TAPHONOMIC ALTERATION OF AVIAN BONES: IMPLICATIONS FOR BIAS IN THE AVIAN FOSSIL RECORD

by

ELEANOR ELIZABETH GARDNER

(Under the Direction of Sally E. Walker)

ABSTRACT

Modern avian taphonomic studies provide information on disarticulation, weathering, and preservation potential, as well as how remains reflect paleoecology, paleoenvironment, and evolution. However, relatively little inquiry has been conducted in this field. A review of 130 articles shows that disarticulation, environment, and climate bias the avian record; sex and age are unstudied factors. Two taphonomic studies, one on skeletal disarticulation/loss and another on leg bone weathering/degradation, indicate biological processes impact survival of remains greatly; also, preservation potential may be higher in warm temperate versus subtropical/tropical climates. Temperature and humidity are the climate parameters with the greatest effect on leg bone mass loss. The results suggest the avian record is biased toward males. Age did not affect carcass disarticulation/loss, but juvenile leg bones weathered faster than adult bones, indicating possible age-based differential survivorship. A modified avian bone weathering profile stresses differences between patterns observed in semiarid savanna versus humid coastal settings.

INDEX WORDS: Avian, Taphonomy, Preservation, Bias, Weathering, Climate, Sex, Age, Depositional Environment

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DEDICATION

To

Lytt Gardner and Maria Edmondson

For being the most loving, encouraging, and helpful parents I could hope for

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INTRODUCTION AND LITERATURE REVIEW

Introduction and Objectives

Modern taphonomic studies are a crucial component of vertebrate paleobiology and have been employed extensively to develop a better understanding of the biostratinomy and diagenesis of vertebrate carcasses and bones (Shipman 1981; Lyman 1994). The majority of studies (both observational and experimental) have focused on mammalian remains (Brain 1967; Tappen and Peske 1970; Miller 1975; Behrensmeyer 1978; Haynes 1980, 1988; Von Endt and Ortner 1984; Andrews and Cook 1985; Lyman 1984, 1987; Tappen 1994; Crowther 2002; Trueman et al. 2004; Janjua and Rogers 2008; Todisco and Monchot 2008; Western and Behrensmeyer 2009; Fernández-Jalvo et al. 2010). Fewer modern taphonomic studies of avian carcasses and bones have been undertaken (Schäfer 1955, 1962, 1972; Bickart 1984; Oliver and Graham 1994; Davis 1997; Davis and Briggs 1998; Behrensmeyer et al. 2003; Cruz 2007, 2008). The facts that avian remains are frequently preserved in a wide range of paleontological and archaeological deposits (Bickart 1984; Olson 1985) and that avian bone tissue is structurally different from mammal bone tissue (Kaiser 2007; Dumont 2010) underscores the need for more comprehensive taphonomic studies on modern birds. Decay, disarticulation, scavenging, bioerosion, and weathering have been recorded for avian carcasses and bones, but the roles that climate, age, and sex play in biasing the preservation potential of avian remains have been essentially unknown. The purpose of this research is to identify preservational biases in the avian fossil record as documented in the literature and to test the impacts of these biases on avian bone preservation in modern taphonomic experiments. This should provide a more comprehensive view of potential biases affecting the avian fossil record, as well as offer future workers a foundation for more detailed analyses in modern avian taphonomy studies.

This research is unique because the birds used in the experiments are controlled: domestic chickens (*Gallus gallus domesticus*) with known diet, living conditions, sex, and age were utilized. Previous avian taphonomy experiments did not control for these factors. For example, Bickart (1984) killed wild doves and collected partially decayed gull carcasses from the beach for his study. Controlling for diet is especially important because diet strongly affects the composition of both the inorganic mineral portion and organic collagen portion of bone (Krueger and Sullivan 1984; Ambrose and Norr 1993); avian leg bone composition and strength appear to be particularly sensitive to diet (Orban et al. 1999; Wilson et al. 2001; Whitehead 2005). By controlling for diet and living conditions, the effects of sex and age on avian bone preservation potential can be tested with a higher level of confidence than otherwise might be the case.

Avian fossils and avian evolution have recently come to the forefront of popular and scientific inquiry in vertebrate paleontology. Modern avian taphonomic studies, in which observed degradational and/or preservational patterns are extrapolated to the paleontological and archaeological records, can provide a better understanding of the biases that may be affecting these records. Also, avian assemblages are increasingly used as indicators of paleoenvironment and paleoecology (Rasmussen et al. 1987; Baird 1989; Chevenal 1989; Behrensmeyer et al. 2003; Louchart et al. 2009; Prassack 2010). Additional work in the form of modern avian taphonomic studies is clearly needed in order to determine whether ancient avian remains preserved in various environments and climatic regions reflect their original ecological and environmental settings with reliable accuracy.

Thesis Structure

The research focus of the thesis progresses from a broad review of potential preservational biases in the avian fossil record to testing the sources of bias at a smaller, experimental level. Evidence for preservational biases in terms of depositional environments, climate regions, and skeletal elements is presented first (Chapter 2). The results from an experiment testing the roles of environmental (depositional setting and climate) and ecological parameters (sex and age) on avian carcass disarticulation and loss are also presented in Chapter 2. The chapter highlights the facts that sex and age have not been reported in the literature and that climate has not been carefully assessed as an important preservational force in the avian record. Next, the impact of the environmental and ecological parameters designated above on avian leg bone weathering, and on bone mass loss in particular, is examined (Chapter 3). The data support the theory that bone mass loss increases with higher air temperatures and relative humidity. The data indicate that sex and age are potentially important sources of bias in the preservation of avian remains. Avian bone weathering rates in humid coastal environments are also shown to progress slightly faster than those previously documented in semiarid savanna habitats. Finally, a summary of the conclusions drawn from this research is presented in Chapter 4.

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CHAPTER 2

PRESERVATIONAL BIAS IN THE AVIAN FOSSIL RECORD: A REVIEW AND A MODERN TAPHONOMIC FIELD STUDY[1]

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[1] Gardner, E.E. and S.E. Walker. Submitted to *Earth-Science Reviews*, 15 May 2010.

Abstract

Investigations into the avian fossil record have focused largely on the evolution and diversification of birds and on dinosaur-bird relationships. Comparatively little inquiry has been directed toward avian taphonomy and paleoecology, although understanding the impact of depositional environment, paleoclimate, and other ecological factors on the preservation of avian bones is essential for developing accurate insights into the avian fossil record. Inquiry into these areas should provide the foundations for a more robust understanding of avian taphonomy, paleoecology, and, consequently, bird evolution in relation to environmental change.

A review of 130 peer-reviewed articles describing avian fossils from the Late Jurassic to the Recent indicates the following: (1) most of the specimens comprising the avian fossil record are found in marine depositional environments, suggesting a taphonomic bias in favor of coastal marine birds; (2) the majority of those fossils are wing and leg bone elements rather than fully articulated skeletons; (3) sex and age are unstudied as preservational factors in the avian fossil record; (4) warm temperate climates have provided most of the bird fossil record; and, (5) climate has not been carefully assessed as a force shaping preservational bias within the avian fossil record. The last finding underscores the need for modern taphonomic experiments to better interpret the role of climate in bird bone preservation. To that end, a field study was conducted to investigate the weathering and degradation of age- and sex-grouped bird carcasses in three different depositional settings in two different climatic regions.

The goal of these field experiments was to gain insight into the role of environmental and paleoecological factors that affect avian preservation in two climatically different regions (warm temperate vs. subtropical). Results of the field study revealed that bird carcass disarticulation occurs within 12 months in both the subtropical and warm temperate sites in siliciclastic

lithologic settings. The carcasses in the subtropical climate experienced greater skeletal element loss than those in a warm temperate climate. Of the carcasses deployed in the subtropical climate, 66% were completely lost and the remaining 33% were poorly preserved; in the warm temperate climate, only 33% percent were lost and 25% of the remaining carcasses were relatively well preserved. Skeletal disarticulation and bone element loss was due mostly to scavenger activity. Because the subtropical region experienced more extensive biological activity than the warm temperate location, such activity may be overprinting the impact of climate on preservation. Additionally, male carcasses survived better than female carcasses, but age (juvenile vs. adult) did not appear to affect survival. The role of sex and age on bone preservation has not been previously evaluated; these factors, in addition to depositional environment and climate, need to be studied in more detail to fully understand the preservational biases that affect the avian fossil record.

Introduction

Storrs Olson, in his second chapter of *Avian Biology*, notes a common misconception among scientists that the hollow and lightweight nature of avian remains leads to their being rarely preserved in the fossil record (Olson, 1985). In fact, bird bones, although pneumatic, are relatively hearty; they are frequently heavier and denser than the bones of similarly sized mammals (Proctor and Lynch, 1993; Dumont, 2010). Bickart (1984) also reports the perception of several previous investigators that the fragility of bird bones limits the potential utility of detailed study of the avian fossil record (Matthew and Granger, 1917; Van Tyne and Berger, 1959; Rickleffs and Gill, 1980). However, both Olson and Bickart point out that avian remains not only make up a substantial portion of many fossil assemblages, but also are very well preserved in some localities and worth careful study.

One of the best recognized avian fossil localities in the world is the Jurassic Solnhofen limestone where *Archaeopteryx* was discovered (Owen, 1863). While the effectiveness of the carbonate Solnhofen deposits in the preservation of the primitive bird's bones is widely recognized, relatively little is known about the entire range of depositional environments in which avian fossils are preserved and how climate may influence skeletal-element destruction. Recent findings indicate that physical weathering processes are important in avian taphonomy and paleoecology (Behrensmeyer et al., 2003). However, climate-related differences in these physical weathering processes are not well documented. Taphonomic (preservational) studies are crucial for deciphering the avian fossilization process across different biogeographic and climatic settings.

This review of 130 scientific articles on the avian fossil record was undertaken to answer the following questions:

(1) Are certain depositional environments, such as the carbonate lagoons of *Archaeopteryx*, quintessentially important for bird fossil preservation, or have other environments also proved important in specimen preservation? What are the characteristics of environments that best facilitate avian fossilization?

(2) Is the bird fossil record built on complete skeletons or primarily on particular skeletal elements?

(3) Is the avian fossil record biased in terms of sex (i.e., male or female bones) or age (i.e., adult vs. juvenile bones)?

(4) Can the effects of climate on bone preservation be determined?

No experimental taphonomic studies of how environment, climate, sex, and age differentially affect bird carcass preservation are known. Our study seeks to investigate the destruction of age- and sex-grouped avian carcasses in two climatically different environments, to provide increased insights into the interplay of these factors.

Background

Avian taphonomy: a review

Taphonomy is the study of the "laws of burial" and all related processes which combine to move an organism from the biosphere to the lithosphere (Behrensmeyer and Hill, 1980). Recent fossil bird discoveries have sparked renewed interest in the taphonomy of avian carcasses, bones, and feathers. Taphonomic studies of modern birds can provide clues to the biological, physical, and mineralogical changes that bird elements undergo prior to fossilization, along with important paleoecological information. Such studies can aid in properly interpreting the existing avian fossil record. Over the past seven decades, only a small number of taphonomic studies of modern bird carcasses and individual bones have sought to investigate the decay, disarticulation, weathering, ecology, and overall preservation potential of avian fossil elements.

Avian carcass decay and disarticulation. – Schäfer conducted the first taphonomic studies of modern bird carcasses, those of the herring gull (*Larus argentatus*), in open sea off the Germanic coast of the North Sea (1955, 1962, 1972). From his investigations, Schäfer was able to describe the taphonomic sequence from the death of a gull to its final deposition. He found that carcasses tend to float for about a month, then sink with limited disarticulation, and finally rest on the seafloor, relatively intact, after approximately 60 days. Schäfer also briefly reported in 1972 on the process of drying/mummification and disarticulation of a few carcasses deployed on land.

Bickart (1984) studied the taphonomic effects of scavenging, transport, disarticulation, and decay on modern bird carcasses in a floodplain environment. He observed rock dove (*Columba livia*), ring-billed gull (*Larus delawarensis*), and herring gull (*Larus argentatus*) carcasses in both protected and unprotected conditions at his site in Baltimore County, Maryland, U.S.A. Bickart reported that unprotected carcasses were easily lost to scavengers and flooding events while carcasses that he had protected, using cages, became stuck to the ground and thus were not easily transported by floodwaters. Bickart also reported that while carcass disarticulation varied widely among the birds (from 13 days for juveniles to six months for large adults), evidence of bone weathering was nonexistent for the adult bones and minor for the juvenile bones.

Oliver and Graham (1994) documented the decay, disarticulation, and impact of scavengers on bird carcasses in an icy lake in Illinois, U.S.A. American coots (*Fulica americana*) were trapped in the lake as it froze over, dying and providing a unique natural taphonomic situation for observation. The researchers found that different scavengers left distinctive patterns of carcass dismemberment and bone damage. Mammal scavenging was concentrated on the hind limbs, with evidence of bone breakage and crushing, while avian scavenging was directed primarily to the head and neck, with little observed bone breakage. Scavenger-related actions and decay were important in the early stages of carcass disarticulation, but anatomical characteristics of the individual bird (the strength of various joints, muscle mass, etc.) determined later disarticulation.

Davis and Briggs (1998) examined taphonomic processes affecting bird carcasses in both swamp and shallow marine settings in south Florida, U.S.A. They deployed protected and unprotected carcasses from a variety of avian species (24 species, 23 genera from 13 orders) in brackish swamp waters in the Florida Everglades and in a marine bay site on Key Largo. They documented the influence of bacterial decay and scavenger-related taphonomic loss. They also described five morphological stages of degradation observed in the protected carcasses and three in the unprotected carcasses. Comparing their observed degradational stages to fossil birds from four famous avian Lagerstätten, Davis and Briggs found that their experiments closely mirrored the carcass configurations in three of the four fossil avifaunas.

Avian bone weathering and the need for further studies in avian taphonomy. – Physical weathering stages and paleoecological signs from modern bird and mammal bones, exposed subaerially in Amboseli National Park, Kenya, were analyzed by Behrensmeyer et al. (2003). Typically, the bird bones weathered more rapidly than did the mammal bones and could not be observed at the advanced weathering stages noted in the mammal samples. The Behrensmeyer et al. analysis indicated that larger-sized (body weight of 1.0-10 kg) bird species with robust skeletal elements were more likely to be preserved. They found that the avian bone remains presented a broadly accurate reflection of Amboseli’s living avifauna.

Cruz (2008) compared the taphonomy of a modern avian and mammal bone assemblage from southern Patagonia in South America to that of the Amboseli assemblage in Kenya. She observed that in Patagonia, as in Amboseli, bird bones underwent more rapid weathering than mammal bones. However, the Patagonian bird bones weathered faster than the Amboseli bird bones. The Patagonian avian assemblage was also biased toward small body size. Cruz attributed these taphonomic differences to the dissimilar influences of ecological community composition, as well as predator-prey/scavenger dynamics.

Considerable strides have been made in the field of avian taphonomy, from detailing avian carcass decay and disarticulation to profiling avian bone weathering and ecology. Previous investigators have contributed crucial taphonomic information applicable to the avian fossil record. These studies have covered a wide range of climates and environments. However, no comparative modern taphonomic studies of avian taphonomy have thus far been conducted to investigate the roles that varying climates (e.g., warm temperate, tropical, or cool temperate) may have on avian bone weathering, carcass disarticulation and loss, or the ecological factors that may affect avian fossil preservation. Studies that control for specific variables (e.g., climate, age, sex, or diet) will provide important information on preservational bias in the avian fossil record. Detailed examination of mineralogical and compositional changes in a variety of environments will be key for producing accurate diagenetic models and interpretations of the avian fossil record.

Data sources and methods

This review gathered data from 130 scientific articles on avian fossil remains based on seven descriptive criteria: (1) avian taxonomy, (2) skeletal elements, (3) site locality, (4) geologic age, (5) lithology (if specified), (6) depositional environment (if specified), and (7) climate (if specified). A total of 84 papers fulfilled these criteria. Depositional environment was not specified in 46 papers; in these cases, we looked up the fossil site locality, age, and geologic member/formation from other sources to determine the general depositional environment. Where climate was not specified, information for each region was collected from Christopher

Scotese's Paleomap Project (Scotese, 2002). Data were tallied based on the seven criteria and summed for species counts, skeletal elements, and climatic regions. Lithologic data were subdivided into four major rock groups (siliciclastic, carbonate, mixed siliciclastic-carbonate, or unknown). Sedimentary depositional environment data were grouped into three major environments (continental, transitional, marine) and then further subdivided into 15 different sub-environments (Table 2.1). All data are provided in Appendices A and B.

Marine environments were categorized into three settings: continental shelf, continental slope, and deep (abyssal) marine areas. Continental shelf environments include nearshore and subtidal areas along the edge of continents. They are relatively flat and shallow (less than 200m) and are exposed to waves and tides. Slope environments are relatively steep and deep (1000m and greater) declines that are seaward of the shelf edge. Deep abyssal environments are flat expanses of the deep (4000m) ocean floor.

The oldest paper we cite was published in 1841; the most recent ones were published in 2010. These articles report on avian fossils on all seven continents, in 35 different countries (Figure 2.1), and in 19 localities within the United States (Figure 2.2). The papers document avian fossils from the Late Jurassic to the Recent. Of the 130 papers, 27 (21%) document remains from the Eocene epoch and 68 (53%) document remains from the Miocene to Pleistocene epochs. The reviewed collection represents a large sample size of species, paleobiogeographic regions with associated climates, depositional environments, and geologic time.

