. Historical Biology, 23(1), 5-13.

Heers, A., & Dial, K. (2012). From extant to extinct: locomotor ontogeny and the evolution of avian flight. Trends in ecology & evolution, 27(5), 296-305.

Higgins, J. (1999). Tunel: A Case Study of Avian Zooarchaeology and Taphonomy. Journal of Archaeological Science, 26, 1449-1457.

Horner, J. R. (1982). Evidence for colonial nesting and ‘‘site fidelity’’. Nature, 297, 675-676.

Horner, J. R. (1984b). The nesting behavior of dinosaurs. Sci. am., 250(4), 130 - 137.

Horner, J. R. (2000). Dinosaur Reproduction and Parenting. 28, 19-45.

Horner, Padian, & Riqles, A. d. (2001). Comparative osteohistology of some embryonic and perinatal archosaurs: developmental and behavioral implications for dinosaurs. Paleobiology, 27, 39-58.

Janssen, J. D., Mutch, G. W., & Hayward, J. L. (2011). Taphonomic Effects of High Temperature on Avian Eggshell. Palaios, 26, 658-664.

Jenni, D. A. (1969). A Study of the Ecology of Four Species of Herons during the Breeding Season at Lake Alice, Alachua County, Florida. Ecological Monographs, 39 (3), 245-270

Kandel, A. W. (2004). Modification of ostrich eggs by carnivores and its bearing on the interpretation of archaeological and paleontological finds. Journal of Archaeological Science, 31, 377-391.

Krebs, J. R. (1974). Colonial Nesting and Social Feeding as Strategies for Exploiting Food Resources in the Great Blue Heron (Ardea herodias). Behaviour, 51(1/2), 99-134.

Leggitt, V. L. (1996). An avian botulism epizootic affecting a nesting site population of Presbyornis: on a carbonate mudflat shoreline of eocene fossil lake. Doctoral dissertation, Loma Linda University.

Livingston, S. J. (1989). The taphonomic interpretation of avian skeletal part frequencies. Journal of Archaeological Science, v. 16, p. 537-47.

Mabee, T. J. (1997). Using Eggshell Evidence to determine nest fate of shorebirds. Wilson Bull, 109(2), 307-313.

Naish, D. (2000). 130 years of tree-climbing dinosaurs: Archaeopteryx, ‘arbrosaurs’ and the origin of avian flight. The Quarterly Journal of the Dinosaur Society, 4(1), 20-23.

Naish, D. (2000). Theropod dinosaurs in the trees: a historical review of arboreal habits amongst nonavian theropods. Archaeopteryx, 18, 35-41.

Naish, D. (2012, December). Did Velociraptor and Archaeopteryx climb trees? Claws and climbing in birds and other dinosaurs. Scientific American.

Naish, D. (2013, November). Flight of the Microraptor. Scientific American.

Nice, M.M. (1962). Development of behavior in precocial birds. Transactions of the Linnaean Society of New York 8:1–211.

Padian, K. & Chiappe, L. (1998). The origin and early evolution of birds. Biological Reviews of the Cambridge Philosophical Society, 73, 1-42.

Padian, K. & Dial, K. (2005). Origin of flight: Could 'four-winged' dinosaurs fly? Brief Communications Arising, Nature 438.

Peck, S. (2012, May 01). Retired Cascade Game Warden. (A. McGrath, Interviewer)

Prassack, K. A. (2011). The effect of weathering on bird bone survivorship in modern and fossil saline-alkaline lake environments. Paleobiology, 37(4), 633-654.

Pratt, H. M. (1970). Breeding Biology of Great Blue Herons and Common Egrets in Central California. The Condor, 72, 407-416.

Quinn, T., & Milner, R. (n.d.). General Range and Washington Distribution. Retrieved May 15, 2013, from rentonwa: http://www.rentonwa.gov/uploadedFiles/Business/EDNSP/planning/PHS_great_bluheron.pdf

Rich, P. (1980). Preliminary report on the fossil avian remains from Late Tertiary sediments at Langebaanweg (Cape Province). South Africa: South African Journal of Science, 76, 166-170.

Sclater, P.L., (1862). The Ibis: Journal of British Ornithologist Union. 4. Wiley-Blackwell Publishing. 6.

Selby, P.J., Babington, C.C., Gray, J. E., & Francis, W., (1860). The Annals and Magazine of Natural History. 6 (3), p.449.

Sereno, P. C. (1999). The Evolution of Dinosaurs. Science, 284, 2137-2147.

Serra, A. S., Margalef, C. R., Perez, J. V., Ripoll, M. P., Cunat, C. T., Marco, Y. C., . . . Marques, J. B. (2013). Towards the identification of a new taphonomic agent: An analysis of bone accumulation obtained from modern Egyptian vulture (Neophron percnopterus) nests. Quarternary International, 1-14.

Shufeldt, R.W., (1889). Osteological Studies of the Subfamily Ardeinae: Part II. The Journal of Comparative Medicine and Surgery. 10 (4), 287-317.

Smith, D. L., & Hayward, J. L. (2010). Bacterial Decomposition of Avian Eggshell: A Taphonomic Experiment. Palaios, 25, 318-326.

Species Profile: Great Blue Heron (Ardea herodias). (2013, April 19). Retrieved from EPA: http://www.epa.gov/region1/ge/thesite/restofriver/reports/final_era/B%20-%20Focus%20Species%20Profiles/EcoRiskProfile_great_blue_heron.pdf

Starck, J. (1992). Evolution of avian ontogenies. (S. US, Ed.) In current orinthology.

Starck, J. R. & Ricklefs, R.E. (1998). Avian growth and development: evolution within the altricial-precocial spectrum (Vol. 8). Oxford University Press.

Terry, R. C. (2004). Owl Pellet Taphonomy: A Preliminary Study of the Post-Regurgitation Taphonomic History of Pellets in a Temperate Forest. Palaios, 19, 497-506.

Varricchio, D. J., & Jackson, F. D. (n.d.). Two Eggs Sunny-Side Up: Reproductive Physiology in the Dinosaur Troodon formosus.

Varricchio, D. J. (1995). Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana. Paleogeography, Palaeoclimatology, Paelaeoecology, 114, 297-323.

Varricchio, D. J., Jackson, F., Borkowski, J. J., & Horner, J. R. (1997). Nest and Egg clutches of dinosaur Troodon formosus. Nature, 385(16), 248-250.

Varricchio, D. J., Jackson, F., & Trueman, C. N. (1999). A Nesting Trace with Eggs for the Cretaceous Theropod Dinosaur Troodon formosus. Journal of Vertebrate Paleontology, 19(1), 91-100.

Varricchio, D. J., Horner, J. R., & Jackson, F. D. (2002). Embryos and eggs for cretaceous theropod dinosaur troodon formosus. Journal of Vertebrate Paleontology, 22(3), 564-576.

Varricchio, D. J., & Jackson, F. D. (2004). A phylogenetic assessment of prismatic dinosaur eggs from the cretaceous two medicine formation of montana. Journal of Vertebrate Paleontology, 24(4).

Varricchio, D. J. (2005). Bringing Up Baby: The evidence mounts that some dinosaurs were attentive parents. Naturalist at Large, 30-32.

Varricchio, D. J., Moore, J. R., Erichson, G. M., Norell, M. A., Jackson, F. D., & Borkowski, J. J. (2008). Avian Paternal Care Had Dinosaur Origin. Science, 322, 1826-1828.

Varricchio, D., Jackson, F., Jackson, R., Zelenitsky, & Darla. (2013). Porosity and water vapor conductance of two Troodon formosus eggs: an assessment of incubation strategy in maniraptoran dinosaur. Paleobiology, 39(2), 278-296.

Vennesland, R. (2004). The Great Blue Heron (Ardea herodias). Accounts and Measures for Managing Identified Wildlife.

Vennesland, R. G., & Butler, R. W. (2011). Great Blue Heron (Ardea herodias), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved May 21, 2013, from http://bna.birds.cornell.edu.proxybz.lib.montana.edu/bna/species/025

Vermont Fish and Wildlife. (2013, April 19). Retrieved from vtfishandwildlife.com: http://www.vtfishandwildlife.com/.%5Clibrary%5CReports_and_Documents%5CNonGame_and_Natural_Heritage%5CGuidelines%20for%20Great%20Blue%20Heron%20Rookeries.pdf

Wang, P., Jackson, F., & Varricchio, D. (2013). Nest taphonomy of common terns (Sterna hirundo) on Poplar, Island Chesapeake Bay, Maryland. Historical Biology: An International Journal of Paleobiology.

APPENDICES

APPENDIX A

WEATHER DATA

Weather from April 1, 2012 to August 24, 2013. The blue cells indicate a day the colony was visited. The green cells indicate extreme weather (e.g., temperature (max and min), and wind). These data were taken directly from the online source (http://weathersource.com) using the Great Falls International Airport Weather Station. To uphold the integrity of the primary reporting source, none of these values have been converted to metric.

Day	Max. Temp.	Mean Temp.	Min. Temp.	Precipitation	Max. Wind Speed	Avg. Wind Speed	Min. Wind Speed	Max. Feels Like Temp.	Avg. Feels Like Temp.	Min. Feels Like Temp.
4/1/2012	55	43	31	0.12	39.13	19.18	10.36	49.2	38.2	26
4/2/2012	52	40.5	29		25.32	12.11	6.9	49.6	34	19.2
4/3/2012	64	46.5	29		29.92	12.99	4.6	63	44.2	23.6
4/4/2012	71	52	33		41.43	15.73	4.6	66.9	51	28.9
4/5/2012	51	42	33		12.66	5.94	0	49.3	36.9	26.6
4/6/2012	39	33	27	0.53	12.66	7.64	0	33.8	25.5	22.5
4/7/2012	48	35	22		29.92	14.42	9.21	39	26.8	13.7
4/8/2012	53	37.5	22		9.21	8.34	5.75	49.2	35.5	14.4
4/9/2012	55	40	25		11.51	6.42	0	53.8	37.1	23.2
4/10/2012	61	44.5	28		5.75	2.06	0	54.9	36.5	25.1
4/11/2012	68	49.5	31							
4/12/2012	55	44.5	34	0.53						
4/13/2012	60	47.5	35		29.92	12.75	5.75	60.1	47.7	31.6
4/14/2012	62	45	28	0.07	29.92	10.02	0	62.1	42.4	23.6
4/15/2012	36	32	28	0.18	21.87	7.63	0	35.6	25.8	17.5
4/16/2012	58	45	32		26.47	11.37	0	52.5	40.8	28
4/17/2012	59	50	41		31.07	14.1	5.75	57.2	44.4	33.9
4/18/2012	53	44	35	0.16	28.77	4.98	0	50	40	30.3
4/19/2012	59	46	33		20.71	9.49	0	55.5	41.6	29
4/20/2012	69	54	39		49.48	20.67	5.75	68	52.4	35.2
4/21/2012	63	52	41		10.36	3.26	0	62.1	51.8	39.5
4/22/2012	82	59.5	37		18.41	6.9	0	82	60.2	38
4/23/2012	84	64.5	45		21.87	9.78	3.45	84	65	43.1
4/24/2012	80	68	56		44.88	16.02	8.06	77	67.4	56.4
4/25/2012	76	62.5	49		18.41	7.68	0	75	62.7	46.3
4/26/2012	75	62.5	50	0.15	47.18	9.01	3.45	75.9	58.1	46
4/27/2012	52	44.5	37	0.39	37.98	16.55	3.45	49.2	34.7	26.1
4/28/2012	50	43.5	37	0.2	42.58	10.74	0	44.1	36.3	29.6
4/29/2012	61	50	39		25.32	10.89	3.45	60.1	45.3	34.7
4/30/2012	64	52	40	0.18	36.83	13.43	3.45	62.1	45.9	32.3
5/1/2012	56	44.5	33		56.39	20.52	10.36	48.2	39.8	27.5
5/2/2012	56	42	28		34.52	10.45	0	51.6	36.3	20.4
5/3/2012	59	43.5	28		31.07	8.3	0	77.2	41.5	21.9
5/4/2012	65	52	39	0.28	33.37	11.89	0	64.9	49.6	34.5
5/5/2012	56	47.5	39	0.02	39.13	16.84	0	49.6	40.2	33.3
5/6/2012	58	46	34		33.37	12.13	0	53.3	41.9	27.9
5/7/2012	66	50.5	35		18.41	8.3	3.45	64.9	47.1	27.9
5/8/2012	77	57.5	38		23.02	9.25	3.45	77	57	32.8
5/9/2012	80	65	50		40.28	16.26	4.6	80.1	64.8	49.4
5/10/2012	56	44.5	33		46.03	14.05	3.45	53.1	44	28.5
5/11/2012	64	44.5	25		24.17	9.07	0	63	41.4	16.8
5/12/2012	72	49.5	27		17.26	6.31	0	70	50.8	20.8
5/13/2012	80	58	36		13.81	8.71	0	80.1	58.8	31.5
5/14/2012	79	59	39		16.11	8.3	3.45	79	61.1	34.3
5/15/2012	86	65	44		14.96	7.39	0	86	66.9	42.6
5/16/2012	85	66	47		27.62	11.31	6.9	84	68.1	45
5/17/2012	64	56.5	49	0.14	17.26	6.62	0	63	54.2	43
5/18/2012	57	49	41	0.18	28.77	7.15	0	54.2	47.6	40
5/19/2012	65	49	33		23.02	6.9	0	64	49	28
5/20/2012	75	55	35		26.47	7.68	0	75	56.9	31.1
5/21/2012	77	66	55	0.06	14.96	8.16	0	76.7	64	54.7
5/22/2012	64	53	42	0.15	44.88	17.6	6.9	63	52.7	36.6
5/23/2012	62	51	40		35.67	14.72	0	60.8	46.3	35.7
5/24/2012	50	42	34	0.1	19.56	8.92	3.45	44.2	38	30.3
5/25/2012	52	41.5	31		29.92	11.84	0	46.6	38	25.6
5/26/2012	43	38	33	0.5	31.07	12.08	0	39.2	31.7	26.6
5/27/2012	37	35	33	0.8	24.17	9.45	0	33.8	27.7	24.8
5/28/2012	54	43	32	0.04	19.56	7.19	0	51.4	37.3	27.1
5/29/2012	66	49.5	33		35.67	8.01	0	64	50.6	34

5/30/2012	65	51	37		32.22	10.93	5.75	64.9	50.7	32.8
5/31/2012	67	54.5	42		29.92	12.33	8.06	66	54.3	37.2
6/1/2012	73	59.5	46		31.07	11.31	4.6	75.2	59.7	42.5
6/2/2012	80	64	48		32.22	12.42	5.75	76.8	62.7	47.7
6/3/2012	74	60.5	47		17.26	8.49	0	74.4	59.7	44.1
6/4/2012	79	62.5	46		39.13	7.77	0	78.6	62.3	45.4
6/5/2012	77	64.5	52	0.36	40.28	9.87	0	77	62.1	47.1
6/6/2012	63	51	39	0.04	49.48	22.64	8.06	62.1	48.9	35.5
6/7/2012	72	54.5	37		21.87	9.07	5.75	72.1	55.4	30.4
6/8/2012	73	60	47	0.02	37.98	8.47	4.6	73.9	56.7	43.9
6/9/2012	63	50.5	38		33.37	13.86	4.6	63	48.4	34.5
6/10/2012	51	47.5	44	0.56	32.22	16.97	11.51	46.9	41.8	38
6/11/2012	72	60	48		20.71	10.16	4.6	74.7	56.7	43.9
6/12/2012	77	59.5	42		33.37	9.54	4.6	75.1	61.2	40.6
6/13/2012	70	61	52		44.88	20.62	12.66	69.1	59.1	48.9
6/14/2012	72	57	42		20.71	8.83	4.6	73.5	59	43
6/15/2012	73	60	47		27.62	9.25	4.6	73.3	60.5	48.5
6/16/2012	80	61	42		48.33	13.56	0	79	62.6	39.5
6/17/2012	80	66	52		51.79	20.14	10.36	78.1	69.4	54.1
6/18/2012	72	58.5	45		37.98	13.04	0	70	58.3	45.9
6/19/2012	65	55	45	0.07	32.22	12.08	3.45	63	50.2	39.3
6/20/2012	70	59	48	0.01	11.51	7.1	3.45	69.1	56.9	45
6/21/2012	79	61	43		18.41	7.77	0	79	62.9	43
6/22/2012	79	63.5	48		12.66	7.39	0	78.6	63.8	46.2
6/23/2012	85	70.5	56		44.88	13.67	3.45	84	71.8	56.7
6/24/2012	82	67.5	53		21.87	8.87	3.45	82.7	69.4	51.6
6/25/2012	84	73	62		27.62	6.53	0	84.3	73.3	63
6/26/2012	81	66.5	52		50.64	16.4	0	80.8	66.6	47.7
6/27/2012	76	63	50		43.73	18.22	0	75	59.9	44.2
6/28/2012	89	65.5	42		17.26	8.49	0	88	69.2	43.9
6/29/2012	89	70	51		32.22	9.78	0	87.1	72.1	48.8
6/30/2012	89	68	47		13.81	6.42	0	88	72.3	46.7
7/1/2012	82.9	69.4	55.9		29.92	9.46	0	82.9	70.3	55.3
7/2/2012	87	71	55		19.56	7.61	0	87.1	71.4	52.7
7/3/2012	86	70	54		46.03	15.11	0	84.9	71.4	55.8
7/4/2012	84	62.5	41		32.22	12.66	3.45	82.9	64.5	37.7
7/5/2012	80	62.5	45		14.96	4.7	0	79	65.1	42.5
7/6/2012	90	70	50	0.56	56.39	8.96	0	90	69.6	49.1
7/7/2012	94	73	52		14.96	6	0	93	73.3	52
7/8/2012	93	77	61		10.36	6.33	0	93	78.5	61
7/9/2012	98	77.5	57		24.17	6	0	97	81.9	61
7/10/2012	95	79.5	64		37.98	9.74	0	93	81.4	64.9
7/11/2012	94	76	58		18.41	7.63	3.45	93.9	77.5	56.8
7/12/2012	98	78.5	59		18.41	6.86	0	97	81.4	59
7/13/2012	91	75	59		17.26	7	0	90	76.4	60.1
7/14/2012	82	72.5	63	1.09	20.71	5.56	0	82.2	72	64.9
7/15/2012	85	72.5	60	0.1	43.73	8.44	0	82.9	70.9	62.6
7/16/2012	84	69	54		17.26	5.9	0	84	70.4	54.4
7/17/2012	87	74.5	62	0.26	24.17	5.62	0	84.9	72.7	63
7/18/2012	96	76.5	57		26.47	11.17	4.6	96.1	78.9	62.1
7/19/2012	97	77	57		19.56	6.53	0	96.1	79.5	57.7
7/20/2012	93	76	59	0.01	20.71	6.19	0	93	74.7	60.1
7/21/2012	92	75	58		37.98	11.6	3.45	91	74.9	56.8
7/22/2012	93	72	51		31.07	7.86	0	91	75	52
7/23/2012	94	76.5	59		37.98	14.96	4.6	93	80.1	64.9
7/24/2012	87	69	51		33.37	11.66	4.6	86	70.2	47.6
7/25/2012	84	66.5	49		24.17	7.48	0	84	68.4	47.8
7/26/2012	85	67.5	50		34.52	6	0	82.9	70.1	48.5
7/27/2012	91	71.5	52		28.77	6.9	0	90	71.5	53.1
7/28/2012	97	77	57		31.07	8.49	0	97	78.8	58.5
7/29/2012	93	73.5	54		13.81	7.15	0	91	75.4	57.2
7/30/2012	98	76.5	55		73.65	7.96	0	97	76.5	52.5
7/31/2012	93	75.5	58		10.36	5.87	0	93	75.3	57.7
8/1/2012	88	72	56	0.01	16.11	6.28	0	87.1	72.2	55
8/2/2012	84	66.5	49		35.67	12.52	4.6	82.9	67.1	49.2
8/3/2012	71	58.5	46	0.12	20.71	9.4	0	70	56.5	42.5
8/4/2012	84	65.5	47		11.51	6.53	0	82.9	65.5	42.5
9/22/2012	84	63.5	43		9.21	5.71	0	82.9	63.4	43.8
10/27/2012	37	31	25	0.05	9.21	5.22	0	33.8	25.4	19.1
4/1/2013	62	43	24		11.51	5.22	0	61	40.7	21.9
4/2/2013	72	49.5	27							
4/3/2013	58	47	36		26.47	10.74	0	56.1	44.9	33.4
4/4/2013	62	43	24	0.01	10.36	6.05	0	60.1	40.1	19.3
4/5/2013	64	52	40		41.43	18.7	9.21	64	48	35.6
4/6/2013	60	49	38		36.83	16.73	11.51	53.9	44.5	36.4
4/7/2013	50	38	26	0.18	31.07	10.55	0	66.2	33.4	16.8