Results

Avian evolution and a potential bias toward coastal marine birds in the fossil record

Since the unearthing of *Archaeopteryx* in 1861, the origin and evolution of birds has remained a hotly debated topic, one further fueled by more recent discoveries of additional Mesozoic bird species and feathered dinosaurs. Currently, two main camps of scientific opinion exist: those who consider birds to be direct descendants of theropod dinosaurs (e.g., Hu et al., 2009) and those who consider birds to have had an ancestor in common with dinosaurs, but to have evolved on their own separate path (e.g., Ruben, 2010). In this review, we consider *Archaeopteryx* to be the most ancient bird; it possesses a mosaic of characteristics, albeit primitive, that define the clade of birds. Thus, we follow the phylogenetic relationships presented by Chiappe and Dyke (2006). The majority of the avian fossil record that is covered in this review is composed of neornithine (modern) birds, with anseriform (duck-like) and pelecaniform (pelican-like) birds predominating. Shallow aquatic avian species, particularly diving anseriform species, are the fossils most commonly recovered. Based on these papers, there appears to be an overall taphonomic bias favoring a few orders of coastal marine birds, and this may be influencing our understanding of avian evolution. Although different avian groups appear to be preferentially preserved in different geologic time units (e.g., Mayr (2009) points out that terrestrial birds dominate the Paleogene fossil record), this review found that the overall avian record is biased toward coastal marine species.

Differential preservation of avian skeletal elements and developmental influences on avian bone taphonomy

Our review found that the three most commonly preserved avian skeletal elements across all depositional environments were, in order of abundance: the humerus, the tarsometatarsus, and the tibiotarsus (Figure 2.3). These bones are likely to have microstructural characteristics, such as greater density, which result in preferential preservation (Livingston, 1989). However, the influence of such characteristics on avian bone taphonomy is essentially unknown.

The impact of sex and age on avian fossil preservation has not been well studied in the literature either. Only four articles reviewed for this paper documented juvenile avian remains, and no articles listed the sex of the fossil bird specimens. This may be a result of difficulty in identifying these factors in fossil samples; nevertheless, both sex and age are potentially productive pieces of the avian fossil puzzle deserving of greater attention in future studies. To elucidate some of the possible taphonomic biases inherent in avian fossilization, a discussion of the varying developmental influences on bird bone preservation is warranted.

Avian bones are complex; they vary in structure by the age and sex of the bird, as well as by individual skeletal element. Thus, certain types of avian bones are more likely than others to be preserved in the fossil record. Avian bone, like that of all vertebrates, is composed of compact bone and cancellous bone (mostly restricted to the epiphyses). However, compared to mammals of similar size, birds have bones which are denser and more pneumatic (Dumont 2010). Like all vertebrates, the bones of birds undergo remodeling throughout their life spans. Passageways called Haversian canals and canaliculi develop as bone cells are grown, resorbed, and grown again (Currey 2002). After death and deposition of a carcass, bacteria, which are largely responsible for the bone fossilization process, use these avenues to progress through the tissue (Briggs, 2003). As they break down much of the organic matter, the bacteria can either actively or passively cause mineralization to occur, enabling preservation of the bone (Briggs, 2003). Cancellous bone is much more porous than compact bone, leading to decreased preservation potential because very porous bones are more likely to be crushed, damaged, or completely disintegrated, leading to decreased preservation potential.

The preservation potential of avian bones is not limited to compact versus cancellous bone tissue. Both forms of bone can be further subdivided into the following bone types:

(1) Woven bone – bone that is laid down quickly and is very porous and weak, with randomly oriented collagen fibrils and mineral associations; it is rapidly replaced with other bone types (Currey, 2002).

(2) Lamellar bone – bone that is laid down slowly and is relatively non-porous and strong, with precisely oriented collagen fibrils and mineral associations; it is the bone type of most adult bird bones (Currey, 2002).

(3) Fibrolamellar bone (also known as laminar or plexiform bone) – bone that consists of alternating layers of lamellar and woven bone, and is the bone type of most juvenile bird bones (Currey, 2002).

These types of bones have different densities and porosities, possibly causing differential preservation in the fossil record. Whether a particular bone type is present in a bird depends on its age and the growth rate of its individual skeletal elements. Infant bird bones grow very quickly, laying down woven and fibrolamellar bone; with age and slowing hydroxyapatite accretion rates, more and more lamellar bone is deposited (Currey, 2002). However, different skeletal elements have different accretion rates. Bones that grow rapidly for a long time have high accretion rates and tend to remain fibrolamellar, while those that grow slowly have low accretion rates and tend to be lamellar (Currey, 2002). For example, mallard duck humeri grow extremely fast, with high accretion rates, and are completely fibrolamellar for much of the duck's life; its phalanges, on the other hand, always appear to have low accretion rates and never display fibrolamellar bone structure (Castanet et al., 1996; Currey, 2002). Thus, differences in avian bone types may be at least partially responsible for differential preservation in the fossil record. Juvenile birds tend to have woven and fibrolamellar bone types, so their bones are more porous and may be subject to increased weathering and taphonomic loss. Adult bird bones, usually composed of the comparatively stronger lamellar bone type, may be more likely to survive taphonomic processes and therefore have better preservation potential in the fossil record. The humerus bone, despite being fibrolamellar in many avian species, may have the perfect combination of strength, porosity, and density that enables it to be preferentially preserved, which may explain its abundance in the fossil record.

Sex may also play a role in the preservation potential of avian bones. Females of reproductive age grow medullary tissue in their long bones for use in mobilizing calcium for eggshell production (Dacke et al., 1993). This leads to a net loss in calcium from the bones, which can cause female birds to develop osteoporosis at an early age (Rath et al., 2000). These reproductive stresses suggest that female bird bones may be less likely to survive in the fossil record compared to adult male bird bones. Since the sex of avian fossils has been unreported in the literature, this theoretical taphonomic bias has not yet been demonstrated empirically.

Developmental, metabolic, and reproductive factors are very likely to affect the taphonomic survival of avian remains. The porous nature of juvenile bird bones may place them at high risk for weathering and loss, while the depleted strength of adult female bird bones may increase their chances for taphonomic destruction. Thus, the avian fossil record may be biased toward adult males. More detailed study of the nature of different bird bones and their taphonomic advantages or disadvantages will be required for a more adequate future understanding of the role of these factors in the fossil record.

Environmental distribution of avian fossils biased toward marine settings, siliciclastic sediments, and warm temperate climates

Our review indicates that avian fossils are most frequently preserved in marine environments. Of the marine settings, continental shelves contain the most avian fossils and this preservational bias in the fossil record may be influencing our understanding of avian evolution. More avian fossils appear to be preserved in siliciclastic environments than in any other lithologic type, including carbonates. Climate also appears to play a substantial role in these preservational trends: avian fossils are preserved most frequently in environments with warm temperate climates. Past climate variation may thus have produced a distinct taphonomic bias in the avian fossil record, so that further study will be needed for more complete assessments in the future.

Avian fossils are found in a wide variety of depositional environments. – Living birds inhabit and frequent a wide variety of environments, so a keen understanding of those environments which best favor bird bone preservation is important for a clearer understanding of the avian fossil record. In this review, we found bird remains to be documented in 15 different depositional environments (Table 2.2 and Appendix B).

A large portion of the avian fossil record is derived from marine deposits. Of 1,537 total fossil bird specimens reported, 466 individual bones, one fully articulated skeleton, two partial articulated skeletons, 11 associated skeletons, and three dissociated skeletons were documented in marine sediments. Continental-shelf marine environments were reported as preserving the most bird fossils, with 455 individual bones, one articulated skeleton, two partial articulated skeletons, four associated skeletons, and three dissociated skeletons (Figure 2.4). Avian fossil material is also found in slope (9 bones and 7 associated skeletons) and deep (2 bones) marine environments.

Bird fossils are less frequently encountered in floodplain, fluvio-lacustrine, and lacustrine paleoenvironments. Floodplain environments preserved the second greatest number of bird fossils, with 243 individual bones (Table 2.2). Only weathered and fragmentary bones are preserved in floodplain environments, suggesting that long exposure times (which subject remains to scavenging and weathering) and fluvial- and flood-related processes may play a significant taphonomic role in the disarticulation and subsequent preservation of avian remains in those settings. Fluvio-lacustrine environments preserved the third-most number of avian fossils, with 233 individual bones and one associated skeleton (Table 2.2). Lacustrine settings contained the fourth greatest number of bird fossils, with 227 individual bones, eight fully articulated skeletons, 13 partial articulated skeletons, four associated skeletons, and one dissociated skeleton (Table 2.2). Lacustrine environments provided the best preservation (in terms of complete skeletons) due to their calm, anoxic bottom waters and fine sediment layers.

A taphonomic bias toward continental shelf marine environments exists in the avian fossil record, indicating that coastal shore birds and other marine birds that forage in shelf waters may make up the bulk of the avian fossil record. This might be related to the wide range of depositional settings in shelf environments and increased erosion in upshelf settings. The diversity of marine bird species that comprise shore and sea bird communities is also a strong contributing factor.

More avian remains are preserved in siliciclastic environments than carbonate. – The majority of avian fossils are found in siliciclastic sediments and environments: 63 of the analyzed papers described bird fossils from siliciclastic sediments, whereas only 22 papers described fossils from carbonate sediments (Figure 2.5); 18 papers documented avian fossils in mixed siliciclastic-carbonate settings, and 27 papers lacked adequate lithological information to identify geologic facies. Although Lagerstätten, or truly exceptional fossil deposits, of bird bones are frequently found in carbonate sediments (e.g., the Solnhofen, Germany, lagoon limestone; the Las Hoyas, Spain, lacustrine limestone; or the Nammoura, Lebanon, marine limestone), equally exceptional preservation can occur in siliciclastic Lagerstätten. For example, the siliciclastic lacustrine mudstones of Liaoning, China, have yielded exceptionally preserved specimens of the primitive bird, *Jeholornis prima*, along with numerous other birds and feathered dinosaurs (Zhou and Zhang, 2002). Articulated avian skeletons were also retrieved from the siliciclastic beds at the Messel pit in Hessen, Germany (Mayr, 1999a; 1999b; 2001), and from the biosilica diatomites of the Fur Formation in Jutland, Denmark (Dyke et al. 2004; Leonard et al., 2005). Other Lagerstätten occurring in siliciclastic-dominated environments include the lacustrine Florissant Formation in Colorado (Chandler, 1999) and the marine London Clay Formation of England (Dyke, 2001; Dyke and Cooper, 2000; Owen, 1841). Mixed siliciclastic-carbonate settings, like the lacustrine Green River Formation in Wyoming, Utah, and Colorado, have yielded Lagerstätten as well (Eastman, 1900; Mayr and Daniels, 2001; Wetmore, 1926a). However, it is important to note that siliciclastic sedimentary rocks are more abundant than carbonate sedimentary rocks, which partially influences the results reported here (Railsback, 1993).

Mode of preservation is also important to consider. Asphalt pits provide extraordinary preservation of original avian bone material. The asphalt pits at Rancho La Brea have yielded extremely high-quality preservation of many thousands of individual bird bone fossils (Howard, 1933). Saturation of the bones with the asphalt prevented biological decay and decomposition, so many of the bones are in near-original condition (Akersten et al., 1983). Other areas that are prime locations for exceptional preservation include low-energy siliciclastic and carbonate lacustrine facies. The siliciclastic lacustrine setting of Liaoning, China, proved to be perfect for the preservation of avian remains because of its quiet muddy waters and the occasional volcanic eruptions that would blanket the area in ash, slowing bacterial decay rates (Hou et al., 1995). Carbonate lacustrine settings, like the Las Hoyas limestones of Cuenca, Spain, have also been excellent areas for avian fossil preservation, due to the continuous accumulation of fine-grained carbonate sediments and anoxic bottom waters that prevent disarticulation and bacterial decay (Sanz et al., 1988). The majority of avian fossils, however, are not preserved under such exceptional circumstances. They endure scavenging, disarticulation, decay, and weathering in harsher settings before burial and mineralization. These taphonomic processes have thus far been relatively incompletely documented in their effects on the preservation of avian remains.

Climate: warm temperate climates house most of the avian fossil record. – Climate is a relevant, but relatively understudied, aspect of avian taphonomy. A region's temperature, humidity, precipitation, and soil pH can substantially influence diagenetic processes affecting the preservation of fossils (Lyman, 1994). Understanding the effects of these factors on modern bird bone taphonomy could provide important information about how ancient climates have influenced taphonomic bias in the avian fossil record. Unfortunately, in the articles we reviewed for this paper, climate is rarely discussed. When it is mentioned, it is presented only as background information relating to the fossil's depositional environment.

While modern avian taphonomy studies may reference climate, they seldom present climate as a parameter for study. For example, Bickart (1984) provided data on the climate of Baltimore County during his yearlong experiment, but did not relate that data to his results. He documented daily average precipitation and temperature in the floodplain setting for his study, but did not incorporate those elements into the study or relate them to the apparent lack of avian bone weathering.

Detailed investigations of how specific climate factors impact avian bone preservation are needed. This kind of work has been done for modern avian eggshells, as illustrated in a study conducted by Clayburn et al. (2004). They compared the effects of natural weathering to those of laboratory temperature- and pH-controlled weathering of eggshells from the modern glaucous-winged gull *(Larus glaucescens)*. Ambient temperature and sediment pH have been suggested as important variables for bone weathering (Lyman, 1994), which is why the Clayburn investigators tested the taphonomic effects of these factors on eggshell weathering. They found that increased temperature and acidity levels caused corrosion that was extensive and similar to the taphonomic effects on eggshells weathered naturally for up to 2 years on the sediment surface of a gull colony observed in Jefferson County, Washington, USA. Based on their experimental results, Clayburn and his colleagues proposed a classification scheme for the taphonomic stages of the avian (and thus dinosaurian) eggshell corrosion observed in the fossil record, thus linking environmental factors to preservation condition.

In the examined sample of published avian remains, we found that environments in warm temperate zones preserve the most avian fossils, while environments in cold temperate zones preserve the least (Figure 2.6). Subtropical and temperate environments preserve the second and third most avian fossils, respectively. Exceptional preservation of avian remains, however, occurs disproportionately in warm temperate regions compared to other climate zones. Interestingly, most of these warm temperate fossil localities are siliciclastic or biosilica in lithology.

Experimental work that investigates the role of climate in avian taphonomy is crucial for developing a more detailed comprehension of the elements involved in the preservation of avian remains. Future studies should examine the taphonomic impact of the specific climate-related factors of temperature, pH, moisture/humidity, and seasonality, on the weathering and degradation of avian bone. Furthermore, studies comparing the rates of avian carcass and bone degradation and weathering in different climates and environments are needed, so that we can better understand the range of settings that preserve avian fossils.

Field study in experimental avian taphonomy: does climate, age, or sex affect avian carcass weathering and degradation?

Field study introduction. - Our review indicates that coastal warm temperate siliciclastic depositional environments house the majority of the avian fossil record and that much of the best fossil preservation also occurs in these settings. We designed a yearlong experiment to test these perceptions. Our goal was to investigate the impact of climate, environment, age, and sex on avian carcass weathering and degradation in two distinct siliciclastic regions.

Field study materials and methods. – The carcasses and wings from twenty-four freshly-dead chickens (*Gallus gallus domesticus*) of known age, sex, diet, and living conditions were used to document disarticulation, bone weathering, and scavenger effects specific to each environment and climate. The birds were grouped into four categories (juvenile male, juvenile female, adult male, and adult female) to examine whether they would have distinct age- or sex-related taphonomic signatures. Since our review identified coastal depositional environments as containing the most avian fossils, we chose two coastal settings (marsh and dune), as well as and one lacustrine-like setting (freshwater pond) for our field sites in a warm temperate and a subtropical climate region.

The carcasses and wings were deployed in siliciclastic coastal and lacustrine habitats in three locations: Sapelo Island, Georgia; Rookery Bay, Florida; and Fort Myers, Florida, in May of 2008 (Figure 2.7). At Sapelo Island (warm temperate climate), experiments were placed in the following habitats: sandy dune, freshwater pond, and *Spartina*-covered saltwater marsh. At Rookery Bay (subtropical climate), experiments were deployed in a vegetated back-beach and a *Rhizophora mangle* mangrove marsh. In Fort Myers (subtropical climate), experiments were deployed in a temporary freshwater pond on the campus of Florida Gulf Coast University. The wings were removed from the carcasses at the glenohumeral joint for separate observation. The legs were removed for another taphonomic experiment, the results of which are not reported here. The carcasses and wings, protected by staked-down plastic crates, were positioned on the sediment surface.

Mass was determined based on a precision scale in grams. Climate data was gathered from the NOAA/NWS and NERRS meteorological databases. Sediment temperature was taken with a soil thermometer. Signs of decay, disarticulation, and physical weathering of the carcass and wing bones, along with descriptions of scavenging (bite/gnaw marks, tracks, scat, cage destruction) were reported by field associates at the sites during the first month after deployment. Investigator photographs, taken every two months for the yearlong period of the study, provided documentation of the condition of the deployed specimens. Non-parametric Wilcoxon Rank Sum tests, done in SAS version 8.2, were used to analyze the data. Data were log-transformed to manage unequal variation.

Field study results. – Warm temperate (coastal Georgia, USA): Carcasses and wings were deployed in a sandy dune, a saltwater marsh, and a freshwater pond on Sapelo Island, Georgia. Unlike either the dune or marsh site, no bone elements were present at the Georgia freshwater site after twelve months. At this site, the crates were all crushed, damaged, or overturned, very likely by juvenile alligators in the area (Figure 2.8). It appears that the bones in the freshwater pond suffered the same fate as several of Davis' and Briggs' (1998) birds which were deployed in similar aqueous sites: alligators may have eaten or buried the carcasses/wings. Therefore, we can present only the dune and salt marsh results here. (Subtropical Florida results are presented later.)