4/8/2013	28	21	14	0.14	18.41	10.16	0	21.2	9.1	0.6
4/9/2013	34	21.5	9		10.36	5.56	0	28	16.4	-0.9
4/10/2013	60	42.5	25		36.83	14.96	9.21	53.3	35.4	15.6
4/11/2013	53	43	33	0.01	34.52	12.52	0	49.2	37.5	22.5
4/12/2013	49	39.5	30							
4/13/2013	53	40.5	28	0.01						
4/14/2013	31	26	21	0.03	36.83	18.99	9.21	17.7	13.3	9.2
4/15/2013	31	24.5	18	0.07	21.87	11.8	6.9	18.2	12.4	7.3
4/16/2013	31	24.5	18	0.09	20.71	7.86	0	26.6	15.5	7.9
4/17/2013	40	27.5	15	0.01	11.51	5.75	0	34.5	21.1	8.2
4/18/2013	56	40.5	25		23.02	12.37	0	51.1	32.8	14.2
4/19/2013	57	45	33		36.83	15.69	9.21	50.8	37.9	24.1
4/20/2013	62	44.5	27	0.12	52.94	17.6	8.06	60.1	40.4	16.1
4/21/2013	27	23.5	20	0.21	18.41	9.25	0	26.6	15	10.1
4/22/2013	35	22.5	10		10.36	6.13	0	29.8	17	5.1
4/23/2013	49	35	21		24.17	12.18	5.75	42.7	27.5	9.2
4/24/2013	59	43.5	28	0.09	36.83	14.05	0	53.2	36.4	18
4/25/2013	66	51.5	37		35.67	15.16	8.06	66	47.9	31.5
4/26/2013	72	55	38		35.67	16.2	9.21	71.7	53.4	31.8
4/27/2013	71	61	51		47.18	22.35	0	70	57.3	48.1
4/28/2013	64	54	44		40.28	17.26	3.45	64	49.4	41.6
4/29/2013	58	44	30		55.24	24.45	11.51	51.4	39.1	23
4/30/2013	39	30	21	0.04	27.62	10.55	0	29.3	22.5	15.2
5/1/2013	51	32	13		21.87	6.62	0	45	29.4	7.7
5/2/2013	67	48	29		32.22	13.38	5.75	64.9	42.7	19.3
5/3/2013	49	42	35	0.32	26.47	10.69	0	44.6	38.8	33.3
5/4/2013	58	47.5	37	0.09	24.17	6.28	0	53.1	43.2	31.5
5/5/2013	68	48.5	29							
5/6/2013	73	54	35		10.36	4.6	0	73.3	55.2	31.1
5/7/2013	74	56	38							
5/8/2013	73	52	31		11.51	5.85	0	73.4	53	26.2
5/9/2013	77	58	39		23.02	6.57	0	75	58.8	38.4
5/10/2013	67	54.5	42		42.58	11.95	0	66	52.6	38.2
5/11/2013	80	60	40		31.07	8.39	0	79	58.6	37.1
5/12/2013	83	66.5	50		34.52	13.04	5.75	81	67.4	48.1
5/13/2013	85	65.5	46							
5/14/2013	70	55	40		42.58	14.19	0	69.1	53.9	38.8
5/15/2013	68	50.5	33		10.36	4.94	0	66.9	53.4	34
5/16/2013	68	55	42		20.71	6.95	0	66	55.7	36.6
5/17/2013	65	50.5	36	0.1	14.96	6.66	0	63	48.9	31.6
5/18/2013	65	56	47	0.03	23.02	6.53	0	64	51.1	44.9
5/19/2013	54	50.5	47	0.21	13.81	8.58	3.45	51.6	46.8	41.4
5/20/2013	64	52.5	41	0.24						
5/21/2013	73	54	35							
5/22/2013	63	55	47	0.03	36.83	19.23	12.66	62.1	50.7	38.8
5/23/2013	54	48.5	43	0.22						
5/24/2013	65	53	41	0.01	43.73	14.76	3.45	64	47.4	34.9
5/25/2013	68	54	40		29.92	7.72	0	64.9	51.1	36.6
5/26/2013	70	51.5	33	0.24	29.92	4.6	0	68	52.5	29.3
5/27/2013	63	53	43		16.11	7.81	0	60.1	48.8	39.3
5/28/2013	63	51	39	0.09	16.11	6.33	0	62.1	50.8	39.2
5/29/2013	63	54.5	46	0.01	16.11	5.13	0	88.9	50.9	43.8
5/30/2013	55	51	47	0.58	17.26	8.21	0	52	46.4	41.4
5/31/2013	51	48	45	0.62	29.92	11.27	5.75	46.5	42.3	38.9
6/1/2013	68	54.5	41		11.51	6.66	0	66.9	53.4	36.6
6/2/2013	65	55	45	0.76	25.32	5.95	0	63	52.1	43.9
6/3/2013	48	44.5	41	0.75	37.98	12.81	0	44.6	39.3	36.7
6/4/2013	58	48	38	0.01	6.9	5.42	0	54.9	44.7	34
6/5/2013	73	55.5	38		11.51	6.42	0	73.9	56.4	34.5
6/6/2013	75	61	47		11.51	6.04	0	75.6	60.3	46.7
6/7/2013	79	65.5	52		37.98	13.14	5.75	79	66.4	52.2
6/8/2013	76	62.5	49		10.36	5.47	0	75.4	62.7	48.5
6/9/2013	81	63.5	46							
6/10/2013	76	57.5	39		23.02	7.8	0	75	58.8	34
6/11/2013	66	57.5	49		16.11	7.63	0	64	56.8	44.6
6/12/2013	73	64.5	56	0.25	11.51	5.35	0	76.1	58.7	41.1
6/13/2013	58	53.5	49	0.13	27.62	8.49	0	57	50.9	44.4
6/14/2013	65	55	45							
6/15/2013	75	59	43		26.47	10.02	0	73.9	58.5	38.5
6/16/2013	73	56.5	40		10.36	6.13	3.45	75.1	58.7	36.4
6/17/2013	80	62	44		17.26	6.38	0	78.6	64.9	44.8
6/18/2013	84	68.5	53		29.92	7.39	0	82	68.4	50.9
6/19/2013	74	62	50	0.37	48.33	8.91	0	76.6	58.9	44.9
6/20/2013	65	53.5	42							
6/21/2013	68	55	42	0.01	10.36	5.8	0	66.9	53.2	37.2
6/22/2013	70	55.5	41	0.06						

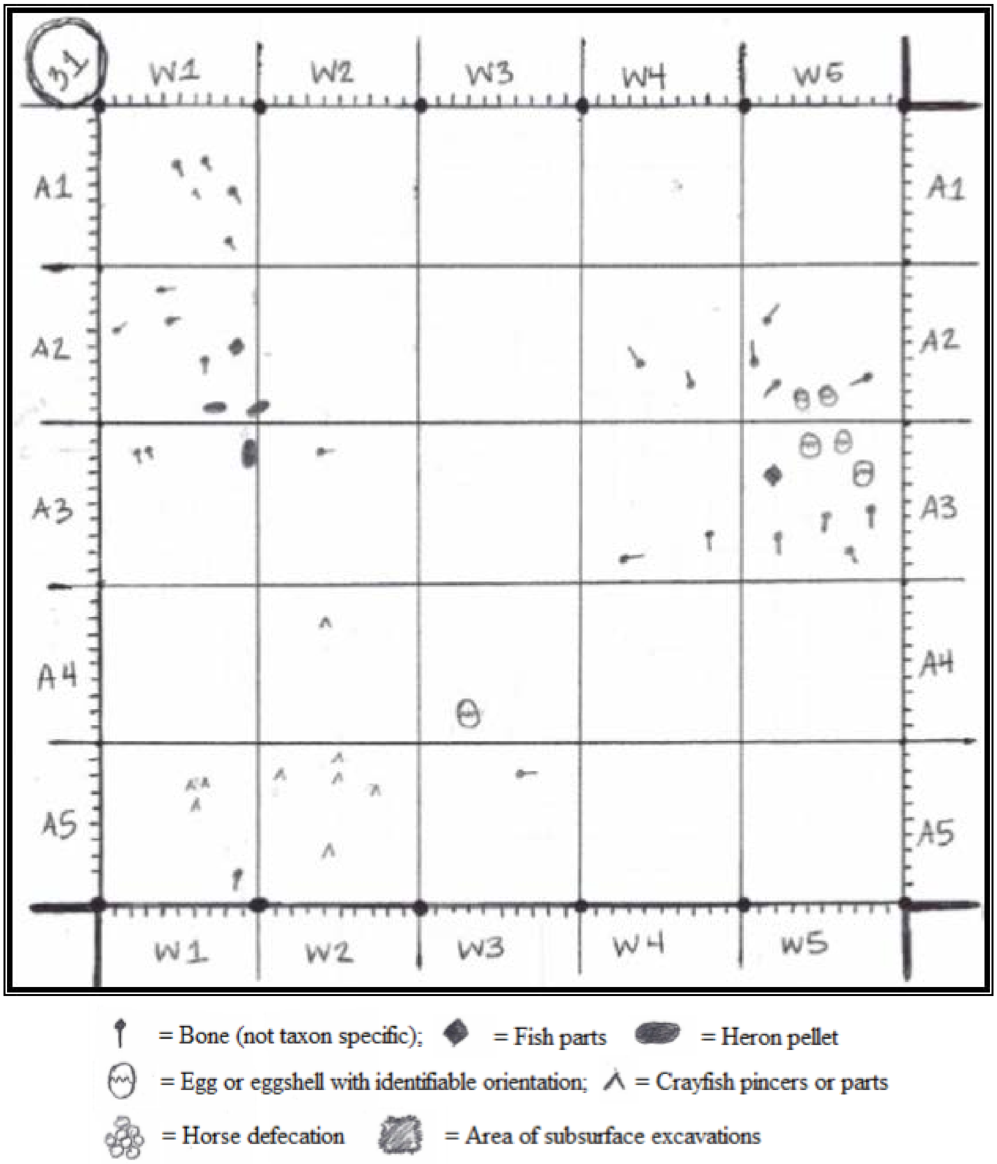
6/23/2013	75	59	43							
6/24/2013	78	64	50		10.36	4.56	0	78.1	64.7	49.2
6/25/2013	76	64.5	53	0.02	37.98	13.76	0	76	63.7	51.9
6/26/2013	79	65	51		35.67	15.01	6.9	78.1	64.2	48.4
6/27/2013	85	68.5	52		21.87	8.72	0	84	69	50.2
6/28/2013	88	68.5	49		21.87	7.63	0	88	71.6	47.2
6/29/2013	88	69.5	51		11.51	6.13	0	88	72.8	49.6
6/30/2013	90	74	58		12.66	6.04	0	88	75.7	60.1
7/1/2013	90	73.5	57							
7/2/2013	99	77.5	56		11.51	6.19	0	98.1	81.8	57.7
7/3/2013	98	81.5	65							
7/4/2013	91	76	61							
7/5/2013	80	66.5	53							
7/6/2013	75	60	45		17.26	7.24	3.45	76.1	63	44.2
7/7/2013	82	65	48							
7/8/2013	84	66.5	49	0.07	56.39	8.96	0	82.4	63.5	49.6
7/9/2013	82	64	46		12.66	5.18	0	82	65.4	44.3
7/10/2013	97	72.5	48		41.43	7.43	3.45	95	74.3	46.7
7/11/2013	91	74.5	58		37.98	12.85	3.45	90	76.8	57.7
7/12/2013	88	72	56	0.01	41.43	10.31	0	86	71	56.6
7/13/2013	78	64	50		25.32	8.44	0	75.9	64.7	49.6
7/14/2013	87	71.5	56		16.11	6.66	0	86	70.5	55
7/15/2013	96	74.5	53		40.28	15.73	9.21	96.1	75.7	52.5
7/16/2013	78	62.5	47		23.02	7.1	0	77.2	63.4	48
7/17/2013	92	73.5	55	0.14	44.88	5.9	0	90	70.2	54.9
7/18/2013	90	73.5	57		20.71	10.55	5.75	90	75.1	57.7
7/19/2013	91	71.5	52		25.32	9.25	5.75	90	74.3	51.2
7/20/2013	91	70.5	50		11.51	5.47	0	90	72.6	46.7
7/21/2013	89	70.5	52							
7/22/2013	91	70.5	50							
7/23/2013	88	68	48		20.71	7.05	0	87.1	70.3	43.5
7/24/2013	95	73.5	52							
7/25/2013	86	69.5	53							
7/26/2013	93	74	55		24.17	10.16	3.45	91.9	73.9	51.6
7/27/2013	93	72	51		29.92	9.11	0	91.9	73.7	50.5
7/28/2013	81	65.5	50	0.08	16.11	8.23	4.6	80.1	66.2	48.5
7/29/2013	69.1	59.5	50	0.15	24.17	7.16	0	68	56.9	46.3
7/30/2013	74	63	52		97.82	8.21	3.45	75.6	62.5	50.5
7/31/2013	86	66	46		20.71	7.83	0	84.9	67.5	46.9
8/1/2013	72	63	54	0.3	24.17	8.49	0	70	62.7	52.5
8/2/2013	74	64	54	0.43						
8/3/2013	74	60	46	0.07						
8/4/2013	82	64.5	47		18.41	5.75	0	81	65.7	46.5
8/5/2013	86	67.5	49	0.06	27.62	6.76	0	84.9	64.9	46.3
8/6/2013	84	65.5	47		20.71	7.34	0	82	65.9	45.9
8/7/2013	84	66	48		17.26	8.63	0	82.9	67.5	46.5
8/8/2013	81	65	49							
8/9/2013	81	66.5	52		10.36	6.38	0	79.1	65.2	49.2
8/10/2013	85	69.5	54		31.07	7.1	3.45	84	71.1	53.8
8/11/2013	80	68.5	57		8.06	4.6	0	78.7	69.5	56.4
8/12/2013	88	69.5	51							
8/13/2013	87	68.5	50	0.03						
8/14/2013	88	71	54							
8/15/2013	97	74.5	52		14.96	5.26	0	95	75.4	52.9
8/16/2013	101	77.5	54		37.98	7.72	0	100.9	76.8	54.9
8/17/2013	94	75.5	57		20.71	8.25	0	91	75.7	55.7
8/18/2013	92	73	54		33.37	9.74	0	91	75.2	53.3
8/19/2013	93	74.5	56							
8/20/2013	90	72.5	55		27.62	7.57	0	89.1	73.4	56.7
8/21/2013	82	64.5	47		12.66	6.25	0	81	65.7	46.7
8/22/2013	90	69.5	49		13.81	5.95	0	88	70.9	49.6
8/23/2013	90	77.5	65							
8/24/2013	90	74	58							
Criteria	**>90**		**<32**		**>30**					
Day the colony was visited										

APPENDIX B

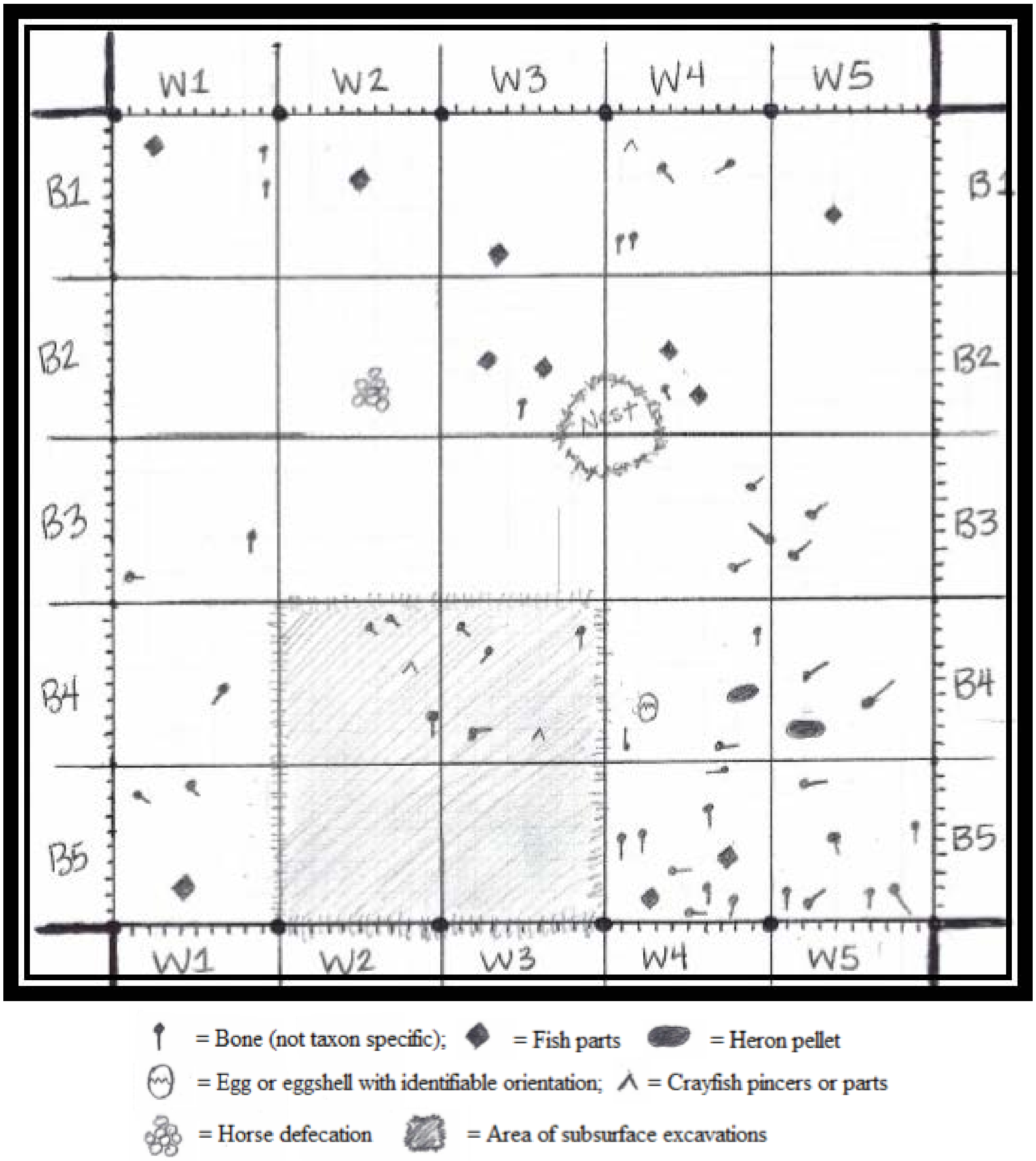
PLOT A-1 2013 MAPS

The base map used for this figure was taken from an aerial photo in Google Earth (2011). The right hand side plot map (A-I) was created using ArcGIS Explorer and coordinates taken with RTK methodologies from the Cascade Heron Colony. The dashed line indicates the plot which is magnified in the upper left hand corner. Each plot (5x5 m) is depicted with a flag and box. The upper left hand image is the plot representation of the biological material found in the plot during the time limited bi-weekly site visitations prior to the final site collection and subsurface excavations. Visitations were limited to minimize human disturbance on nesting herons.