Carcasses and wings at the sandy dune were preserved in large numbers, along with feather remnants, compared with the marsh and freshwater localities (Table 2.3). After twelve months at the dune site, all carcass and wing bones were completely disarticulated and scattered on the sediment surface, except for the adult male carcass, which remained partially articulated (Figure 2.9). All of the bones became desiccated and relatively fragile. Application of the avian bone weathering stage classification of Behrensmeyer et al. (2003) indicates that, by the end of this experiment, the bones at the dune were in weathering stage 1.5-2 (Figure 2.10).

At the dune site, bone elements from the carcasses were preserved in greater numbers than wing bone elements (Table 2.3). Cervical vertebrae and ribs were the first and second most frequently recovered bone types. The juvenile male carcass retained the most bone elements of all the carcasses deployed at the site. The associated juvenile male wings also retained the most bones of all the wing sets deployed here.

Bone element loss is a reduction in the number of bone elements originally deployed. At the dune site, each carcass lost between 20-40% of its original number of elements (Table 2.3). Each set of wings lost between 15-30% of the original number of elements (Table 2.3). We attribute these losses to scavenging and disintegration.

Mass loss is a measurement of the difference between the weight at deployment and the weight of remaining material after 12 months of exposure. Mass loss was most directly affected by the removal and decay/loss of soft tissue. Soft tissue was completely gone after the first month of exposure; that loss is attributed to scavenging and decay. The individual bones themselves later lost mass due to intense weathering. Figure 2.11 shows the mass loss per avian carcass or wing set.

Evidence of dune scavengers included raccoon tracks and scat, along with cottonmouth snake sightings. Cottonmouth snakes in the southern U.S. are documented as scavengers who frequently eat carrion (Lillywhite and McCleary, 2008). One set of adult male wings was highly disturbed by scavenger activity – the meaty portion with bones was removed within 24 hours of deployment, leaving only a mass of strewn feathers.

In contrast to the comparatively well-preserved carcass and wing materials at the dune site, fewer bone elements and feather remnants were preserved at the marsh site on Sapelo Island. After twelve months in the marsh, all of the carcasses and wings were completely disarticulated except for the adult male carcass, which retained an articulating pelvic girdle and keel/sternum (Figure 2.12). All of the bones preserved at this site were covered in a thick layer of sulfur-rich marsh mud. According to Behrensmeyer’s physical weathering classification, the bones preserved at this site were in weathering stages 1 to 2 at the end of the twelve-month period (Figure 2.13).

As with the dune site, carcass bone elements at the marsh site were preserved in greater numbers than were wing elements (Table 2.3). However, the bone type recovered most frequently from the marsh site was the radius, a wing element. The adult male carcass retained the greatest number of bone elements of all the carcasses; it was preserved in the best condition of all the carcasses deployed at the Sapelo marsh site.

Each carcass deployed at the marsh site lost between 75-99% of all the original bone elements (Table 2.3). Wing element loss was similar: between 85-99% loss for each set of wings (Table 2.3). The high element loss percentages are attributed to intense scavenger activity.

Mass loss at the marsh site was similar to that at the dune site. The carcasses and wings lost the majority of their weight when scavengers removed the soft tissue within the first month of exposure. Later, the individual bones were affected by crab-related scavenging, which caused further mass loss. Figure 2.14 shows the amount of mass lost per carcass and wing set.

The bones preserved at the marsh site showed evidence of substantial scavenging. Mud crabs scratched the shafts and crushed the epiphyses of the bones. Fiddler crabs appeared to incorporate some of the smaller bone pieces into their burrows (Figure 2.15). Other evidence of scavenging included gnawing, raccoon sightings, and tracks around the experiments.

Subtropical (coastal Florida, USA): Carcasses and wings were deployed in a vegetated beach, a mangrove marsh, and a freshwater pond in subtropical Florida. At both the beach and mangrove marsh sites at Rookery Bay, no carcass or wing bones were preserved. Raccoon scavenging wrecked the beach site. The stakes holding down the crates were pulled up and the carcasses and wings were dragged away, evidenced by the fact that feather piles were found at separate locations around the area. Additional evidence of raccoons at the beach site included tracks, scat, and sightings. Humans also disturbed the site, indicated by the presence of beer bottles and cigarette butts. Tidal fluctuations and scavenger activity devastated the mangrove marsh site before the year of observation was concluded. Earlier in the experiment, at the six-month point, three bones from the adult male carcass were present in the mangrove marsh; they showed signs similar to those of wet-rot in timber and mud-crab scavenging marks were also observed on them. With the influx and outgo of the tide, those bones eventually washed and/or rotted completely away. Only the Florida freshwater site retained carcass bones throughout the twelve months of our study of subtropical sites; thus, only the results from that location can be presented.

At the freshwater pond in Fort Myers, Florida, various carcass and wing bone elements were preserved. The carcasses and wings were deployed on the silty substrate at the bottom of a temporary pond, which thereafter deepened through flooding to a depth of 6-7 feet for nine months of the twelve-month exposure time. All of the bones that remained at this site were well-preserved and in weathering stages 0 to 1 (Figure 2.16). The carcasses and wings were highly disarticulated. More carcass bone elements than wing elements were preserved at this location (Table 2.3). Cervical vertebrae and coracoids were the first and second bone types most frequently preserved at the site. The juvenile male carcass retained the most bone elements of all the carcasses deployed here; it also was the best preserved specimen at the site.

Bone element loss at the freshwater site was substantial. The wing bone elements were lost more rapidly than the carcass bone elements. Each carcass lost between 75-99% of its original elements. Each set of wings lost between 90-100% of their original bones (Table 2.3).

Mass loss at the Florida pond site occurred at a slower rate than at any of the sites in Georgia. It took longer (approximately two months) for the soft tissue to decay. Scavenging and weathering processes did not have as great an impact on the individual bones as at the Georgia sites. Figure 2.17 shows the mass loss per carcass and wing set at this site.

Tilapia lived in the temporary pond for nine months before evaporation of the water caused them to die. While they were alive, they probably consumed much of the decomposing soft tissue from the deployed chicken carcasses and wings. Tilapia have been shown to eat a wide variety of nutriment, including decomposing organic matter (Popma and Masser, 1999). The presence of alligators at the site was suggested by damage to three of the eight crates covering the carcasses; their accompanying stakes were missing or damaged. Since the area serves as a seasonal breeding ground for alligators, this seems reasonable as an explanation for the observed damage.

Can climate be separated from depositional environment and scavenger-related taphonomic signatures?. – Avian carcass and wing disarticulation and loss were widespread in both the warm temperate and subtropical climates. The main climatic difference between the regions during the year of study was average annual temperature: Sapelo Island was six to seven degrees cooler than Rookery Bay and Fort Myers (Table 2.4). Both regions received approximately the same amount of precipitation and had similar relative humidities (Table 2.4). Of the carcasses deployed in the subtropical climate, 66% were completely lost and the remaining 33% were poorly preserved (few bone elements remaining); in the warm temperate climate, only 33% percent were lost and of the remaining carcasses, 25% were relatively well preserved. Carcass bone element loss was much greater in the subtropical region, due mostly to a higher intensity of scavenger activity. A preservational bias in the avian fossil record in favor of warm temperate areas may be inferred from these observations, especially if scavenger activity is higher in subtropical habitats.

Both climate zones had similar carcass mass loss trends, however. There was no statistically significant difference in carcass mean mass loss between the climate regions (Wilcoxon test, p-value of 0.11). This indicates that soft tissue loss, primarily occurring during the initial month of exposure via scavenging and bacterial decay, is similar across the two climate regions. Additionally, it suggests that soft tissue loss may be overshadowing climate-specific weathering patterns. Later mass loss, attributed to physical weathering, may be too similar in these climate regions to see a significant difference. These results are most likely due to the similarity of the climates themselves, as indicated by the data in Table 2.4. In order to see significant differences in climate-related weathering patterns, future field experiments should be conducted in disparate climate regions (e.g., subtropical vs. cool temperate).

Although no differences in avian carcass mean mass loss could be discerned when the data were grouped by climate, mass loss did differ significantly among the dune/beach environments and the pond environments. When the carcass data was grouped according to depositional environment type, we found that the carcasses in the Georgia dune environment lost significantly less mean carcass mass than those in the Florida pond environment (p-value of 0.028). There were no significant differences between the Florida pond and Georgia marsh environment or the Georgia dune and Georgia marsh environments. Figure 2.18 shows the mean mass differences by environment. This is directly linked to the intensity of scavenger activity: the Georgia dune experienced less scavenger-related loss than the Florida pond, so the carcass mean mass loss was smaller.

In summary, the taphonomic disarticulation, loss, and weathering patterns of the experimental avian carcasses were similar in the warm temperate and subtropical climate zones. Carcass mean mass loss was not significantly different among the climates, but was among the individual dune and pond environments. Scavenger activity was greater in the Florida environments, indicated by the preservation of bone elements only in the pond environment. Additionally, the Florida pond setting very likely experienced greater scavenger activity (alligators) compared to the Georgia dune setting, explaining the significant difference in mean carcass mass loss between those sites. In this experiment's field locations, biological activity in each habitat may be overprinting climate-related taphonomic signatures. Future avian taphonomic experiments would benefit from comparing more disparate climates, as well as having meteorological data stations in each habitat.

Sex and age may affect taphonomic degradation of avian carcasses. – Sex and age did not significantly affect the mean mass loss of the carcasses (Wilcoxon test, p-value of 0.69). Any sex- or age-related taphonomic patterns may be overshadowed by the initial loss of soft tissue. Nevertheless, the best-preserved carcasses in each depositional environment were those of the males. In the Georgia marsh, the adult male carcass remained partially articulated, lost the fewest number of bone elements, and showed the least amount of physical weathering. In the Georgia dune, the adult male carcass remained partially articulated and the juvenile male carcass lost the fewest number of bones. The juvenile male carcass in the Florida pond also lost the fewest number of bone elements. This suggests that sex may well play a role in avian fossil preservation.

Our field experiment appears to, at least partially, support the taphonomic predictions about the influence of avian sex and age on preservation potential. Overall, adult male carcasses best survived the yearlong exposure period. Juvenile male carcasses also faired relatively well. Female carcasses, both juvenile and adult, experienced greater taphonomic damage and loss. Thus, the avian fossil record may be biased toward adult male birds. More detailed experiments focusing on these factors should be conducted in order to understand the possible biases in the avian record.

Discussion

Preservational biases in the avian fossil record

Preservational bias dominates the vertebrate fossil record and the avian record is no exception. Our review of the literature indicates that the majority of the avian record is preserved in siliciclastic facies. Aquatic (shallow marine, lacustrine, etc.) settings comprise most of these environments. Burial in fine-grained sediments also reduces biological and physical degradation, increasing the potential for fossilization. Compared to marine environments, lacustrine settings are more likely to preserve articulated skeletons because their waters are generally calm and undisturbed by wind, wave, and storm activity. We found that articulated avian skeletons, particularly anseriform species, are found in much greater numbers in lacustrine-type environments.

The largely fragmentary nature of the avian record is widely acknowledged, but the limitations in our understanding of the taphonomic processes affecting bird fossil preservation have not been fully explored. Although the avian record is based primarily on disarticulated skeletal elements, especially the humerus, tarsometatarsus, and tibiotarsus bones, why these particular wing and leg bones are preferentially preserved has not been effectively investigated. Archeological studies of avian skeletal element distribution have suggested several theories for the abundance of certain bones in natural assemblages (Bovy, 2002). These range from differential preservation due to greater bone density (Livingston, 1989; Lyman, 1984), to scavenger-specific damage (Oliver and Graham, 1994), to analytical collection-based bias (Crockford et al., 1997). The bone density theory has the greatest number of adherents, but very little data on bone density are known for most bird groups and few studies have produced solid support for this theory (Bovy, 2002). Investigations of avian bone density and microstructure in varying skeletal elements should yield insight into why the bird fossil record is dominated by certain elements.

The impact of age and/or sex on the preservational potential of avian skeletal elements is also poorly known. Only four articles noted juvenile remains, suggesting either the scarcity of these remains or that they are understudied. Bone density, porosity, and strength of skeletal elements could all be affected by whether the bones came from a male or female bird, thereby skewing the potential for preservation of male versus female bird bones. Thus, there may be an unrecognized sex-based taphonomic bias in the avian fossil record.

Lastly, our review found that environments in warm temperate climates contain the majority of avian fossils. Paleoclimate is an understudied factor in the taphonomy of bird fossils, and future studies need to address how climate affects the preservation of avian remains.

Experimental study implications

Our field study indicated that avian carcass and wing destruction is greater in subtropical climates than in warm temperate climates. The interconnectedness of climate, depositional environment, and biological activity, rather than climate alone, may be determinative. In each of the experimental field locations of our study, scavengers provided the initial and most substantial impact on carcass disarticulation and loss. In both climate regions, raccoons and crabs were the most damaging to the avian carcasses in the terrestrial settings, while in the aquatic settings, alligators were the most damaging. Taphonomic clues left on the bones by the raccoons included bite/gnaw marks; crabs left evidence of scratching and crushing. Alligator-related evidence included extensive damage to the protective crates and stakes.

Bone weathering varied substantially depending on the environment in which the bones from our study were exposed. At Sapelo Island, bones were preserved in both the salt marsh and the vegetated dune locations. The bones from the salt marsh were covered in mud and heavily degraded by mud-crab scavenging marks. The crabs tended to target the epiphyses of the bones and appeared to use them in building their burrows. Bones at the dune site were subject to high heat and frequent rain; this wet/dry pattern caused them to become desiccated, fragile, and cracked. In the Florida environments, bones were preserved only in the temporary freshwater pond. The bones which remained in the pond were covered by anoxic silt sediments and a thick layer of periphyton. This limited their exposure to oxygen and to wet/dry cycles, so those bones – initially black in color and slimy to touch upon collection – were in remarkably good condition. However, a significant difficulty was that of partitioning climate-based bone weathering from depositional-environment-based bone weathering. Having individual weather stations in each depositional environment could help to create more separation between localized climate and depositional environment.

Conclusions

In this review we found that marine shelf environments dominate the avian fossil record: 63 of the 84 papers with sufficient lithlogical information described bird fossils from siliciclastic environments; only 22 papers described fossils from carbonate sediments. Wing and leg bones dominate the fossils reported in the papers we reviewed. Age was not studied enough in these papers to allow us to draw any conclusion as to its potential function in avian bone preservation and the sex of bird fossils was not reported in any of the papers. Climate plays a relatively unknown role in the preservation of avian fossils, since the majority of their record is housed in environments from warm temperate climate zones.

Our field study indicates that avian carcass disarticulation occurs rapidly within 12 months in both subtropical and warm temperate climates, but that carcasses in subtropical climates experience greater taphonomic loss. Of the carcasses deployed in the subtropical climate, 66% were completely lost and the remaining 33% were poorly preserved; in the warm temperate climate, only 33% percent were lost and 25% of the remaining carcasses were relatively well preserved. Scavengers played a primary role in the taphonomic damage and loss of avian skeletal elements; thus, scavenging may be overprinting climate- and depositional-environment-based weathering. Overall, the terrestrial site in warm temperate Georgia contained the greatest number of skeletal elements after a yearlong period of exposure, despite showing the most physical weathering. Thus, avian bone element preservation may be favored in warm temperate siliciclastic settings with few scavengers.

There is some evidence for a sex-based bias in the results of our study. In all environments, the adult and juvenile male carcasses fared much better than either the adult or juvenile female carcasses. This indicates that female carcasses may be more likely to become weathered and lost, while the more robust physical characteristics of male carcasses increase their chances of being preserved in the fossil record. Small sample size, however, limits our ability to make any definitive statement as to the role of sex in the survival of avian bone elements. Age did not appear to play a role in our results, which was surprising.

More studies examining the effects of climate on modern bird bone taphonomy could provide essential data about how ancient climates have influenced taphonomic bias in the avian fossil record. Further taphonomic studies on modern avian remains are needed to develop a more detailed understanding of the avian fossil record and the physical, scavenger-related, and diagenetic processes affecting the preservation of bird bones. Future investigations should examine taphonomic processes in a variety of paleobiogeographical settings, document the weathering stages bird bones undergo in a wide array of depositional environments, and investigate the important, but so far relatively understudied, biogeochemical aspects of bird bone preservation.

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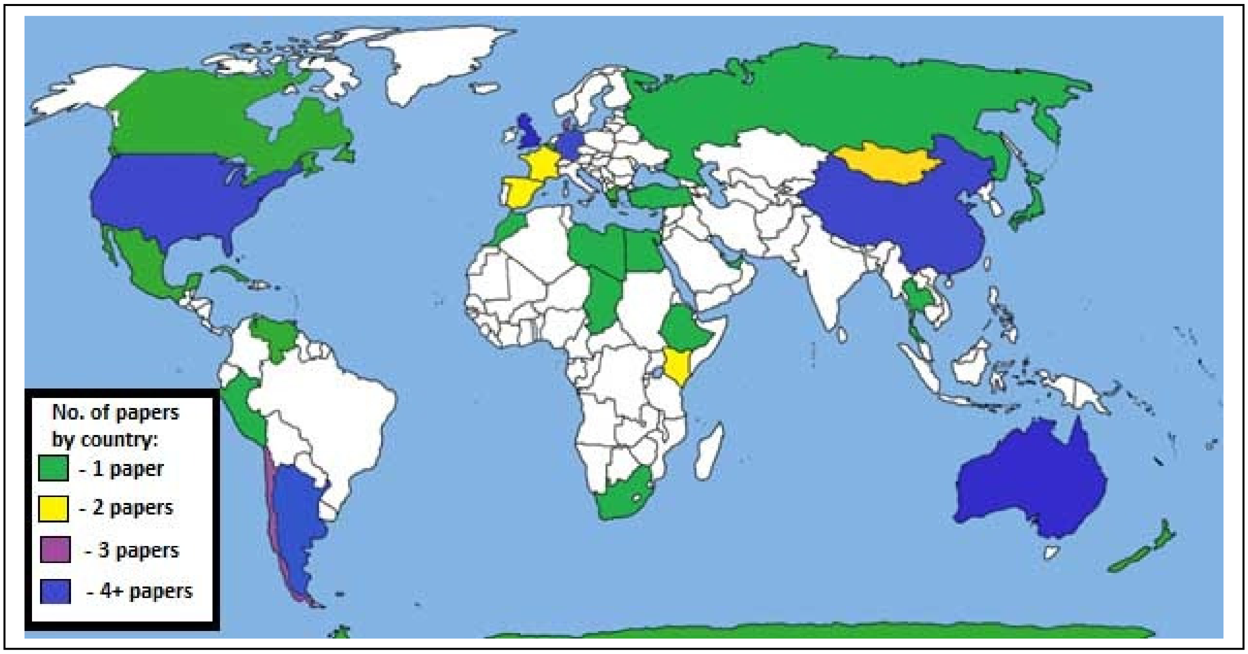

Figure 2.1 - World map indicating where fossil avian remains were documented. Different colors represent the number of papers from each country. See Appendix A for site information and references. (Modified from Brimelow, 2006.)