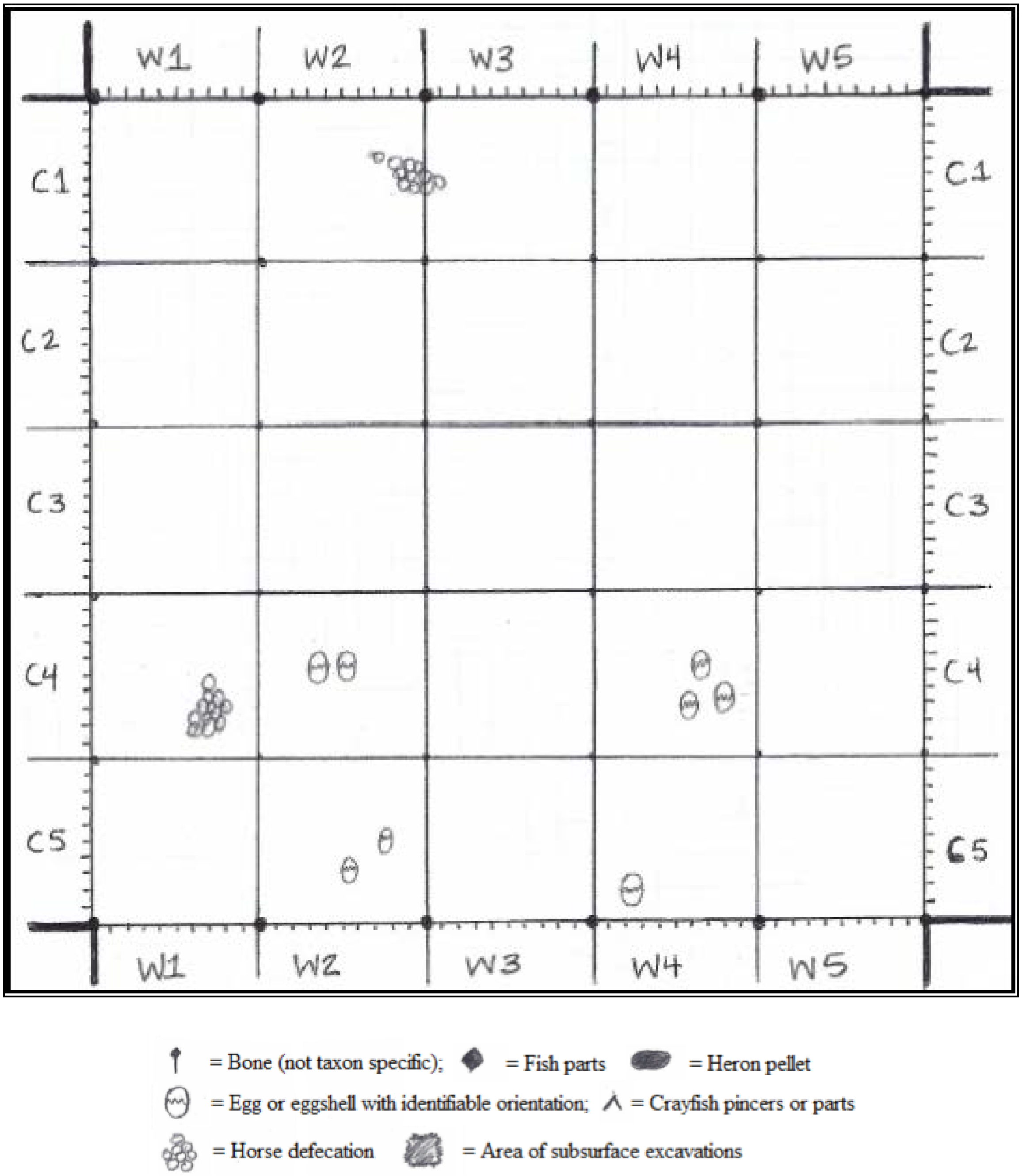
Plot A



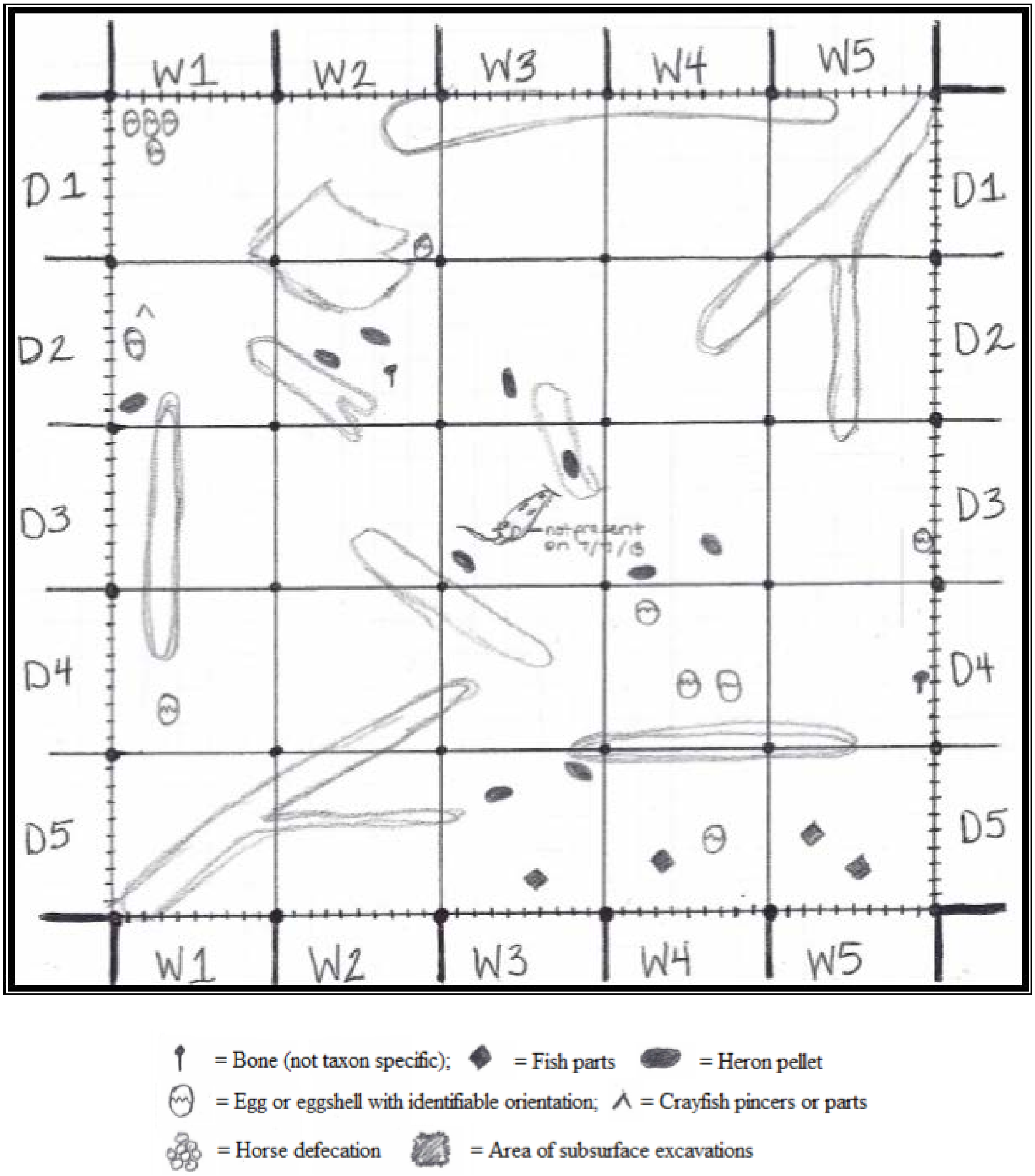
Plot B


W1
W2
W3
W4
W5
B1
B2
B3
B4
B5
Nest B
= Bone (not taxon specific);
= Fish parts
= Heron pellet
= Egg or eggshell with identifiable orientation;
= Crayfish pincers or parts
= Horse defecation
= Area of subsurface excavations

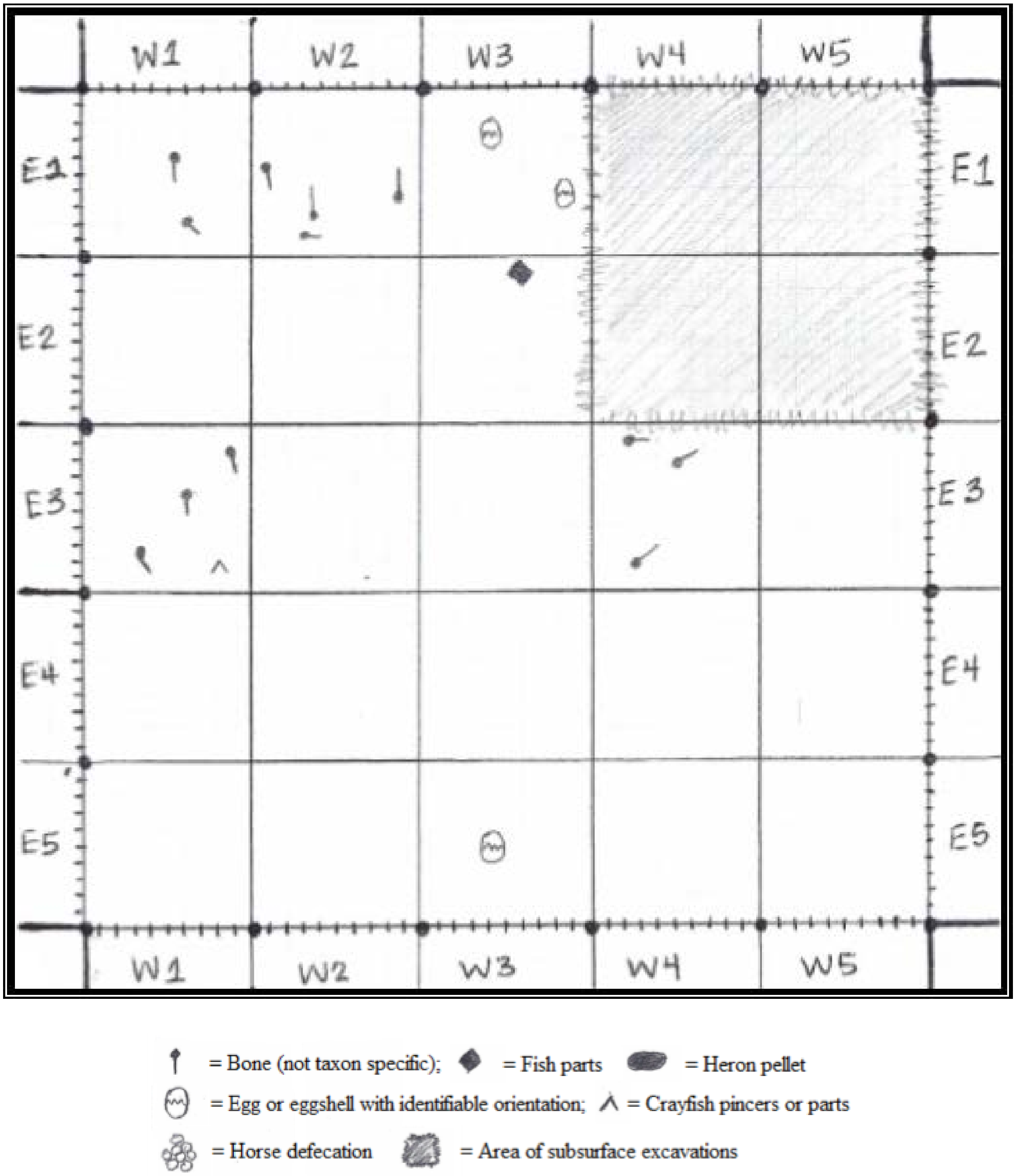
Plot C


W1
W2
W3
W4
W5
C1
C2
C3
C4
C5
= Bone (not taxon specific);
= Fish parts
= Heron pellet
= Egg or eggshell with identifiable orientation;
= Crayfish pincers or parts
= Horse defecation
= Area of subsurface excavations