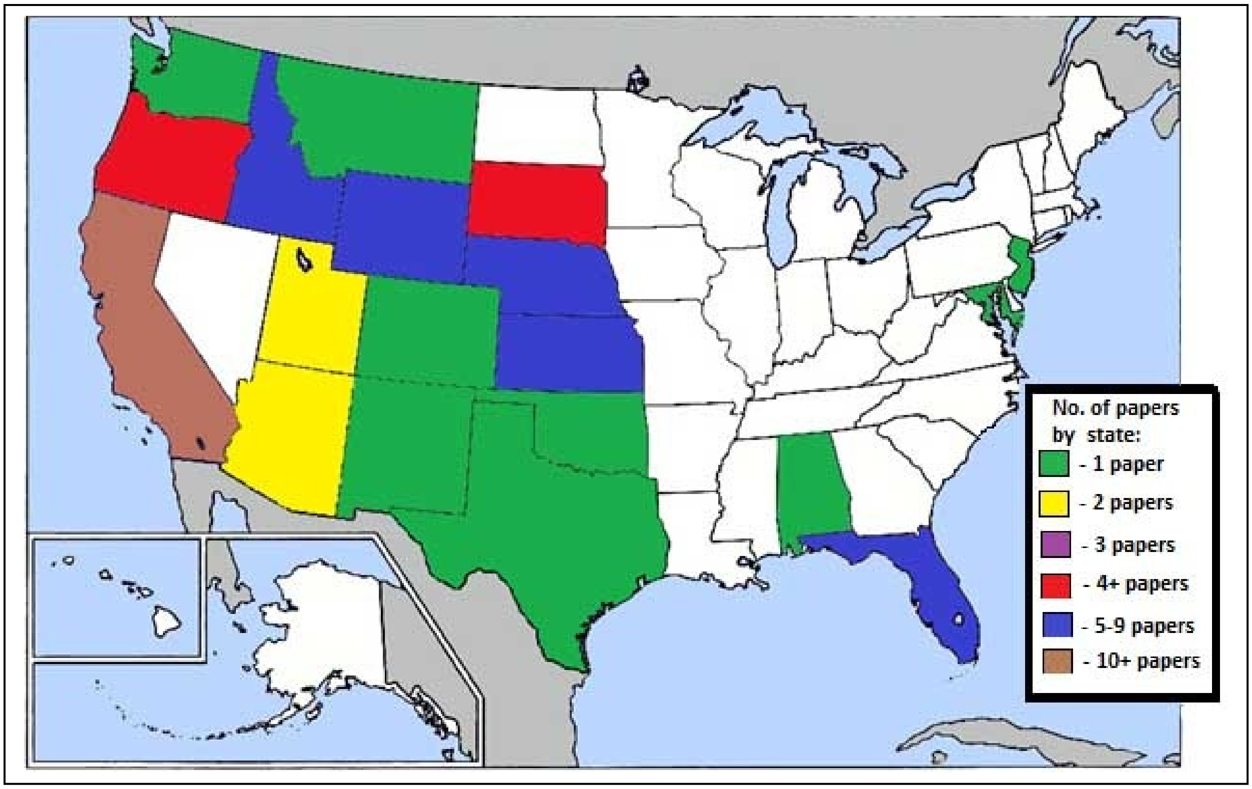

Figure 2.2 - United States map showing where fossil avian remains were documented. Different colors indicate the number of papers from each state. See Appendix A for site information and references. (Map courtesy of the University of Texas Libraries, The University of Texas at Austin.)

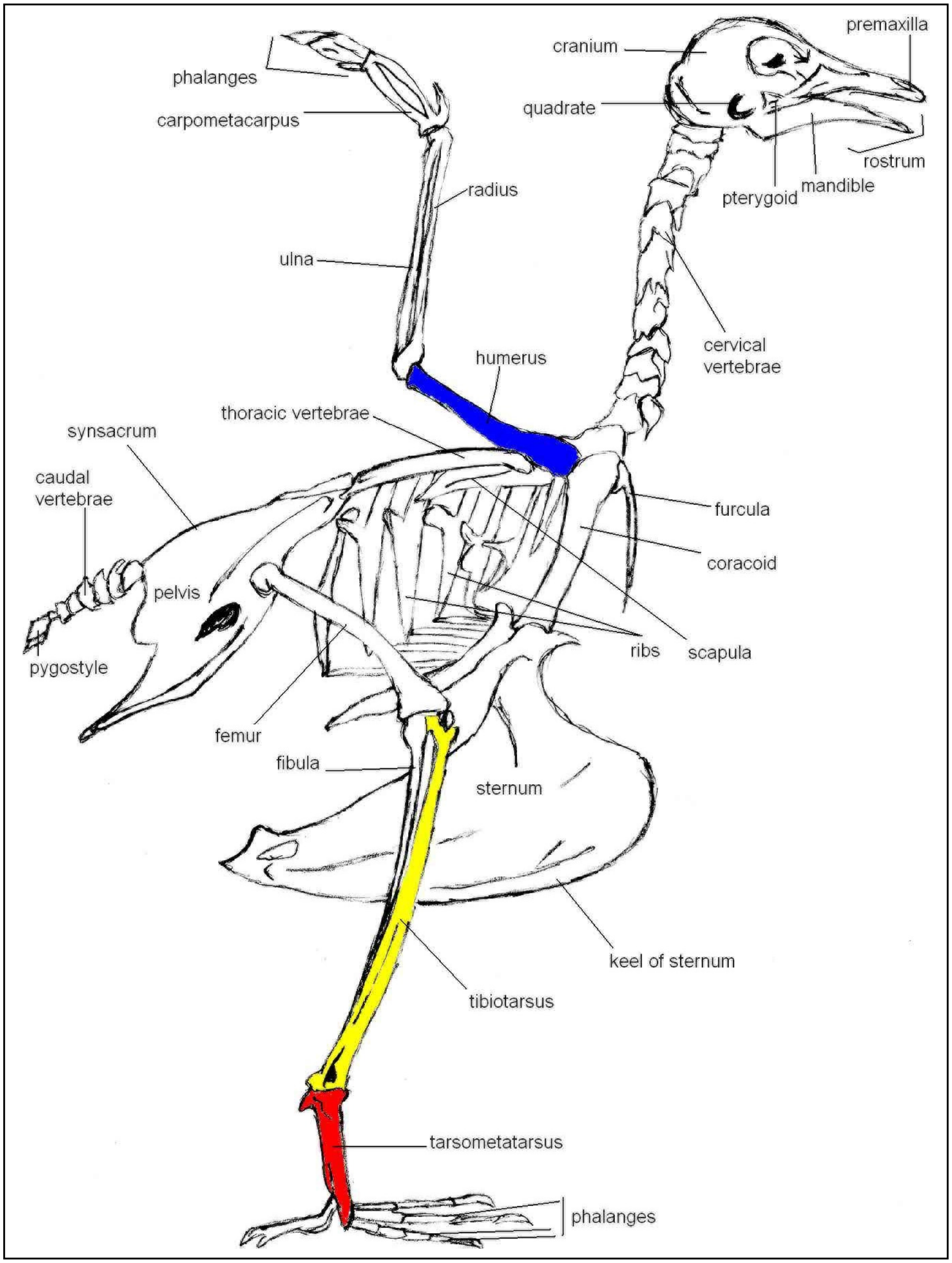

Figure 2.3 - Generalized bird skeleton. The bone types documented in the reviewed papers are indicated. The humerus, tarsometatarsus, and tibiotarsus are the three most abundant avian bone elements preserved in the fossil record. Blue = most abundant (239), red = second most abundant (192), and yellow = third most abundant (175). (Adapted from Proctor and Lynch, 1993.)

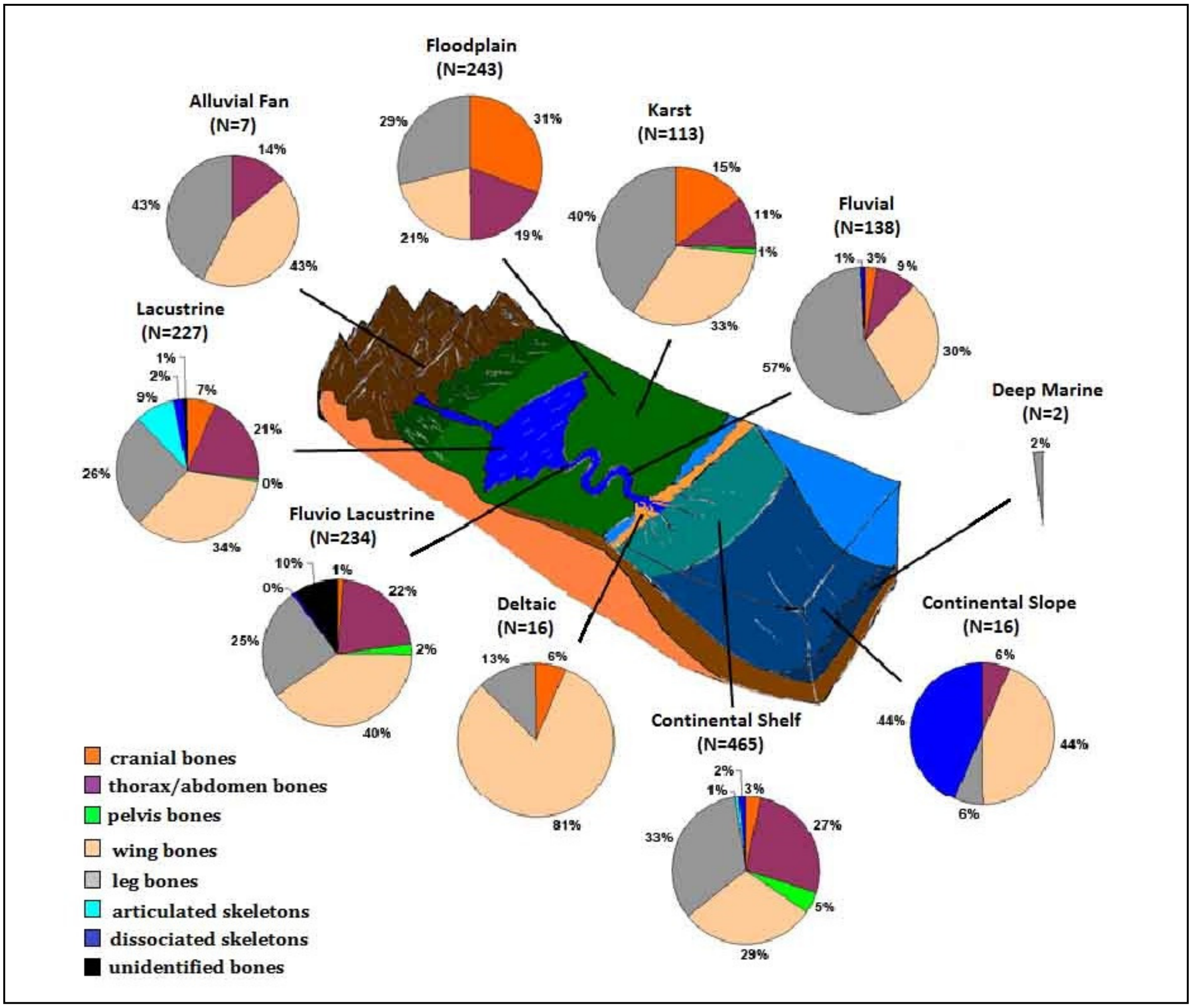

Figure 2.4 - Schematic of ten depositional environments which preserve most of the avian fossil record. Each environment has an associated pie chart showing the percentage of skeletal elements preserved there. See Appendix B. (Center graphic adapted from Press and Siever, 1986.)

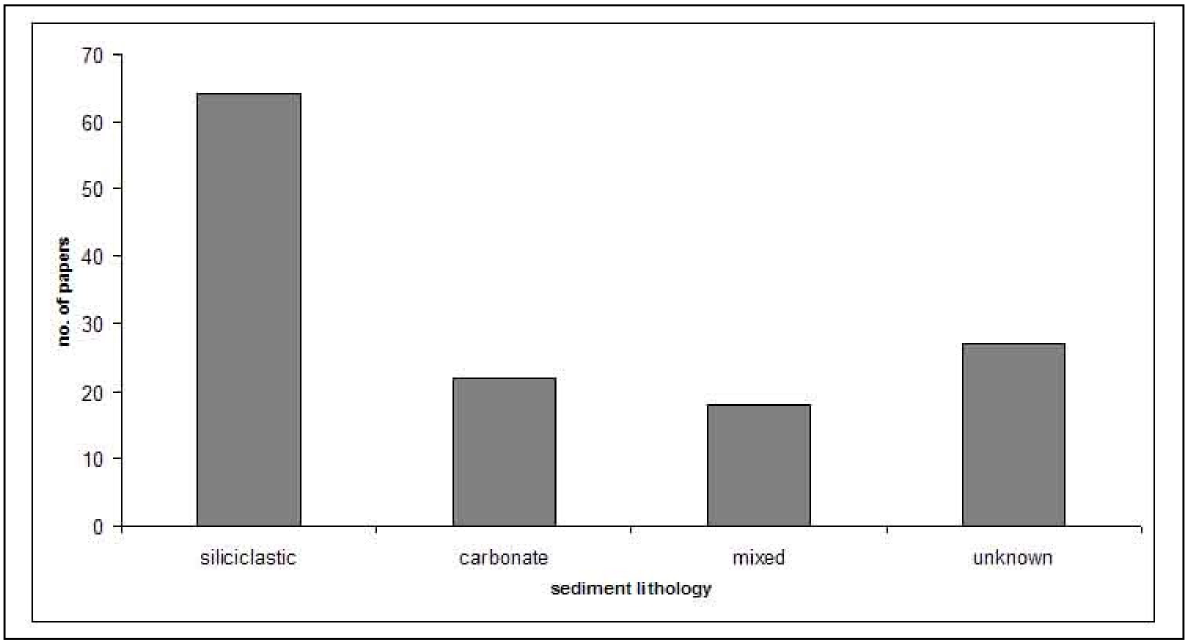

Figure 2.5 - Number of papers documenting fossil avian remains in each lithology. Sediment lithologies are siliciclastic, carbonate, mixed siliciclastic-carbonate, or unknown.

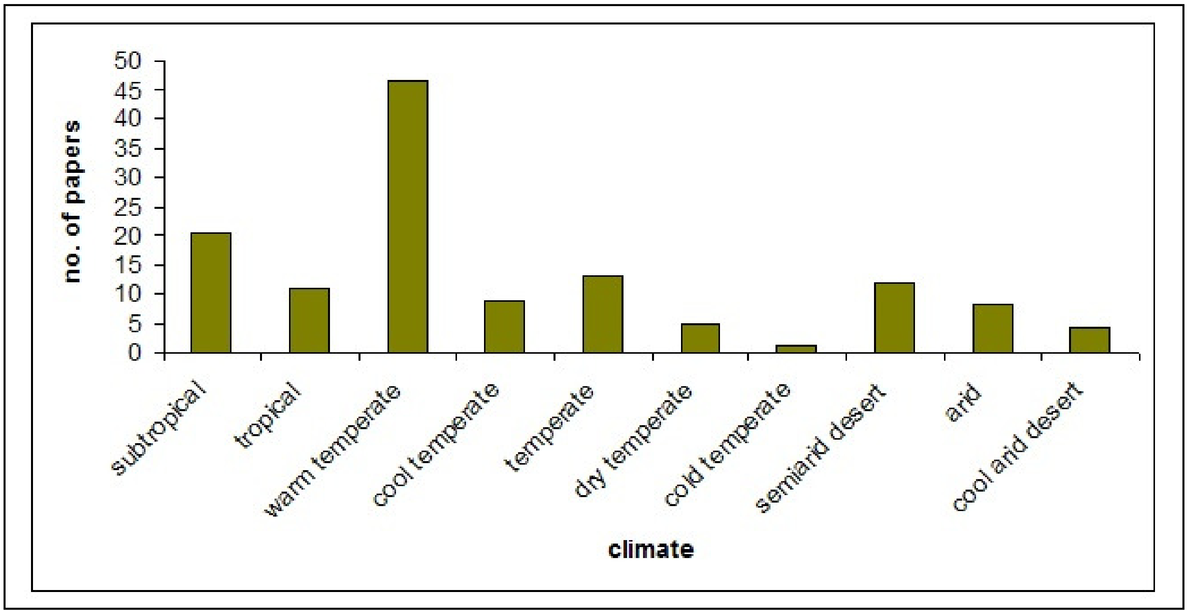

Figure 2.6 – Distribution of climatic regions in the reviewed papers.