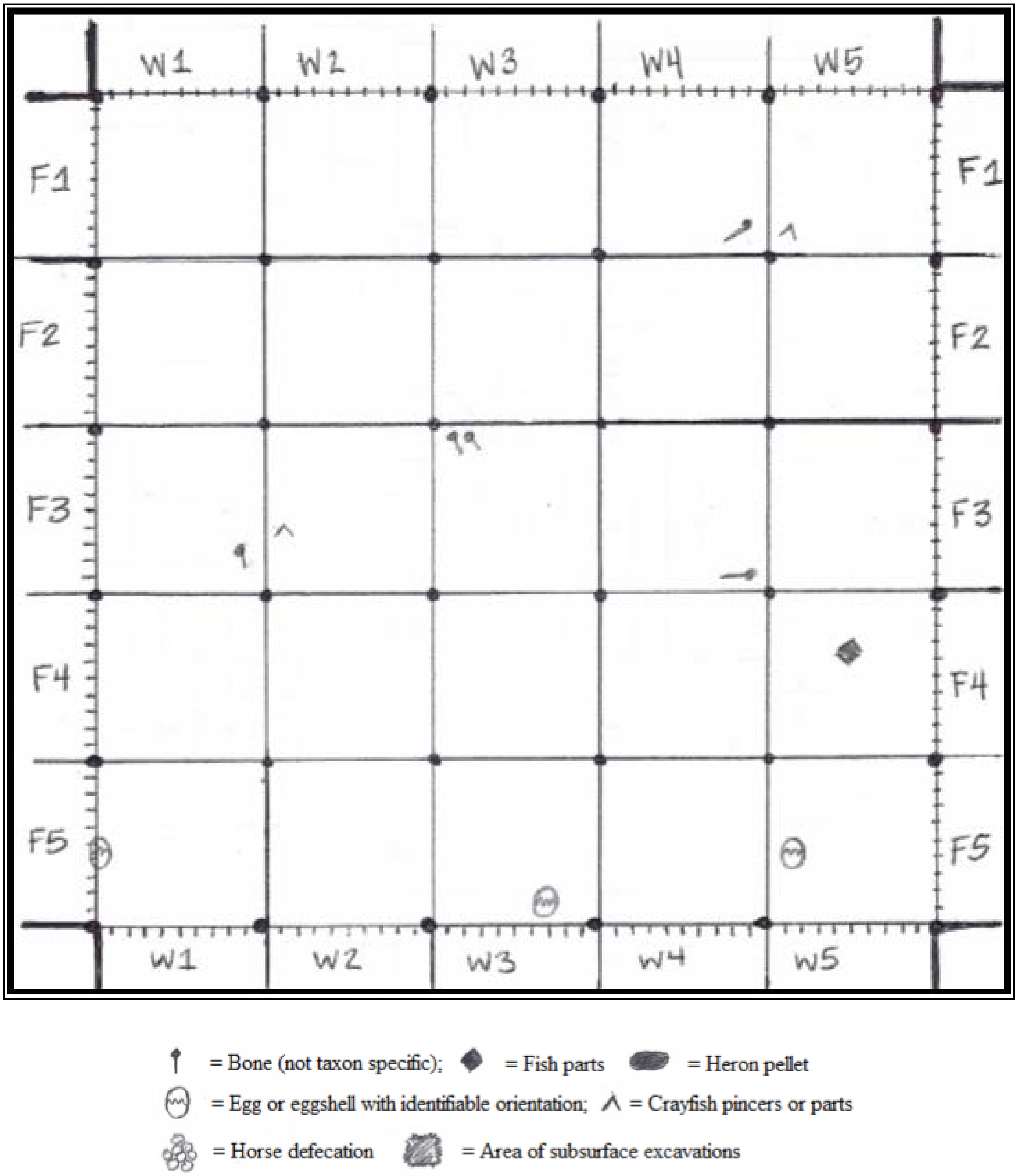
Plot D


W1
W2
W3
W4
W5
D1
D2
D3
D4
D5
not present on 7/13/13
= Bone (not taxon specific);
= Fish parts
= Heron pellet
= Egg or eggshell with identifiable orientation;
= Crayfish pincers or parts
= Horse defecation
= Area of subsurface excavations

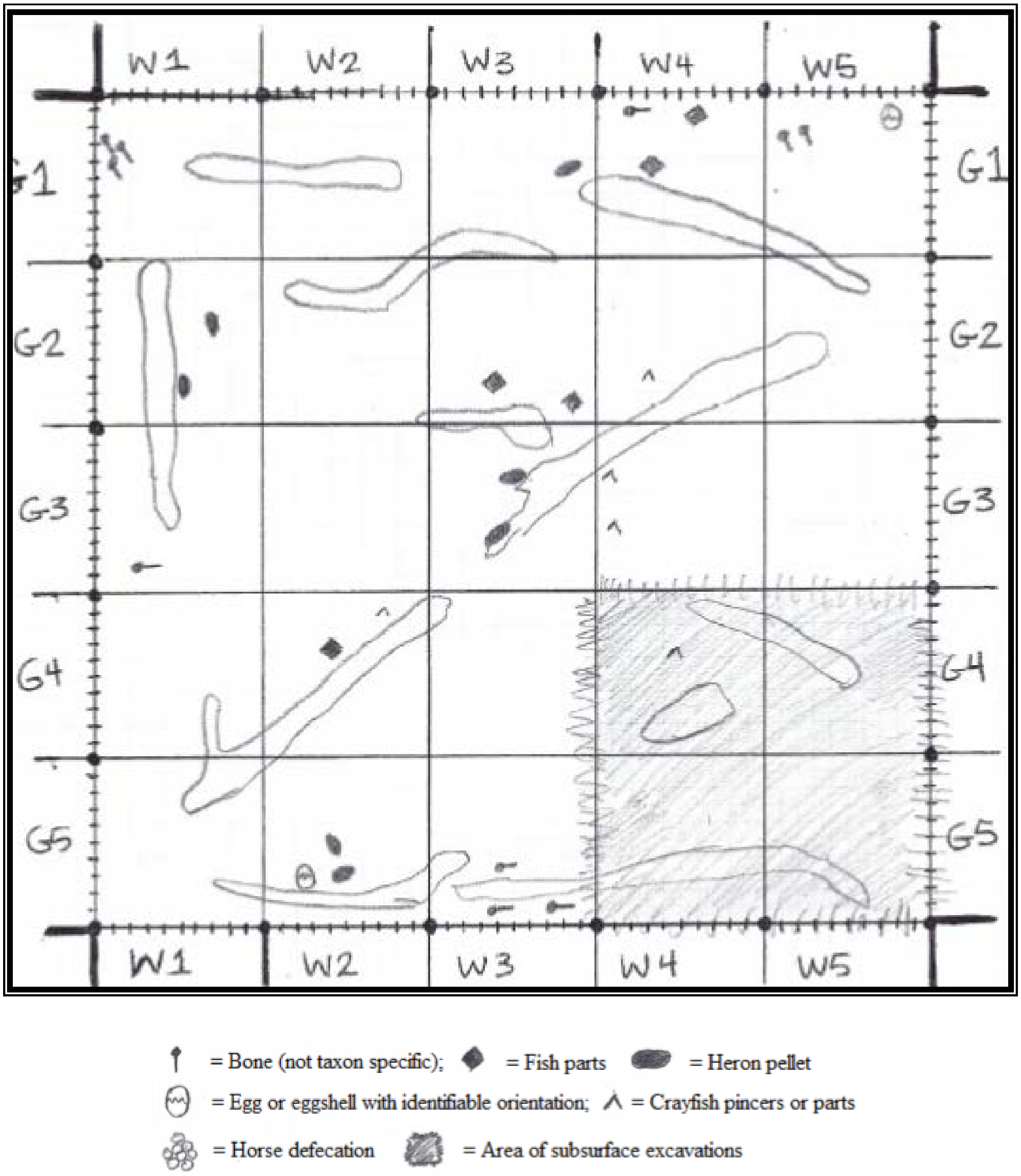
Plot E


W1
W2
W3
W4
W5
E1
E2
E3
E4
E5
= Bone (not taxon specific);
= Fish parts
= Heron pellet
= Egg or eggshell with identifiable orientation;
= Crayfish pincers or parts
= Horse defecation
= Area of subsurface excavations

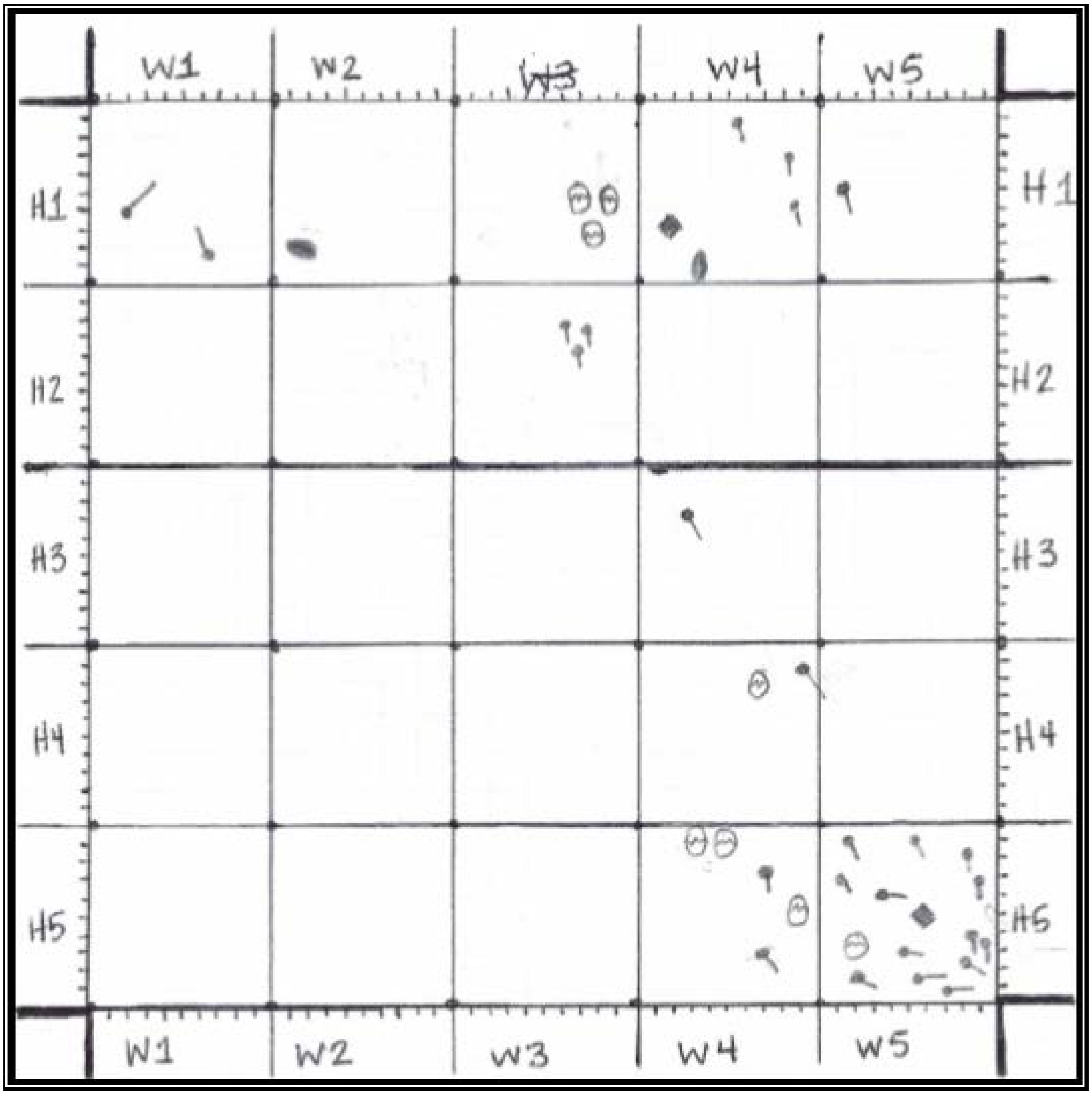
Plot F


W1
W2
W3
W4
W5
F1
F2
F3
F4
F5
F1
F2
F3
F4
F5
W1
W2
W3
W4
W5
= Bone (not taxon specific);
= Fish parts
= Heron pellet
= Egg or eggshell with identifiable orientation;
= Crayfish pincers or parts
= Horse defecation
= Area of subsurface excavations

Plot G


W1
W2
W3
W4
W5
G1
G2
G3
G4
G5
= Bone (not taxon specific);
= Fish parts
= Heron pellet
= Egg or eggshell with identifiable orientation;
= Crayfish pincers or parts
= Horse defecation
= Area of subsurface excavations

Plot H

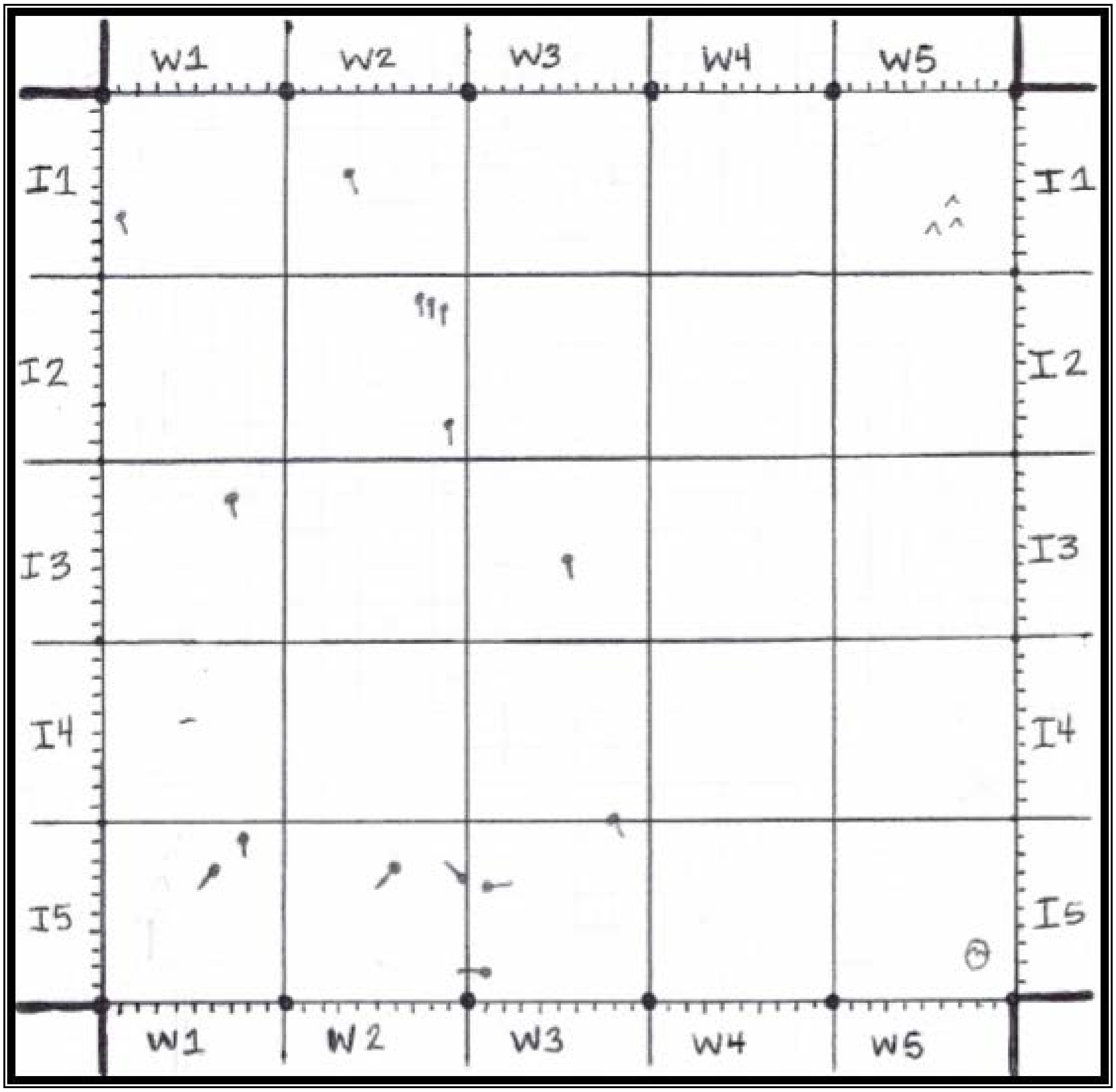


† = Bone (not taxon specific); ◆ = Fish parts ● = Heron pellet

○ = Egg or eggshell with identifiable orientation; ⋏ = Crayfish pincers or parts

⁂ = Horse defecation ▨ = Area of subsurface excavations

Plot I



† = Bone (not taxon specific); ◆ = Fish parts ⬬ = Heron pellet

◯ = Egg or eggshell with identifiable orientation; ⋀ = Crayfish pincers or parts

⁂ = Horse defecation ▨ = Area of subsurface excavations

APPENDIX C

COLONY 2012 & 2013 BIOLOGICAL MATERIAL PLOT REPRESENTATIONS

Element representation of the biological material found below the great blue heron nest from 2012 to 2013. All MNI are shown in italics with an asterisk. The question marks following taxa were suspected to be this taxon.

Plots	**A**		**C**		**E**		**G**		**H**		**I**		**B**	**D**	**F**				
Year	**2012**	**2013**	**2012**	**2013**	**2012**	**2013**	**2012**	**2013**	**2012**	**2013**	**2012**	**2013**	**2013**			**2012 NISP Total**	**2013 NISP Total**	**Total**	**Percent of Total (%)**
HERON	**121**	**49**	**76**	**2**	**76**	**75**	**48**	**202**	**61**	**30**	**23**	**12**	**154**	**5**	**0**	**405**	**529**	**934**	**52.24%**
CARPOMETACARPUS					3											**3**	**0**	**3**	**0.17%**
CLAW		1				1		2								**0**	**4**	**4**	**0.22%**
CORACOID	4	2	3		5	3	3	8	2	1		2	8	1		**17**	**25**	**42**	**2.35%**
CRANIUM	2		2		2		1	3	1		1		5			**9**	**8**	**17**	**0.95%**
CRANIUM?		2						1								**0**	**3**	**3**	**0.17%**
DIGIT	4	6			3	3		25		2		1	22	1		**7**	**60**	**67**	**3.75%**
FEMUR	6	1			5	5	8	5	1				13			**20**	**24**	**44**	**2.46%**
FIBULA	1				2	1	1	1								**4**	**2**	**6**	**0.34%**
FURCULA	1				1			1					2			**2**	**3**	**5**	**0.28%**
HUMERUS	3		1		3	1	2	4	5	1			4	1		**14**	**11**	**25**	**1.40%**
ILLIUM	4				1	4	1	10	3				6			**9**	**20**	**29**	**1.62%**
ISCHIUM						4		2					2			**0**	**8**	**8**	**0.45%**
MANDIBLE	4	8	3	2	1		3			2	3		4			**14**	**16**	**30**	**1.68%**
METACARPEL						2										**0**	**2**	**2**	**0.11%**
PARIETAL													2			**0**	**2**	**2**	**0.11%**
PATELLA								3								**0**	**3**	**3**	**0.17%**
PHALANX								1					1			**0**	**2**	**2**	**0.11%**
PUBIS	1		2			2		2	1							**4**	**4**	**8**	**0.45%**
PUBIS?								1								**0**	**1**	**1**	**0.06%**
QUADRATE	1					1		2								**1**	**3**	**4**	**0.22%**
RADIUS	3				3	1		1	2							**8**	**2**	**10**	**0.56%**
RIB	13	2	1			1		5	5	2	5		3	1		**24**	**14**	**38**	**2.13%**
RIB?								1								**0**	**1**	**1**	**0.06%**
SCAPULA	3				3		1	4		2			5			**7**	**11**	**18**	**1.01%**
STERNUM													1			**0**	**1**	**1**	**0.06%**
TARSAL								1					1			**0**	**2**	**2**	**0.11%**
TARSOMETATARSUS	4	3			1	5	3	9		3			13			**8**	**33**	**41**	**2.29%**

*TIBIA**	4	1	3		5	6	7	18	1	6			18		**20**	**49**	**69**	**3.86%**
ULNA	3		1		4	1	1	7	2		1		2		**12**	**10**	**22**	**1.23%**
UNIDENTIFABLE BONE	4	17	43		1	14			12	8	3	1	1	1	**63**	**42**	**105**	**5.87%**
VERTEBRAE	56	6	17		33	20	17	85	26	3	10	8	41		**159**	**163**	**322**	**18.01%**
HERON?						**1**		**34**					**17**		**0**	**52**	**52**	**2.91%**
FIBULA						1									**0**	**1**	**1**	**0.06%**
SCAPULA								1							**0**	**1**	**1**	**0.06%**
UNIDENTIFABLE BONE								33					16		**0**	**49**	**49**	**2.74%**
VERTEBRAE													1		**0**	**1**	**1**	**0.06%**
NONHERON		**3**				**5**		**2**							**0**	**10**	**10**	**0.56%**
UNIDENTIFABLE BONE		3						2							**0**	**5**	**5**	**0.28%**
CARPOMETACARPUS						1									**0**	**1**	**1**	**0.06%**
*FEMUR**						2									**0**	**2**	**2**	**0.11%**
MANUS						1									**0**	**1**	**1**	**0.06%**
TARSOMETATARSUS						1									**0**	**1**	**1**	**0.06%**
MAMMAL						**2**		**3**							**0**	**5**	**5**	**0.28%**
CALCANIUM						1									**0**	**1**	**1**	**0.06%**
*FEMUR**								1							**0**	**1**	**1**	**0.06%**
PELVIS						1									**0**	**1**	**1**	**0.06%**
UNIDENTIFABLE BONE								2							**0**	**2**	**2**	**0.11%**
RODENT	**5**	**26**				**14**	**4**	**4**	**13**				**5**	**2**	**22**	**51**	**73**	**4.08%**
CLAW								2					1		**0**	**3**	**3**	**0.17%**
*FEMUR**		3				4			2						**2**	**7**	**9**	**0.50%**
HUMERUS		1							1					1	**1**	**2**	**3**	**0.17%**
JAW		6							1					1	**1**	**7**	**8**	**0.45%**
MANDIBLE	2					5	3	1	1				1		**6**	**7**	**13**	**0.73%**
PELVIS		6													**0**	**6**	**6**	**0.34%**
RADIUS		2				2									**0**	**4**	**4**	**0.22%**
SCAPULA?						1									**0**	**1**	**1**	**0.06%**
TEETH		6				2		1	5						**5**	**9**	**14**	**0.78%**
TIBIA		2													**0**	**2**	**2**	**0.11%**
UNIDENTIFABLE BONE	3						1		3				3		**7**	**3**	**10**	**0.56%**
RODENT?		**3**													**0**	**3**	**3**	**0.17%**
JAW		3													**0**	**3**	**3**	**0.17%**