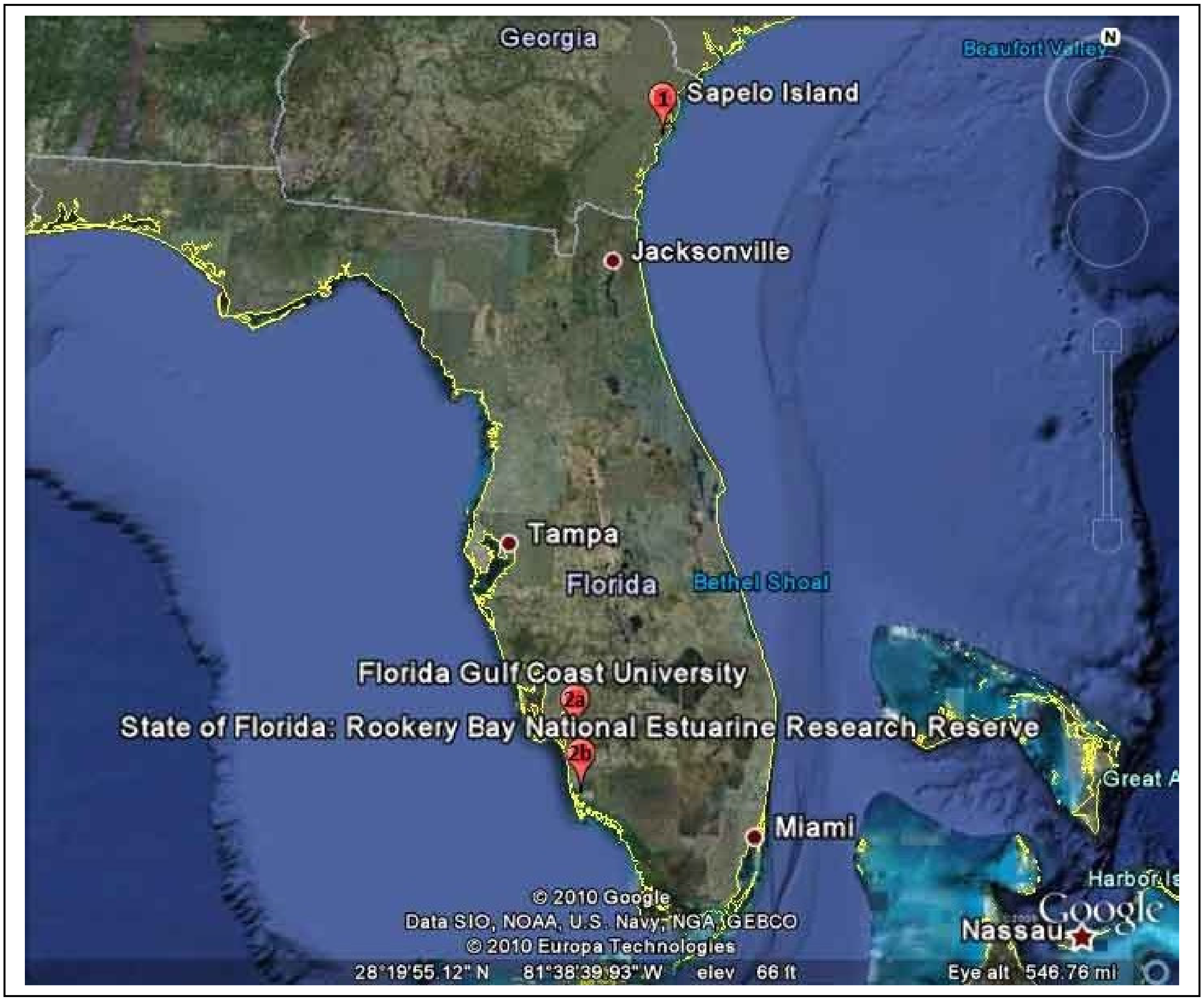

Figure 2.7 - Map of the experimental field sites. Site 1 is at the University of Georgia Marine Institute on Sapelo Island, Georgia. Site 2a is on the campus of Florida Gulf Coast University in Fort Myers, Florida. Site 2b is at Rookery Bay National Estuarine Research Reserve in Naples, Florida. (Image from Google Inc., 2010.)

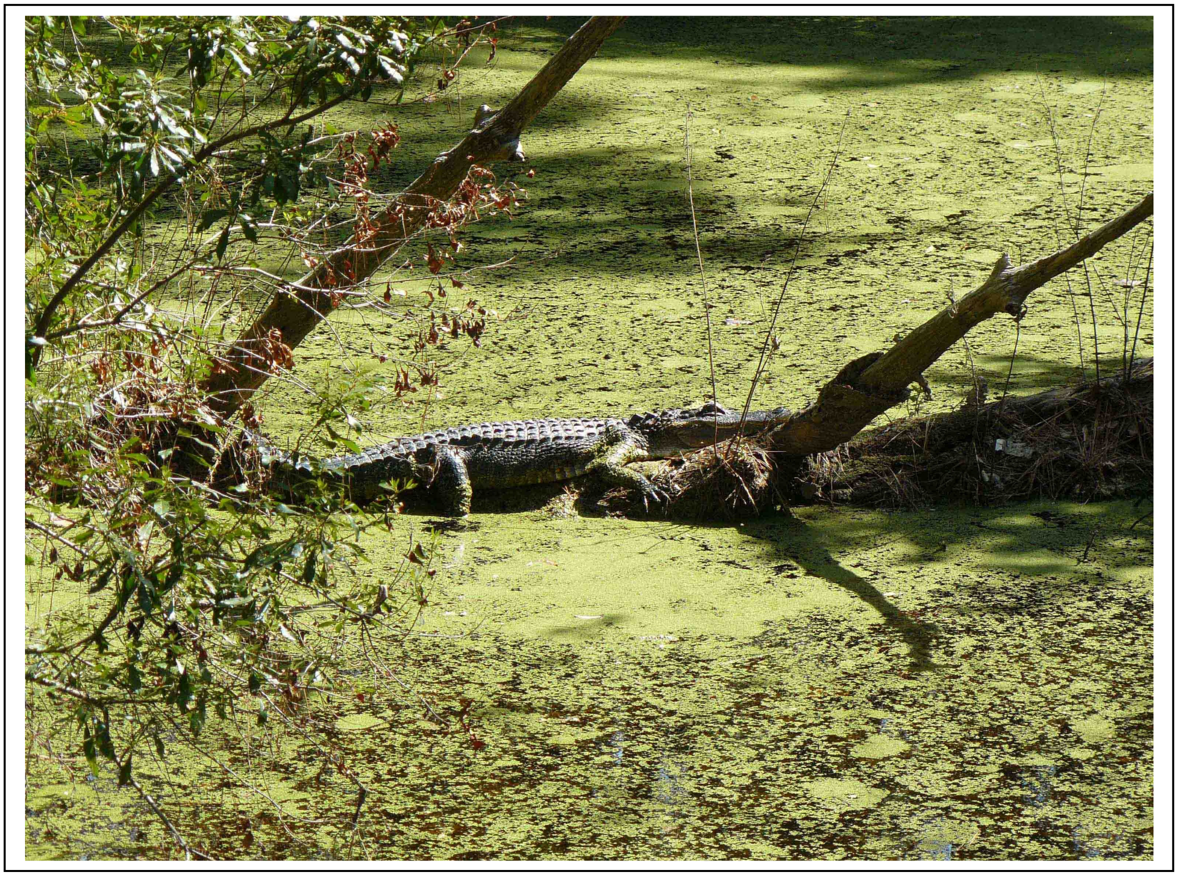

Figure 2.8 - Juvenile alligator in the pond on Sapelo Island, Georgia.

Figure 2.9 - Intact pelvic girdle of an adult male carcass at the Sapelo Island, Georgia, dune site. This is after 12 months of exposure. Scale in cm.

Figure 2.10 - Disarticulated carcass bones at the Sapelo Island, Georgia, dune site. The bones are in weathering stage 2 after 12 months of exposure. Scale in cm.

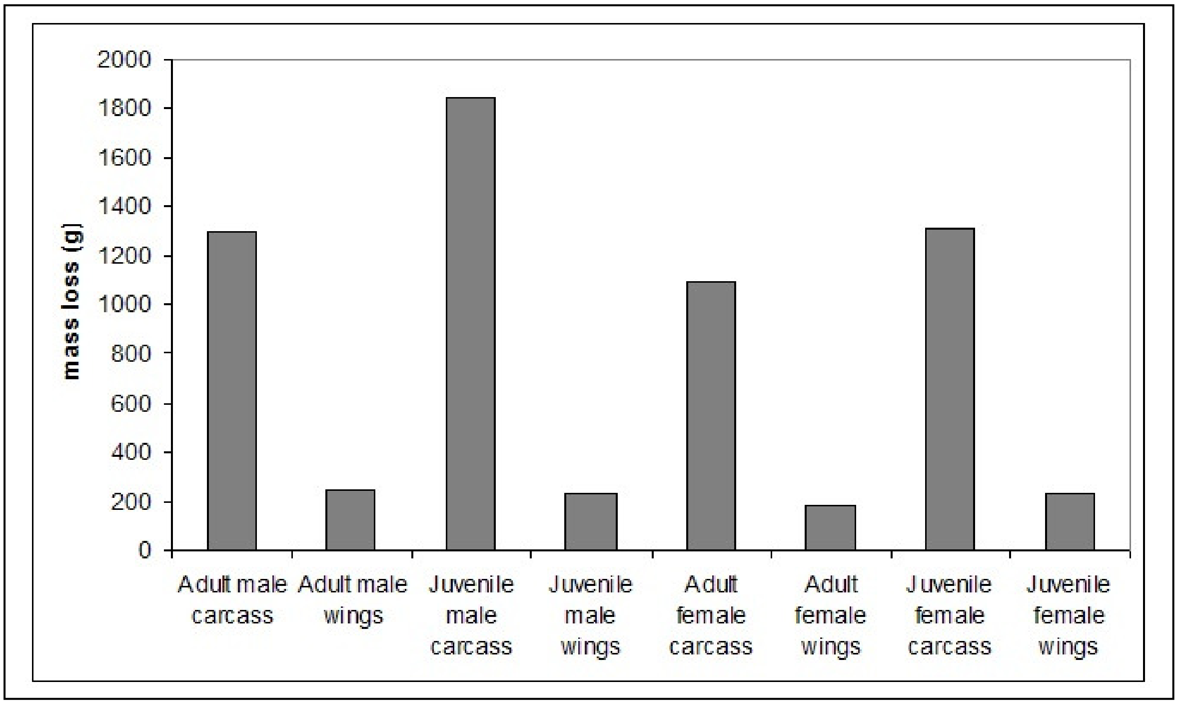

Figure 2.11 - Mass loss per bird carcass or wing set at the Sapelo Island, Georgia, dune site. This is after 12 months of exposure. N = 1 per bar. Mass loss was determined by taking the ending mass (weight of any remaining bones after exposure period) and subtracting it from the initial mass (weight of freshly dead carcass or wing set).

Figure 2.12 - Intact pelvic girdle of an adult male carcass at the Sapelo Island, Georgia, marsh site. This is after 12 months of exposure. Scale in cm.

Figure 2.13 - Humerus bone at the Sapelo Island, Georgia, marsh site. This bone reached weathering stage 1 after 12 months of exposure. Scale bar = 2cm.

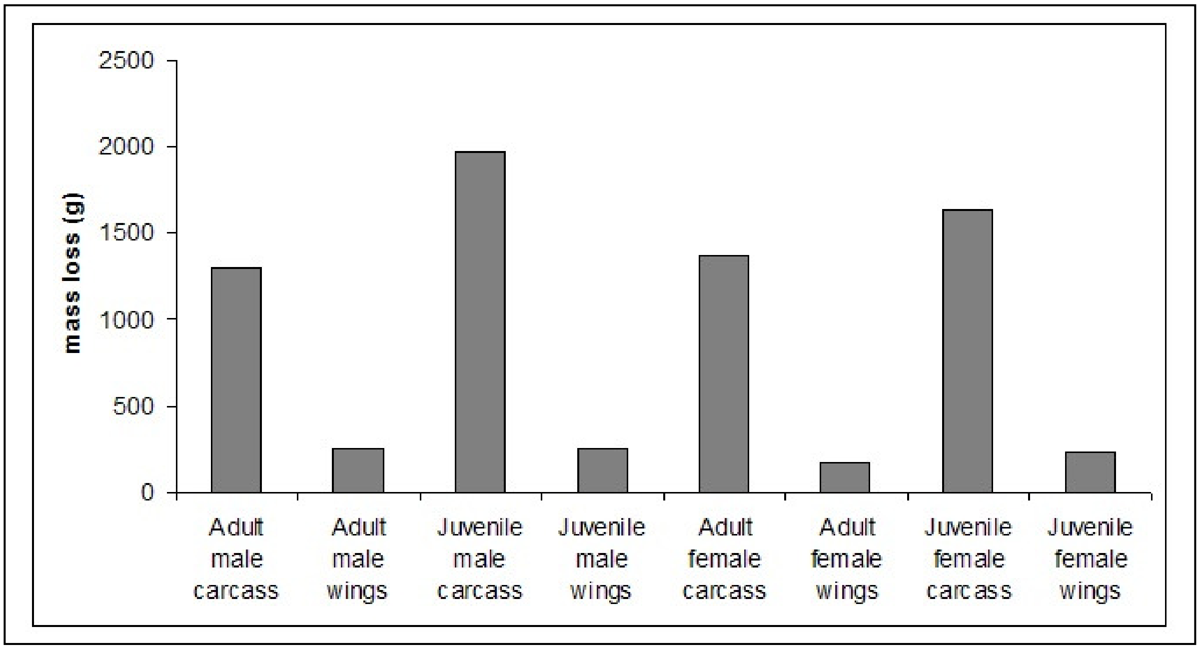

Figure 2.14 - Mass loss per bird carcass or wing set at the Sapelo Island, Georgia, marsh site. This is after 12 months of exposure. N= 1 per bar. Mass loss was determined by taking the ending mass (weight of any remaining bones after exposure period) and subtracting it from the initial mass (weight of freshly dead carcass or wing set).

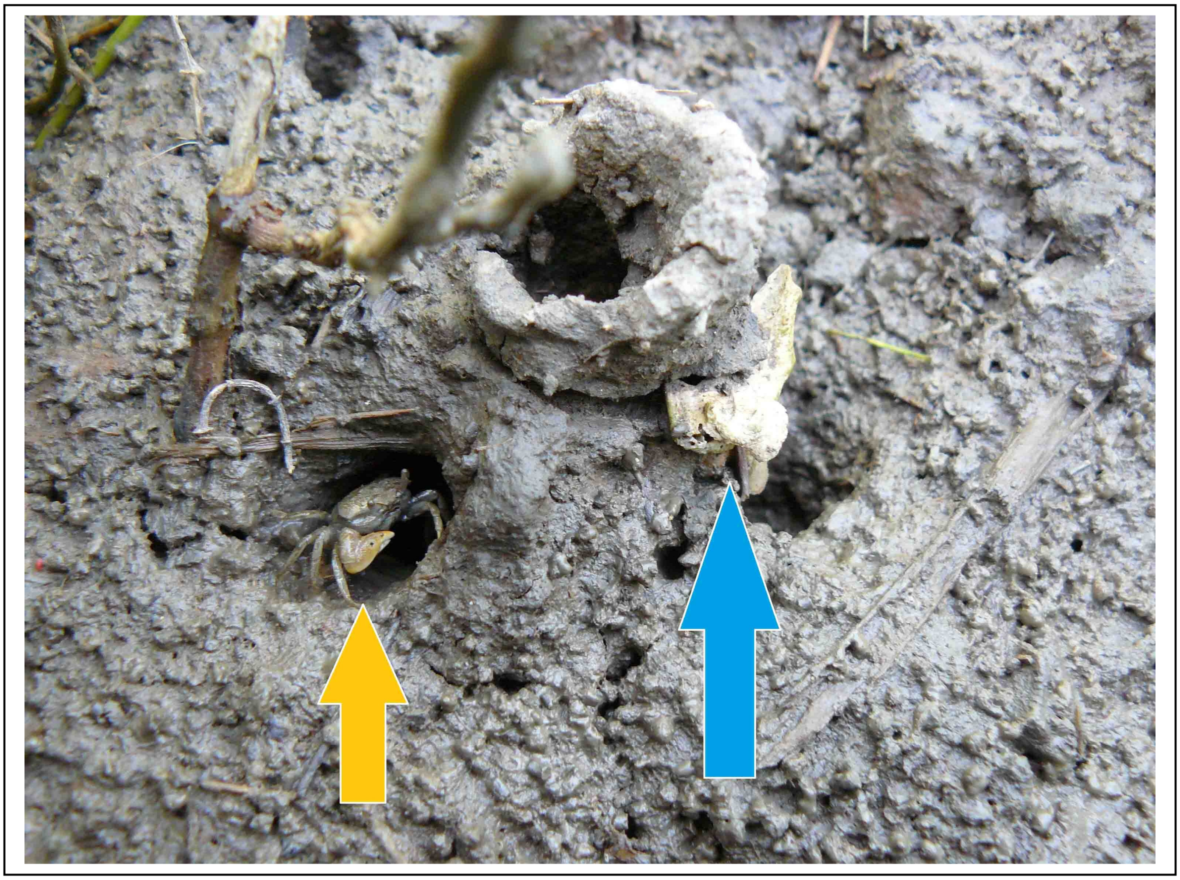

Figure 2.15 – Mud crab with scavenged vertebra at the Sapelo Island, Georgia, marsh site. Mud crab is indicated by the orange arrow and the scavenged vertebra attached to its burrow is indicated by the blue arrow.

Figure 2.16 - Ulna bone at the Fort Myers, Florida, pond site. This bone reached weathering stage ½ after 12 months of exposure. Scale bar = 2cm.

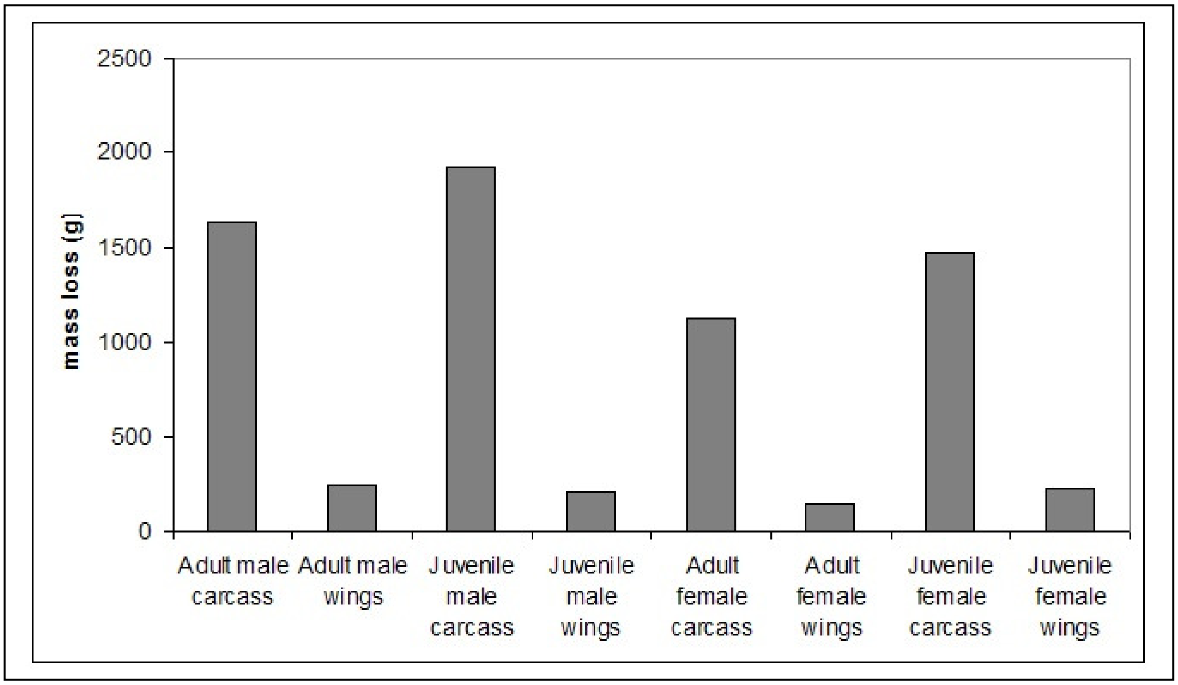

Figure 2.17 - Mass loss per bird carcass or wing set at the Fort Myers, Florida, pond site. This is after 12 months of exposure. N = 1 per bar. Mass loss was determined by taking the ending mass (weight of any remaining bones after exposure period) and subtracting it from the initial mass (weight of freshly dead carcass or wing set).

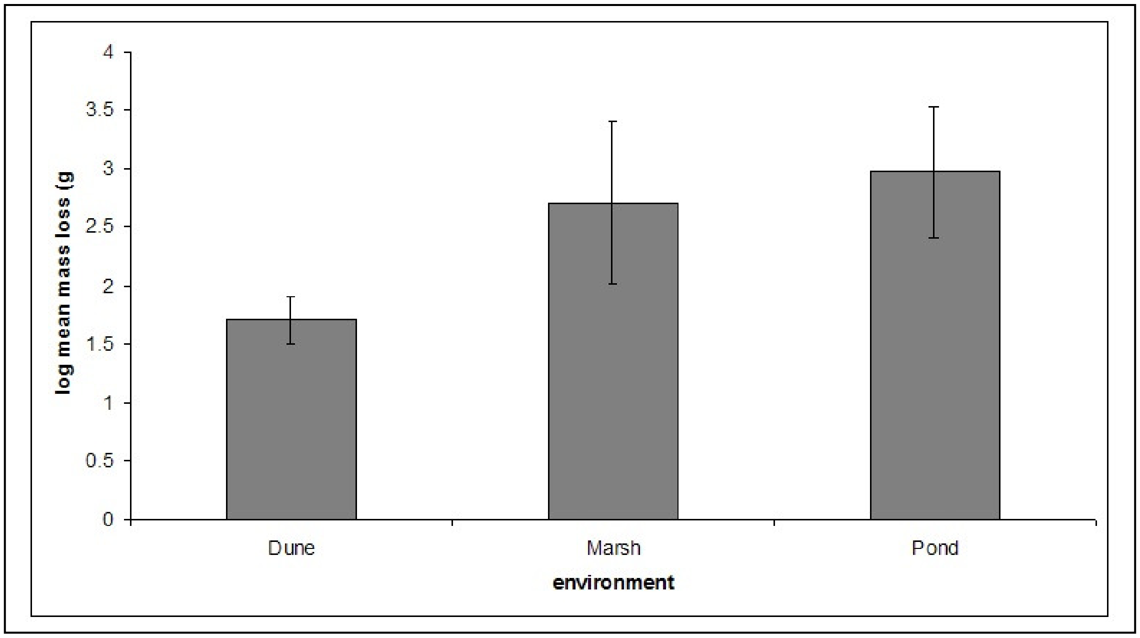

Figure 2.18 - Log mean mass loss in each environment. The environments consist of the Georgia dune, the Georgia marsh, and the Florida pond.

Table 2.1 - List of reviewed depositional environments.

Major Environment	Sub-environment
Continental	
	Alluvial
	Lacustrine
	Fluvial
	Floodplain
	Fluvio-lacustrine
	Glacio-fluvio-lacustrine
	Karst
Transitional	
	Deltaic
Marine	
	Continental shelf
	Continental slope
	Deep (abyssal)
Unclassified	
	Hot spring
	Volcanic uplands
	Fissure fill
	Asphalt pit

Table 2.2. – Depositional environments containing the most avian fossils, with the number of each bone type (sorted by body region) preserved in each environment.

	Marine Environment	Continental Environments		
	Continental shelf	Floodplain	Fluvio-lacustrine	Lacustrine
Skeletons				
fully articulated	1	0	0	8
partial articulated	2	0	0	13
associated	4	0	1	4
dissociated	3	0	0	1
Cranial				
rostrum/bill	1	5	0	0
premaxilla/mandible	5	68	0	5
pterygoid	1	0	0	0
quadrate	1	1	1	1
skull/cranium	8	1	2	9
Thorax/Abdominal				
furcula	2	1	0	1
coracoid	40	35	20	33
ribs	6	0	5	0
sternum/keel	5	4	4	2
scapula	15	5	8	5
cervical vertebrae	47	1	14	6
thoracic vertebrae	9	0	0	0
Pelvic Girdle/Tail				
coccyx	1	0	0	0
sacrum	3	0	0	0
synsacrum	9	0	2	1
pelvis	5	0	3	0
caudal vertebrae	2	0	0	0
pygostyle	1	0	0	0
Wing				
humerus	71	37	48	40
ulna	26	3	24	11
radius	8	1	8	3
carpometacarpus	21	11	13	20
phalanges (digits)	11	0	0	3
Leg				
femur	58	6	19	4
tibiotarsus	51	26	16	26
fibula	3	0	0	0
tarsometatarsus	36	31	23	19
phalanges	9	7	0	10
Miscellaneous				
unidentified remains	0	0	23	2
3D body mold	0	0	0	0
Total	465	243	234	227

Table 2.3 - Preserved avian remains from each environment in the Georgia and Florida locations.

Georgia - Warm Temperate Climate

Environment	Carcass or Wings	Initial Mass / Ending Mass	Mass Loss	Skeletal Elements Remaining
Dune	Adult male carcass	1335g / 38.2g	1296.8g	intact pelvic girdle, intact keel/sternum, 2 scapulae, 2 coracoids, furcula, 4 articulating cervical vertebrae, 11 degraded vertebrae, 9 ribs
Dune	Adult male wings	(left) 125.9g / 0g (right) 119.8g / 0g	125.9g 119.8g	--- (degraded feathers)
Dune	Juvenile male carcass	1870g / 22.1g	1847.9g	degraded keel/sternum, 2 ischia, 7 cranium/beak parts, 2 coracoids, 2 scapulae, furcula, 11 ribs, 20 degraded vertebrae
Dune	Juvenile male wings	(left) 115.7g / 6.1g (right) 128.6g / 5.3g	109.6g 123.3g	2 humeri, 2 radii, 2 ulnae, 2 right metacarpals, 3 right phalanges, (degraded feathers)
Dune	Adult female carcass	1129.5g / 35.1g	1094.4g	degraded pelvic girdle, degraded keel/sternum, furcula, right scapula, left coracoid, 3 articulating cervical vertebrae, 5 degraded vertebrae, 12 ribs, (degraded feathers)
Dune	Adult female wings	(left) 98.1g / 4.2g (right) 95.4g / 3.2g	93.9g 92.2g	2 humeri, right radius, left ulna, 2 left metacarpals, 1 left phalange
Dune	Juvenile female carcass	1332g / 20.4g	1311.6g	degraded keel/sternum, 2 ischia, 2 coracoids, 2 scapulae, furcula, 4 articulating vertebrae, 16 degraded vertebrae, 12 ribs
Dune	Juvenile female wings	(left) 112.3g /	108.4g	2 humeri, 2 radii, right

		3.9g (right) 126g / 5.8g	120.2g	ulna, 2 left metacarpals, 3 left phalanges
Marsh	Adult male carcass	1335g / 29.1g	1305.9	intact pelvic girdle, intact keel/sternum, 2 cervical vertebrae, 2 coracoids, 2 scapulae
Marsh	Adult male wings	(left) 121.9g / 3.9g (right) 131.1g / 0.9g	118g 130.2g	left humerus, right radius
Marsh	Juvenile male carcass	1973.5g / 1.8g	1971.7g	keel/sternum
Marsh	Juvenile male wings	(left) 120.7g / 1.1g (right) 130.9g / 0.4g	119.6g 130.5g	left radius, right humerus
Marsh	Adult female carcass	1363g / 1.2g	1361.8g	right scapula
Marsh	Adult female wings	(left) 76.7g / 0.4g (right) 95.3g / 0.4g	76.3g 94.9g	2 radii, (degraded feathers)
Marsh	Juvenile female carcass	1638g / 1.3g	1636.7g	left coracoid
Marsh	Juvenile female wings	(left) 106.7g / 0.2g (right) 125.9g / 2.4g	106.5g 123.5g	left metacarpal, right humerus
Pond	(no carcass or wing bones were preserved in the warm temperate pond)			

Florida - Subtropical Climate

Environment	Carcass or Wings	Initial Mass / Ending Mass	Mass Loss	Skeletal Elements Remaining
Back Beach/Dune	(no carcass or wing bones were preserved in the subtropical dune)			
Mangrove marsh	(no carcass or wing bones were preserved in the subtropical marsh)			
Pond	Adult male carcass	1632g / 0.4g	1631.6g	right scapula
Pond	Adult male wings	(left) 121.8g / 0g (right) 117.3g / 0g	121.8g 117.3g	---

Pond	Juvenile male carcass	1931.5g / 8.6g	1922.9g	2 ischia, 2 coracoids, furcula, 4 degraded vertebrae, 1 rib
Pond	Juvenile male wings	(left) 103.5g / 1.5g (right) 104.9g / 2.4g	102g 102.5g	left humerus, right radius
Pond	Adult female carcass	1218g / 1.4g	1216.6g	left coracoid
Pond	Adult female wings	(left) 75.4g / 0g (right) 68.8g / 0g	75.4g 68.8g	---
Pond	Juvenile female carcass	1475.5g / 3g	1472.5g	furcula, 5 degraded vertebrae
Pond	Juvenile female wings	(left) 107.4g / 0g (right) 113.6g / 0g	107.4g 113.6g	---

Table 2.4 - Climate data for each field site.

Location	Ave. Ann. Air Temp.	Ave Ann. Sediment Temp.	Ave Ann, Precip.	Ave Ann. Humidity
Sapelo Island	67.9^0F	66.71^0F (Dune) 70.14^0F (Marsh) 60.14^0F (Pond)	4.62 inches	73.4%
Rookery Bay	74.6^0F	68.71^0F (Dune) 70.85^0F (Marsh)	4.41 inches	72.4%
Fort Myers	74.9^0F	59.85^0F (Pond)	4.64 inches	70.0%

CHAPTER 3

MODERN AVIAN BONE WEATHERING IN HUMID COASTAL ENVIRONMENTS: IMPLICATIONS FOR BIAS IN THE FOSSIL RECORD[1]

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[1] Gardner, E.E. and S.E. Walker. To be submitted to *Paleobiology*.

Abstract

Avian remains are found in many paleontological and archaeological deposits and recent work has shown their utility in paleoenvironmental and paleoecological reconstructions. However, compared to mammalian taphonomy, avian taphonomy is inadequately understood. Modern avian taphonomic studies are an important tool for exploring preservational biases related to environmental and ecological (i.e., age and sex) factors. In this paper, we explore the weathering and degradation patterns of age- and sex-grouped avian leg bones exposed for one year in three different coastal habitats (e.g., tidal, terrestrial, and freshwater) located in warm temperate, subtropical, and tropical climates. Avian remains experience intense scavenging in warmer climates and larger leg bones are preferentially scavenged in these regions. Warmer climates are associated with greater bone mass loss due to high air temperature and humidity. Overall, physical weathering (cracking and flaking), chemical weathering (dissolution and corrosion), and biological weathering (bacterial attack) are most extensive in terrestrial and marsh environments compared to freshwater environments. Juvenile bones undergo more rapid weathering and loss than adult bones. Male bones are frequently recovered in much better taphonomic condition than female bones. Thus, the avian fossil record may be biased toward preservation of submerged bones, adult male bones, and, depending on scavenger activity, toward preservation in warm temperate climates. Global warming events likely negatively impact the preservation potential of avian remains, but more taphonomic research across a variety of climates, environments, and habitats is needed to evaluate this.

Introduction

Despite the fact that avian remains are frequently preserved in paleontological and archaeological deposits, they are often overlooked because they are considered too small or fragmentary (Olson 1985; Nicholson 1996). Assumptions that birds have poor preservation potential are common, but not based on comprehensive taphonomic examinations (Bickart 1984). Relatively little attention has focused on studying the intrinsic and extrinsic factors that influence avian bone taphonomy, or how these factors may be biasing our interpretation of the avian paleontological and archaeological records. Taphonomic investigations of modern bird remains are necessary for determining whether ancient assemblages adequately reflect depositional environment, ecological community, and species diversity (Howard, 1947; Rasmussen et al. 1987; Behrensmeyer et al. 2003; Louchart et al. 2009; Prassack 2010). Since bone is the predominant material preserved in avian deposits, it is crucial to develop an understanding of the taphonomic biases that affect bird bones.

Studies of carcass decay and disarticulation have traditionally been used to document avian taphonomy. Investigations of carcass decay and disarticulation have provided valuable information on the sequence of events from death to deposition (Schäfer 1955, 1962, 1972), disarticulation and transport (Bickart 1984), skeletal part frequencies (Livingston 1989), scavenging (Oliver and Graham 1994), morphological stages of degradation (Davis and Briggs 1998), and species-specific taphonomy (Cruz 2007). Avian bone weathering studies are less common. Although detailed documentation exists on the weathering of mammalian bone over a variety of environments and time spans (Voorhies 1969; Tappen and Peske 1970; Behrensmeyer 1978; Lyman 1984; Andrews and Cook 1985; Tappen 1994; Janjua and Rogers 2008; Todisco and Monchot 2008; Fernández-Jalvo et al. 2010), only four studies have specifically explored the weathering of bird bones. Nicholson (1996) compared the weathering of buried mammal, fish, and bird bones in a variety of soils from the humid temperate climate of Southern England over a 7-year period. Davis (1997) documented the weathering effects of bioerosion on avian bones in freshwater and marine settings in the subtropical climate of southern Florida over a 2.3-month long period. Behrensmeyer et al. (2003) modified the mammalian bone weathering profile to accommodate for different patterns seen in bird bones exposed subaerially for 2-3 years in the semiarid Amboseli Basin of Kenya. Cruz (2008) applied the weathering profiles from Behrensmeyer (1978) and Behrensmyer et al. (2003) to mammal and bird bones subaerially exposed in a variety of semiarid steppe habitats of Southern Patagonia. The relatively limited number of avian bone weathering studies underscores the need for further investigations covering a variety of depositional settings and climate regions.

It is particularly important to document taphonomic processes by climatic region because weathering rates differ by climate (Janjua and Rogers 2008). A climate's effects on soil characteristics (e.g., temperature and moisture content) have been hypothesized to affect the diagenetic processes that act on bones (Lyman 1994). Bone weathering rates specific to various climates have been established for mammals, but not for birds. Since avian bone responds differently from mammalian bone to varied environmental settings (Nicholson 1996; Cruz 2008), assumptions drawn from weathering studies of mammal bone cannot be confidently applied to avian bone. For instance, Nicholson (1996) found that mammal bone showed extensive cracking, as well as channeling and pitting from bioerosion, while bird bone generally appeared smooth and largely intact. This contrasts with the findings of Behrensmeyer et al. (2003) and Cruz (2008) who found that, over a few years, subaerially exposed bird bones tend to weather more rapidly than mammal bones in semiarid climates. The discrepancies between these results are explained by the difference in method (burial vs. subaerial exposure) (Shipman 1981), but it is clear that more controlled studies across an array of climates are necessary.