FISH	**5**	**9**	**37**	**2**	**2**	**43**	**32**	**69**	**105**		**128**	**1**	**44**	**7**		**309**	**175**	**484**	**27.07%**
JAW		1	3		2	4	1	5	7		4		4			**17**	**14**	**31**	**1.73%**
RIB			11			1							6			**11**	**7**	**18**	**1.01%**
UNIDENTIFABLE BONE	5	1				36	31	59	76		70	1	27			**182**	**124**	**306**	**17.11%**
VERTEBRAE		7	23	2		2		5	22		54		7	7		**99**	**30**	**129**	**7.21%**
FISH?								**11**								**0**	**11**	**11**	**0.62%**
JAW								1								**0**	**1**	**1**	**0.06%**
RIB?								10								**0**	**10**	**10**	**0.56%**
SNAKE							**34**				**21**					**55**	**0**	**55**	**3.08%**
VERTEBRAE							34				21					**55**	**0**	**55**	**3.08%**
CRAYFISH	**8**	**10**			**4**	**2**	**1**	**5**	**2**		**1**	**1**	**3**	**1**	**2**	**15**	**24**	**39**	**2.18%**
ABDOMEN					1											**1**	**0**	**1**	**0.06%**
ARMS		2														**0**	**2**	**2**	**0.11%**
CEPHALOTHORAX					1											**1**	**0**	**1**	**0.06%**
LEG	3															**3**	**0**	**3**	**0.17%**
*PINCER**	5	8			2	2	1	5	2			1	3	1	2	**10**	**22**	**32**	**1.79%**
GASTROPOD	**2**	**2**			**2**		**6**		**2**							**12**	**2**	**14**	**0.78%**
SHELL	2	2			2		6		2							**12**	**2**	**14**	**0.78%**
UNIDENTIFABLE		**22**				**49**	**2**		**25**		**5**	**1**		**4**		**32**	**76**	**108**	**6.04%**
UNIDENTIFABLE BONE		22				49	2		25		4	1		4		**31**	**76**	**107**	**5.98%**
VERTEBRAE											1					**1**	**0**	**1**	**0.06%**
Element by Plot Total	**141**	**124**	**113**	**4**	**84**	**191**	**127**	**330**	**208**	**30**	**177**	**15**	**223**	**19**	**2**	**850**	**938**	**1788**	**Overall Total**
Plot Total	**265**		**117**		**275**		**457**		**238**		**192**		**223**	**19**	**2**	**1788**			
Plot	**A**		**C**		**E**		**G**		**H**		**I**		**B**	**D**	**F**				

APPENDIX D

COLONY OVERALL BIOLOGICAL MATERIAL CHARACTERISTICS

Each survey type listed below was taken as a total of the materials found from 2012 to 2013. The Cascasde Heron Colony produced 2878 biological materials from all surveys combined. From the Intraplot and Extraplot surveys, 894 eggshell fragments were found. Not reported for the eggshells were the number of eggshell with indeterminable orientation. For example, the Intraplot small eggshells had 26 indeterminable fragments and in 2013, 20 eggshell fragments. For the Extraplot small eggshell investigations, there were 34 indeterminable fragments. From the bi-weekly, pellets and final site collections 980 biological materials were considered as Great blue heron prey. From the final site collection, 996 elements were considered as avian bones.

			ORIENTATION SURVEY				2012			2013			OVERALL REPRESENTATION		
REPORTING GROUP	**SURVEY TYPE**	**TAXA**	**CONCAVE UP (CU)**	**CONCAVE DOWN (CD)**	**INDETERMINABLE**	**OVERALL REPRESENTATION (2012 + 2013 DATA)**	**SUB-SURFACE**	**SURFACE**	**YEAR TOTAL**	**SUB-SURFACE**	**SURFACE**	**YEAR TOTAL**	**SUB-SURFACE TOTAL**	**SURFACE TOTAL**	**(2012 + 2013) TOTAL**
EGG & EGGSHELL SURVEY	**INTRAPLOT SMALL EGGSHELL**	**HERON**	**158**	**117**	**22**	**297**	**31**	**31**	**159**	**190**		**107**	**107**	**31**	**297**
	EXTRAPLOT EGGSHELL	**HERON**	**241**	**409**		**650**		**325**			**325**				**650**
	HATCHED SMALL EGGSHELL	HERON	148	352		500		273			227				500
	PREDATED SMALL EGGSHELL	HERON	5	30		35		6			29				35
	HATCHED LARGE EGGSHELLS	HERON	82	24		106		40			66				106
	PREDATED LARGE EGGSHELLS	HERON	6	3		9		6			3				9
NESTS	**FALLEN NESTS**	**HERON**	**5**	**3**		**8**		**7**			**1**				**8**
HERON PREY	**DISSECTED PELLETS**													**136**	**136**
		FISH												1	1
		INVERTEBRATE												26	26
		MAMMAL												109	109
	BI-WEEKLY HERON PREY													**52**	**52**
		CRAYFISH												21	21
		FISH												27	27
		RODENT												4	4
	FINAL COLLECTION NON-AVIAN BONE						**229**	**216**	**445**	**87**	**260**	**347**	**316**	**476**	**792**
		CRAYFISH						15	15	1	23	24	1	38	39
		FISH					189	120	309	49	126	175	238	246	484
		FISH?								11		11	11		11
		GASTROPOD					1	11	12		2	2	1	13	14

		MAMMAL					1	4	5	1	4	5
		RODENT		11	11	22	23	28	51	34	39	73
		RODENT?						3	3		3	3
		SNAKE			55	55					55	55
		UNIDENTIFABLE		28	4	32	2	74	76	30	78	108
AVIAN BONES	**FINAL COLLECTION AVIAN BONE**			**34**	**371**	**405**	**352**	**239**	**591**	**386**	**610**	**996**
		HERON		34	371	405	347	182	529	381	553	934
		HERON?					1	51	52	1	51	52
		NONHERON BIRD					4	6	10	4	6	10

APPENDIX E

FRAGILE VERSUS ROBUST ELEMENTS

There were 934 great blue heron bones that were found in the surface and subsurface. Of these surface and subsurface great blue heron bones several were treated as fragile or robust. These elements were reviewed for how frequently they occurred within the subsurface.

			Subsurface vs. Surface				Broken bones					
Element	**Bone Characteristic**	**Total #**	**Subsurface #**	**Subsurface %**	**Surface #**	**Surface %**	**Nonbroken #**	**Broken Total #**	**Broken Subsurface #**	**Broken Subsurface %**	**Broken Surface #**	**Broken Surface %**
CARPOMETACARPUS		3			3	100.00%		3			3	100.00%
CLAW		4	3	75.00%	1	25.00%	4					
CORACOID	Robust	42	19	45.24%	23	54.76%	23	19	3	15.79%	16	84.21%
CRANIUM	Fragile	17	2	11.76%	15	88.24%	8	9			9	100.00%
CRANIUM?		3	1	33.33%	2	66.67%	3					
DIGIT		67	48	71.64%	19	28.36%	59	8	1	12.50%	7	87.50%
FEMUR	Robust	44	21	47.73%	23	52.27%	20	24	6	25.00%	18	75.00%
FIBULA	Fragile	6	2	33.33%	4	66.67%	2	4	1	25.00%	3	75.00%
FURCULA	Fragile	5			5	100.00%	3	2			2	100.00%
HUMERUS	Robust	25	7	28.00%	18	72.00%	10	15	1	6.67%	14	93.33%
ILIUM	Robust	29	9	31.03%	20	68.97%	20	9	3	33.33%	6	66.67%
ISCHIUM	Robust	8	2	25.00%	6	75.00%	8					
MANDIBLE	Fragile	30	1	3.33%	29	96.67%	16	14			14	100.00%
METACARPEL		2			2	100.00%	2					
PARIETAL		2	1	50.00%	1	50.00%	2					
PATELLA		3	3	100.00%			3					
PHALANX		2			2	100.00%	2					
PUBIS	Robust	8	1	12.50%	7	87.50%	4	4	1	25.00%	3	75.00%
PUBIS?		1			1	100.00%	1					
QUADRATE		4			4	100.00%	3	1			1	100.00%
RADIUS	Fragile	10	2	20.00%	8	80.00%	1	9	1	11.11%	8	88.89%
RIB	Fragile	38	7	18.42%	31	81.58%	13	25	1	4.00%	24	96.00%
RIB?		1	1	100.00%			1					
SCAPULA	Fragile	18	9	50.00%	9	50.00%	11	7			7	100.00%
STERNUM	Fragile	1			1	100.00%	1					

TARSAL		2			2	100.00%	2					
TARSOMETATARSUS	ROBUST	41	26	63.41%	15	36.59%	29	12	5	41.67%	7	58.33%
TIBIA	ROBUST	69	38	55.07%	31	44.93%	44	25	8	32.00%	17	68.00%
ULNA	FRAGILE	22	5	22.73%	17	77.27%	9	13	2	15.38%	11	84.62%
UNIDENTIFABLE BONE		105	19	18.10%	86	81.90%	18	87	13	14.94%	74	85.06%
VERTEBRAE	ROBUST	322	154	47.83%	168	52.17%	127	195	49	25.13%	146	74.87%
OVERALL TOTAL		**934**	**381**	**40.79%**	**553**	**59.21%**	**449**	**485**	**95**	**19.59%**	**390**	**80.41%**