The disparate avian and mammalian bone weathering rates that Nicholson (1996) observed are attributable to fundamental differences in bone structure between the two groups. Avian bone is unlike mammalian bone in several ways. Bird bones tend to have less cancellous bone tissue and their cortical bone layers are thinner but denser (Nicholson 1996; Kaiser 2007; Dumont 2010); they also frequently have a more compact periosteum lining on their outer surface (Nicholson 1996). These differences suggest that avian bone may be less vascularized than mammalian bone and therefore potentially more resistant to weathering. However, it is noteworthy that there was no control over age or sex in Nicholson's study; these two factors that may introduce considerable bias in preservation potential, particularly for birds.

Age affects avian bone in many ways, from mineralization to structure to tensile strength. In the embryonic stages, bird skeletal elements are generated quickly and calcium is rapidly mobilized from the yolk and eggshell for skeletal development (Blom and Lilja 2003). After hatching, infant birds grow swiftly; woven and fibrolamellar bone types, which are very porous, are laid down quickly to accommodate their increasing body mass (Currey 2002). As birds mature from juveniles to adults, hydroxyapatite accretion rates slow and relatively non-porous bone progressively replaces the porous bone (Currey 2002). These differences in bone porosity mean that juvenile avian bone is not as mineralized as adult bone (Nicholson 1996), so a taphonomic bias against juveniles in the avian fossil record is likely. However, no controlled studies comparing the weathering rates of adult and juvenile bird bones have been conducted.

Sex also distinctly affects avian bone. The hormone estrogen causes females of reproductive age to deposit calcium-rich medullary tissue in their long bones (i.e., femur and tibiotarsus), which is later resorbed to mobilize the calcium for eggshell production (Dacke et al. 1993). Medullary tissue is an extremely irregular and porous meshwork that is highly mineralized and has no mechanical purpose (Currey 2002; Lentacker and Van Neer 1996). It grows from the endosteal (inner) surface of the bone out into the red marrow through random fingerlike projections (Lentacker and Van Neer 1996), forms 1-2 weeks prior to egg laying, and then is resorbed over a period of 1-3 weeks (Simkiss 1967). To guarantee a supply of mobile calcium for eggshell formation, cortical bone is frequently depleted in order to create medullary tissue; in some cases, cortical bone reduction can reach 50% (Lentacker and Van Neer 1996). Medullary tissue is unique to female birds and their bone mineral density is thought to vary in relation to the reproductive cycle (Dirrigl 2001). Another sex bias affecting the avian record is that male bird bones are typically bigger and more robust than female bird bones due to sexual size dimorphism (Dirrigl 2001). Such differences may make female bones more susceptible to taphonomic weathering than male bones. On the other hand, if medullary tissue is preserved in some avian remains (as at several archaeological sites documented by Rick [1975], Driver [1982], and Lentacker and Van Neer [1996]), then it can be used as an indicator of sex, enabling a clearer understanding of the dynamics of a particular population, or at least an estimate of the number of reproducing females in it (Lentacker and Van Neer 1996). Despite these potentially fruitful areas for study, there have been no taphonomic studies on the role of sex in avian bone weathering and degradation.

Along with the potential influence of genetic factors on bone weathering rates, variation in depositional environments and their localized conditions can lead to differential bone weathering (Behrensmeyer 1978). Depositional environment encompasses the physical (i.e., wind and water), chemical (i.e., rock lithology and soil pH), and biological (i.e., bacteria and fungi) processes of a particular area. Each of these processes can profoundly impact bone weathering (Trueman et al. 2004).

Evidence of physical avian bone weathering includes drying, longitudinal cracking, and flaking from exposure to heat and moisture (Behrensmeyer et al. 2003). Other potential sources of physical bone weathering are abrasion from small particles, such as quartz grains, or damage from frost wedging (White and Folkens 2005).

Chemical bone weathering is more complex and is closely associated with biological alterations of bone. Bone's collagen protein and other organic materials are initially degraded by bacteria and fungi; then, the mineral portion of bone (a non-stoichiometric carbonate hydroxyapatite, $Ca_{10}(PO_4, CO_3)_6(OH)_2$) undergoes dissolution and recrystallation (Trueman and Tuross 2002; Pfretzschner, 2004; Trueman et al. 2004). These changes occur at different rates in different depositional environments, depending on lithology (e.g., siliciclastic vs. carbonate), hydrology, geochemistry, and soil pH (Trueman et al. 2004). For example, in acidic conditions, dissolution leads to "corrosion" of the bone surface (Fernández-Jalov et al. 2010).

Biological weathering (bioerosion) is also fundamental to the degradation of bone. Intricate tunnels, channels, and pits are formed by microorganisms' digestion of the organic content of bone (Davis 1997). Bacteria and fungi generally colonize pores in the cortical bone quickly after exposure, releasing enzymes that consume the bone's organic matter and some small crystallites (Marchiafava et al. 1974). Loss of organic matter causes shrinkage-related cracks to develop in the bone (Piepenbrink 1986), and so provides more area for the microorganisms to invade. Bioerosion, along with physical weathering, sometimes is so extensive that it leads to complete disintegration of the bone (Davis 1997). Bacterial and fungal communities vary in accord with climate and depositional environment (especially geochemistry and soil moisture), and thus highlight the interconnectedness of the forces that can weather vertebrate bone.

Another important taphonomic factor that impacts the preservation of bone is scavenging. Avian carcasses are attractive to a wide variety of scavenging organisms, including vertebrates – mammals (e.g., hyenas, raccoons, rats), reptiles (e.g., snapping turtles), and birds (e.g., vultures and gulls) – and invertebrates like insects (e.g., flies/maggots and beetles) and mollusks (e.g., land snails). Larger scavengers frequently chew, gnaw, or trample bone, causing fractures (Haynes 1983) and providing increased surface area for microbial and physical weathering. Mammalian scavengers of avian carcasses often disarticulate joints, leaving individual skeletal elements more susceptible to weathering processes (Oliver and Graham 1994).

Documenting both macroscopic (physical weathering and scavenging) and microscopic (dissolution and bioerosion) changes to bone is crucial to a thorough understanding of the factors influencing bone taphonomy. One method for detailed analysis of microscopic changes is electron microscopy/spectrometry. Electron microscopy has been used extensively in studies of mammalian – especially human – bone and tooth diagenesis and taphonomy (Hackett 1981; Bell 1990; Hedges et al. 1995; Greenlee 1996; Nicholson 1996; Pesquero et al. 2010; among others). Scanning electron microscopy (SEM) and backscattered electron (BSE) imaging enable detailed histomorphologic and mineral analysis of both fossil and modern bone (Greenlee 1996). SEM and BSE imaging also allow for targeting of specific areas for chemical analyses such as energy- and wavelength-dispersive spectrometry (Greenlee 1996). Wavelength-dispersive spectrometry (WDS) is particularly useful for documenting variation in bone mineral composition because it quantifies the relative abundance of targeted elements (Greenlee 1996). While WDS has been used in mammalian studies (e.g., Greenlee 1996; Denys et al. 1996; Dauphin et al. 1999), it has not been used before in avian studies.

The current study takes a comprehensive approach for documenting the impact of the taphonomic weathering agents described above on modern avian bones in humid warm temperate, subtropical, and tropical coastal siliciclastic and carbonate locales, in three different environments: terrestrial, marine, and freshwater. Sex and age were investigated as potential sources of bias in avian taphonomy. Backscattered electron imaging and wave-dispersive spectrometry were utilized to document weathering-related histomorphologic and compositional changes to the exposed avian bones. From these observations, the avian bone weathering profile for arid environments from Behrensmeyer et al. (2003) was modified to account for patterns seen in hot, humid coastal environments.

Materials and methods

Animals. – The bird bones used in this study came from 18 sexed adult (1.5 year) White Leghorn and 18 sexed juvenile (8 week) Ross Broiler chickens (*Gallus gallus domesticus*) raised at the University of Georgia's Poultry Farm. Prior to our experiment, the birds were the subjects of a UGA Poultry Science Department nutrition study that received approval by the Institutional Animal Care and Use Committee (N. Dale personal communication 2008). Diet (Table 3.1) and living conditions were carefully monitored, providing control over two important variables that affect avian bone composition. At the end of the nutrition study, the birds were euthanized via cervical dislocation by trained personnel in accordance with the American Veterinary Medical Association guidelines (N. Dale personal communication 2008). The carcasses were frozen at 15^0F in an industrial freezer until needed for our experiment.

Specimen preparation. – After the carcasses were thawed, femora and tibiotarsi were removed and then defleshed by hand as best as possible. A separate study analyzing decay and disarticulation of the carcasses was also conducted, but those results are the subject of another paper (Gardner and Walker, in prep). Leg bones were the focus of the current investigation for three reasons: sex-specific avian medullary tissue is mainly concentrated in the long bones (Dacke et al. 1993); weathering rates are easier to identify in long bones (Behrensmeyer 1978); and both the histology and composition of these avian skeletal elements are fairly well documented (e.g., Enlow and Brown 1957; Simkiss 1967; Suchý et al. 2009). A total of 144 leg bones were collected, with sixteen kept as controls. The leg bones were grouped by sex and age (adult male and female, juvenile male and female). Each bone was cut in half at mid-shaft (Fig. 3.1A-D) with a Dremel tool; this was done to enable six- and twelve-month collections from the same bone. A hole was made in the metaphyseal region so that the bones could be securely attached to the plastic tube arrays with metal wire (Fig. 3.1E). Each bone half was weighed on a precision scale after preparation ("start mass" in results below). Four bone halves – two femur halves and two tibiotarsus halves from the same bird – were attached to each plastic tube array. This set-up was meant to deter scavenging while allowing the bones to remain in contact with the sediment surface. A total of 64 arrays were made.

Experiment locations. – Yearlong experiments were executed at two siliciclastic sites and one carbonate site (Fig. 3.2). Site 1 was at the University of Georgia's Marine Institute on Sapelo Island, Georgia. Sapelo Island is a siliciclastic barrier island featuring a variety of coastal depositional environments, and it is considered to have a humid warm temperate climate (Franks 2003). Site 2 consisted of two locations in southwestern Florida: one in Naples at the Rookery Bay National Estuarine Research Reserve and one in Fort Myers at Florida Gulf Coast

University (FGCU). The southwestern coast of Florida shows a gradation from beach and nearshore siliciclastics to carbonate shelf sediments (Finkl et al. 2006); however, our experiments were only deployed on land and thus in siliciclastic environments. Southwestern Florida has a humid subtropical climate (Obeysekera et al. 1999). Site 3 was at John Pennekamp Coral Reef State Park (JPSP) in Key Largo, Florida. The Florida Keys consist of Pleistocene-age fossil reef platforms and associated carbonate sediments; the climate is considered to be tropical (Duever et al. 1994). Site climate data, gathered from the National Climatic Data Center and National Weather Service for the duration of the experiment, are presented in Table 3.2. The experimental arrays at both siliciclastic sites were exposed for the field season of May 2008 to May 2009; the arrays for the carbonate site were exposed for the field season of May 2009 to May 2010.

At each site, experimental arrays were deployed in three different depositional environments: terrestrial, marine, and freshwater. The environments at Site 1 (Sapelo Island) were a sandy dune, a tidal marsh, and a freshwater pond. Site 2's environments were a vegetated beach and a mangrove marsh at Rookery Bay location and a freshwater pond at FGCU. The environments at Site 3 (JPSP) were a rock barren, a mangrove marsh, and a freshwater pond.

Data collection. – Bone mass, determined on a precision scale in grams, was recorded at periodic intervals throughout a twelve-month exposure period in the field. Sediment temperatures, along with water salinity and chemistry (pH, ammonia, nitrate, nitrite), were also documented at each visit, but not utilized in statistical analyses. Means of these data are listed in Table 3.3. Detailed observations of physical weathering and scavenging were recorded during site visits. Photographs provided documentation of the condition of the bone specimens and their environment at the time of each visit. At six months, one bone half from each leg bone was selected at random for collection and analysis. At the end of the twelve month observation period, all remaining bones were collected and carefully examined with a hand-lens for evidence of surface weathering. Janjua and Rogers' (2008) scavenging categories were used to classify the degree of scavenger-inflicted damage to the bones. The weathering stages from Behrensmeyer et al. (2003) were used as guidelines for observations of physical degradation, but variations were noted as well.

Wave-dispersive spectrometry analyses and backscattered electron imaging. – Samples of control bones and experimental bones that survived the yearlong exposure period at each site were selected for analysis. Due to our interest in sex-based morphological differences, only bones from representative adult males and females were selected. The bone thin-section slides were made by Vancouver Petrographics, Ltd. They removed cross sections from the control and experimental bones with an Isomet low-speed saw. All samples were diaphyseal sections, with the exception of the female control bone, which was accidentally cut as a metaphyseal section. The bone samples were not cleaned prior to thin-section preparation. The slides were made using epoxy resin, petrographic slides, and a small-particle abrasive for polishing. Before analysis, the slides were wiped with ethanol and carbon-coated for conductivity.

BSE imaging and WDS analyses were conducted on a JEOL JXA 8600 Superprobe in the Geology Department at the University of Georgia. The following settings were used: 15 kV accelerating voltage, 5µm beam diameter, and 5nA beam current. Elemental concentrations were established via calibration against a homogenous standard (Durango Apatite). Matrix corrections were made with a Phi-Rho-Z correction routine.

WDS measurements were made in four different areas, following Fernández-Jalov et al. (2010): (1) periosteal cortical layer, (2) medial cortical layer, (3) endosteal cortical layer, and (4) medullary layer, if present. A schematic of these different bone areas, within the context of a whole bone, is provided in Figure 3.3. Calcium (Ca), phosphorous (P), sodium (Na), and magnesium (Mg) were measured. Ca/P and Mg/Ca ratios were calculated from the reported elemental weight percentages. BSE images of each area were taken at the time of WDS measurement. The Oxford Histology Index from Hedges et al. (1995) was utilized to determine micro-level damage to bones. As expected, quartz and clay were identified lining the external and internal portions of bones exposed to the siliciclastic settings. No substantial evidence of framboidal pyrite was found. Even though iron was detected in the samples, contamination from rusting of the wire used to attach the bones to the arrays led us to disregard the iron data.

Statistical analyses. – Results were statistically processed using Statistical Analysis Software (SAS) version 8.2. Significance was accepted at alpha ≤ 0.05.

To understand the relationship between bone mass loss (weathering) and each of the independent variables (e.g., sex, age, environment), regression analyses were performed. Because the data were correlated (longitudinal) repeated measures – each bird contributed multiple bones and each bone contributed multiple data points over time – generalized estimating equations (GEE) methods were used with the linear regression models. This technique is useful for handling repeated measures data (Liang and Zeger, 1986). The GEE models were able to analyze trends despite missing data due to random removal of some bones by scavengers or complete disintegration.

The effect of climate on bone weathering was more difficult to treat analytically. To assess the impact of different climate parameters (temperature, humidity, precipitation, or the number of hot days) on the bone mass-loss trends, we averaged the climate data over the months that preceded each periodic field site visit. For example, bones were deployed in May and weighed during a field visit in July; the weather data for those first three months of exposure were averaged together and applied to the July bone measurements. This approach means that baseline mass (starting weight) was dropped from the GEE model because the bones were not exposed to any climate parameters before deployment.

Although we used regression analyses, R^2 values cannot be reported. This is because R^2 values are calculated for linear models with independent observations using a likelihood estimate. A GEE-based model has no likelihood estimate defined due to the correlated nature of the data and thus measures like R^2 and Akaike's Information Criterion (AIC) cannot be directly used (Pan 2001). Instead, GEE-based models use a Quasi-likelihood Information Criterion (QIC) to fit the model's regression variables (McCullagh and Nelder 1989). In our analyses, the QIC gets smaller – indicating a better fit – when additional variables such as temperature, humidity, age, or sex are added to the model.

For the electron microprobe portion of the study, two test groups were created for statistical analysis: “total bone” (elemental composition of each entire bone cross section) and “bone area” (elemental composition of different histologic areas in each bone cross section). To estimate the effects of lithology and sex on total bone elemental composition, all bone area data from each bird were considered and the resulting data were analyzed with regression models using GEE methods to control for the correlated nature of the data. These analyses address the effects of sex and lithology in the crudest possible way by collapsing across all bone areas. To estimate contrasts between the Ca/P ratios in the different bone areas, the outermost portion of each bone was compared to more interior bone sites (cortical or endosteal). Paired t-tests were used to compare the Ca/P ratios in the different bone areas within each lithology or sex.

Results

Bone mass loss. – Mass loss was considered evidence of bone weathering over time. Overall, bone halves deployed for six months and bone halves deployed for twelve months experienced similar relative mass loss and absolute mean mass loss (Table 3.4). Since there was no statistical difference between the mass loss trends in bone halves exposed for six months versus twelve months, we restricted our attention in further analyses to the bone halves exposed for twelve months.

The following climate parameters were identified as potentially affecting bone mass loss trends: air temperature, humidity, precipitation, and the number of hot days ($\geq 90^0$ F). First, differences in climate parameters among the field sites were analyzed via Student's t-tests; these results are presented in Table 3.5. Key Largo experienced significantly higher temperatures than Sapelo Island (p-value of 0.0244); however, the other site comparisons showed no real differences in temperature. Key Largo had significantly greater relative humidity than Sapelo Island (p-value of 0.0005), Naples (p-value of 0.0022), and Fort Myers (p-value of 0.0001). The Fort Myers location had a greater relative humidity than Sapelo Island (p-value of 0.0419). There were no differences in the amount of precipitation received at the sites. Due to sea breeze cooling effects, Key Largo had significantly fewer hot days when compared to Naples (p-value of 0.0081) and Fort Myers (p-values of 0.0094); similarly, Sapelo Island had significantly fewer hot days than Naples (p-value of 0.0398) and Fort Myers (p-value of 0.0486).

Next, the effect of each climate parameter on the overall mass-loss trend was determined using regression analyses with GEE methods. Only two of the four parameters had a significant relationship with bone mass loss. For every degree increase in air temperature (regardless of site), there was a corresponding 0.0822g loss of bone mass (p-value of 0.0001). For every percent increase in humidity (regardless of site), there was a corresponding 0.0625g loss of bone mass (p-value of 0.0291). The amount of precipitation and the number of hot days did not affect the overall mass-loss trend.

Finally, the effects of site-specific temperature and humidity on each site's mass-loss trend were analyzed. At Sapelo Island, the effect of temperature was significant: for every degree increase, there was a corresponding 0.0763g loss of bone mass (p-value of 0.0001). The effect of humidity was significant and very large at Sapelo Island: for every percent increase, there was a corresponding 3.43g loss of bone mass (p-value of 0.0001). Similarly, temperature and humidity significantly affected the trend of bone mass loss at Naples: for every degree increase in temperature, there was a 0.213g loss in the trend (p-value of 0.0001) and for every percent increase in humidity, there was a 1.2638g loss of bone mass (p-value of 0.0001). At Fort Myers, only humidity affected the trend of mass-loss at the pond (0.3975g loss per percent increase). At Key Largo, no significant relationships were detected between the mass-loss trend and temperature or humidity, but this was probably due to small sample size, a result of intense scavenging at the site.

Overall absolute mean bone mass loss trends and relative mass loss were significant at each site, with p-values of 0.0001 (Fig. 3.4). Additionally, the mass loss trends per site were significantly different from each other. The trends at Site 2 (Naples/Fort Myers) and Site 3 (Key Largo) were significantly steeper than the trend at Site 1 (Sapelo Island), with p-values of 0.0007 and 0.0021 respectively. The trend at Site 3 was significantly steeper than the trend at Site 2 (p-value of 0.0254). Site 3's trend was the steepest and it showed a 0.89g greater loss of mass per unit time compared to the two siliciclastic sites. All three trends began to stabilize after six months, suggesting that microbial degradation may begin to slow down after the more readily-accessible organic material is consumed.

The absolute mean bone mass loss trends over time for the three different depositional environments were significant: each environment yielded a mass loss p-value of 0.0001 (Fig. 3.5). However, the trends were not significantly different from each other. In terms of relative mass loss, bones in the pond environments lost the least, at 53.3%; bones in the terrestrial and marsh environments lost 68.8% and 71.2%, respectively. This is reflected in the taphonomic condition of the bones as well (see Weathering section).

Age-based trends were complicated by the fact that the juvenile birds came from a large breed of chicken (Ross Broilers). This meant that the juveniles' leg bones weighed more than those of the adults at the start of the experiment (see Figs. 3.6-3.8). Nevertheless, juveniles lost more mass than adults at two of the three sites. At Site 1, juvenile bones lost significantly more absolute mean mass and relative mass than adult bones (p-value of 0.0125; see Fig. 3.6). Similarly, at Site 3, juvenile bones lost significantly more absolute mean mass and relative mass than adult bones, although the relative mass loss is strongly affected by small sample size at 12 months (p-value of 0.0001; see Fig. 3.7). However, at Site 2, there was no difference between the absolute mass loss trends of juvenile and adult bones, but juveniles lost comparatively more relative mass than adults (see Fig. 3.8). Each site also displayed significantly different juvenile-vs.-adult absolute mean mass loss trends (p-value of 0.0131).

Analysis of the relationship between sex and absolute mean bone mass loss yielded an unexpected result: on average, male bones lost more absolute mass than female bones. Male and female bones both experienced significant loss of mass over time at all three sites (p-value of 0.0001) and the trends were significantly different from each other per site (p-value of 0.0306).

The male bones at Site 1 lost significantly more absolute mean mass than the female bones (p-value of 0.0123; see Fig. 3.9). Similarly, the male bones at Site 2 lost significantly more absolute mean mass than the female bones (p- value of 0.0002; see Fig. 3.10). At Site 3, however, there was no difference between the absolute mean mass loss trends for male and female bones, indicating that mass loss was widespread across both groups (see Fig. 3.11). Interestingly, relative mass loss did not correspond with absolute mean mass loss. Male and female bones at Sites 1 and 2 experienced similar relative mass loss (see Figs. 3.9 and 3.10). At Site 3, scavenger-induced small sample size at 12 months affected the calculated relative mass loss, causing a large difference between relative mass loss of female and male bones (see Fig. 3.11). To better understand the disparities between the absolute mean mass loss trends and relative mass loss, we grouped all male bones together and all female bones together (regardless of site) and then performed a median split. For males, the smaller bones ranged from 4.04g to 8.00g and the bigger bones ranged from 8.15g to 14.16g. For females, the smaller bones ranged from 2.13g to 3.99g and the bigger bones ranged from 4.04g to 10.85g. When we compared the mean mass loss of smaller male bones to that of bigger female bones (a way of matching the bone sizes), we found no difference in absolute mean mass loss. When we compared the mean mass loss of smaller and bigger bones within the males alone, we found a significant difference (p-value of 0.0001). Overall, this indicates that, proportionally speaking, males and females lost similar amounts of bone mass, but in absolute terms, bigger bones lost more mass over time than smaller bones. However, it is important to note that most of the bigger male bones were from juveniles, so an age-based trend may be affecting the sex-based trend.

Scavenging. – Despite the leg bones being attached to arrays, scavenging had a substantial impact on the survival of experimental bones. Intensity of scavenging varied by site location and depositional setting. We used Janjua and Rogers' (2008) carnivore-related scavenging classification (Table 3.6) to rank the extent of observed scavenging on the bones. We also included invertebrate scavenging (detailed below) as evidence of mild or moderate scavenging. Bones deployed at Site 3 (Key Largo - tropical carbonate) experienced the most extensive carnivore-based scavenging, while bones at Site 1 (Sapelo Island - warm temperate siliciclastic) experienced the least. Figure 3.12 shows the number of bones in each site that endured extensive, moderate, mild, and no scavenging. Examples of scavenger damage are presented in Figure 3.13. Raccoons, opossums, and bobcats were the main large scavengers that impacted the marsh and terrestrial sites. Evidence of their presence included chewing of articular bone ends, tracks, scat, and raccoon sightings. Smaller organisms, such as crabs and insects, also intensely scavenged the subaerially-exposed bones. Mud and marsh crabs scratched and crushed the shafts or epiphyses of bones near their burrows. Ants, flies, and beetles began scavenging the bones for any soft tissue within one hour of deploying the arrays; however, insects were not found on the bones after two months. At Site 1's pond environment, one bone array was completely removed by a juvenile alligator. At Site 3's pond environment, all but 2 bones were gone by 6 months; snapping turtles from the pond are thought to be responsible. Overall, terrestrial and marsh/mangrove environments experienced the most extensive scavenging (complete removal), whereas pond environments underwent the least. Notably, scavenging appeared to taper off after about 4 months in all environments; this is contrary to the scavenging activity patterns observed for mammal bones (Janjua and Rogers 2008).

At Sites 2 and 3, juvenile bones were removed by scavengers more than adult bones (see bone counts in Figs. 3.6-3.8). Since juvenile bones started out bigger than adult bones, we tested whether bigger bones were being preferentially scavenged up to the six month point. Baseline bone masses were ranked in tertiles and then we used Fisher's Exact Tests to compare the number of "biggest" scavenged bones across the sites. As expected, Site 1 did not show a significant loss of big bones. However, both Site 2 and 3 did show a significant loss of the big bones (p-values of 0.0136 and 0.0396, respectively).

Surface bone weathering. – Table 3.7 presents the succession of subaerial weathering stages (WS) for bird bones described by Behrensmeyer et al. (2003). In our experiments, relative mass loss appeared to be closely tied with bone weathering stage, which varied by depositional environment. Figure 3.14 gives the total number of bones in each surface weathering stage per type of environment.

Bones with the least amount of relative mass loss were continuously submerged for at least 6 months in the siliciclastic freshwater pond environments. No evidence of exfoliation or cracking was observed on the bones, putting them at WS ½. However, most showed some degree of brown or black staining from sediments/algae; in five samples the marrow cavity was partially filled with a white fungus (Fig. 3.15).

In the terrestrial environments, physical bone weathering was more obvious and seemed to vary by site humidity level. At the warm temperate/siliciclastic dune (Sapelo Island), bones ranged from WS 1-2. Here the bones displayed evidence of bleaching, desiccation/exfoliation, and longitudinal cracking (Fig. 3.16). At the subtropical/ siliciclastic vegetated beach (Naples), the bones ranged from WS ½-1. Light brown staining was observed on the side of the bone in contact with the sediment, but bleaching and exfoliation of the bones was less evident. In the tropical/carbonate rock barren (Key Largo), humidity was very high and the bones remained lightly greasy for up to 6 months. After 12 months, the bones were soft and displayed green and pink microbial stains on both sides, along with a few hairline cracks, putting them in WS ½-1.

Relative bone mass loss and bone weathering were most severe in the marsh/mangrove environments and varied with differences in pH. At the warm temperate/siliciclastic tidal marsh (Sapelo Island), the pH of the water in the area was neutral to slightly alkaline. The bones, which reached weathering stage 2 (Fig. 3.17), displayed bleaching, flaking, and orange staining from sulfate-reducing bacteria (the bones had been covered in a layer of organic-rich mud in the field). The subtropical/siliciclastic mangrove marsh (Naples) had a more acidic pH and the bones there ranged from WS 1-5. The bones showed signs of corrosion (Fig. 3.18A), microbial and fungal activity (Fig. 3.18B), as well as "wet rot," leaving many of them crumbly or disintegrated (Fig. 3.18C). The tropical/carbonate mangrove marsh (Key Largo) had a more alkaline pH and the bones there reached WS 2. They showed evidence of wet rot, exfoliation, and black microbial stains.

As mentioned earlier, juvenile bones experienced greater relative bone mass loss compared to adult bones. This was reflected in their taphonomic condition as well: overall, juvenile bones were more degraded than adult bones. Also, within the same environment, juvenile bones typically reached WS 2 or greater twice as quickly as adult bones.

Relative mass loss was similar in male and female bones, but, overall, female bones showed more evidence of surface weathering than male bones did. Adult male bones were recovered in the best taphonomic condition from all sites. These results indicate that differences in bone composition or microstructure could be biasing the preservation potential of female birds.

Chemical and histological changes. – For the "total bone" WDS analyses testing lithology, no differences were found among control, siliciclastic-exposed, and carbonate-exposed bones for Ca and P weight percents or for Ca/P and Mg/Ca ratios (Fig. 3.19). Figure 3.19

indicates that there is slightly more Na and Mg in the carbonate-exposed bones compared to the control and siliciclastic-exposed bones, but these differences were not significant when analyzed with the GEE model.

In the “total bone” WDS analyses testing sex, the female control bone had slightly greater Ca and P weight percents than the male or female experiment bones, but showed no real difference from the male control bone (Fig. 3.20). The female control bone had a slightly greater Na weight percent than the male control bone, but there were no true differences from the experiment bones; also, there were no differences among the groups for Mg. Figure 3.20 also shows that there were no real differences among the groups for Ca/P or Mg/Ca ratios; the GEE model supported these results.

For the “bone area” WDS analyses, we focused exclusively on the Ca/P ratio because it is a good indicator of changes in hydroxyapatite (Jackes et al. 2001). Rapid mineral precipitation within bones, in association with bacteria, has been documented in laboratory settings (Daniel and Chin 2010), so we thought some of our experimental bones might show mineralogical changes. However, our analyses did not detect any significant differences among the control and experimental groups. Lithology did not affect bone area (Figure 3.21A shows that there is no difference among control, siliciclastic-exposed, and carbonate-exposed bones), but sex might affect the distribution of Ca^{2+} and PO_4^{3-} across the different bone areas. Figure 3.21B indicates that, compared to male bones, female bones have wider Ca/P ratio variation across the measured bone areas. Table 3.8 presents the mean differences between the Ca/P ratios of each bone area within each sex. Male bones have positive mean differences between the Ca/P ratios of each bone area, meaning that the periosteal cortical layer (PCL) has the greatest ratio, the medial cortical layer (MCL) has the second greatest ratio, and the endosteal cortical layer (ECL) has the smallest ratio. On the other hand, female bones have negative mean differences between the Ca/P ratios of each bone area, indicating that the ECL has the greatest ratio, the MCL has the next greatest ratio, and the PCL has the smallest ratio. These differences are not statistically significant, but it is a strong pattern. It suggests that male bones have higher Ca^{2+} and lower PO_4^{3-} relative to each other in the external portion of the bone, while female bones have higher Ca^{2+} and lower PO_4^{3-} relative to each other in the internal portion of the bone. This is likely a result of diet (see Table 3.1) and could mean that the CO_3^{2-} ion is substituting for PO_4^{3-} in the hydroxyapatite crystal lattice during life (Sobel and Hanok 1958). The last bone area that we examined was the female-specific medullary tissue. Figure 3.22 compares the literature-reported Ca/P ratio for avian medullary tissue (Taylor and Moore 1954; Ascenzi et al. 1963) with the observed ratios for medullary tissue in the female experimental bones. There was no difference from the reported value.

The BSE images showed no compositional (i.e., relative mineral density) differences among control and experimental groups, but the images do show some important histomorphological features. The male control sample (Fig. 3.23A) displays intact subperiosteal and cortical bone layers with a few larger areas containing marrow; Haversian and Volkmann’s canals appear enlarged, possibly indicating juvenile osteoporosis (Nicholson 1996). The female control sample (Fig. 3.23B) is, unfortunately, a poorly cut metaphyseal cross section of trabecular (spongy) bone, which makes it hard to use as a comparison point. Despite this problem, several patterns are clear. Subperiosteal bone was lost in all of the experimental bones, explaining some of the observed mass loss. “Destructive foci,” described by Hackett (1981) and Bell (1990), are indicative of bacterial bioerosion (Fernández-Jalov et al. 2010) and were extensive along the periosteal and endosteal cortical layers of male bones in the marsh and mangrove environments (Fig. 3.24F-H). Destructive foci were present only along the periosteal cortical layer in female bones (Fig. 3.25F and 3.25H), except in one case when medullary tissue was not present in the marrow cavity (Fig. 3.25G). Overall, male and female bones generally appeared similar in terms of histology, other than the presence of medullary bone. As expected, depositional environment played the biggest role in experimental bone microstructual degradation. Bones from the terrestrial and freshwater environments displayed the best histomorphology, showing only relatively thin cracks (Figs. 3.24A-E and 3.25A-E). Cracks may be indicative of physical weathering (Nicholson 1996), but Greenlee (1996) points out that some cracks may be an artifact of sample preparation. The Oxford Histological Index (OHI), established by Hedges et al. (1995), is presented in Table 3.9; we used it to determine the degree of histological damage to the experimental bones. For the marsh and mangrove environments, bones were classified as OHI 4, and for the terrestrial and freshwater environments, bones were classified as OHI 5. Within the bones in the marsh/mangrove environments, periosteal cortical layer and endosteal cortical layer (if affected) were classified as OHI 0-1, while the medial cortical layer remained in OHI 4-5. Two types of microscopical focal destruction were observed: linear-longitudinal and budded tunneling; they are the most common types of bacterial alteration of bone (Hackett 1981; Jans et al. 2004). Wedl tunnels, associated with fungal attack (Hackett 1981; Davis 1997), were not observed despite macroscopic evidence of fungal hyphae on some bones.

Weathering profile for avian bones deposited in hot, humid environments. – Based on the comprehensive results of our modern taphonomic experiments, we assembled a bone weathering profile for avian bones deposited in humid warm temperate to tropical coastal environments (Table 3.10). Compared to findings of Behrensmeyer et al. (2003), avian bones subaerially exposed in terrestrial and tidal environments in hot, humid coastal regions undergo slightly more rapid weathering than avian bones subaerially exposed in semiarid to arid environments. The bones that Behrensmeyer and her colleagues examined were exposed for 2-3 years, whereas our experiment lasted only one year. Additionally, in our experiment, we observed surface corrosion and wet rot in the marsh/mangrove environments, as well as extensive scavenging and microbial activity.

Discussion

Bone mass loss as evidence of weathering. – Bone is a complex biological tissue composed of approximately 21% organic material, 70% hydroxyapatite (mineral portion), and 9% water (Pfretzschner 2004). Of the organic material, collagen protein makes up about 18% and lipids (fats) make up the remaining 3% (Pfretzschner 2004). During bone degradation, bacteria rapidly colonize the bone's pore space and release digestive enzymes that drive the hydrolysis of the collagen protein's peptide bones (Hare 1980). As the organic material is digested, this causes shrinkage and tensional stress that leads to some of the surface bone cracking originally identified by Behrensmeyer in 1978 (Piepenbrink 1986). Thus, bone mass loss due to degradation of organic material can be used as evidence of early bone weathering. Bone mass loss can also come from dissolution of the bone mineral itself. Hydroxyapatite, which is composed of small and poorly crystalline mineral grains called crystallites, begins to undergo dissolution and remineralization at the same time that collagen protein is broken down (Trueman and Tuross 2002). One example of this is corrosion of the bone surface when in contact with acidic water or soil (Fernández-Jalov et al. 2010). Due to tidally-influenced fluctuation of pH in the mangrove marsh environment at Site 2, corrosion was observed in some of our bone samples. Although spectrometric analyses of these samples did not indicate significant mineralogical changes, our results do show that early taphonomic changes to bone can occur quite quickly (also see Davis 1997; Janjua and Rogers 2008). We noted no difference between the overall mass loss in bone halves exposed for six months and those exposed for twelve months. This indicates that rapid bacterial degradation of readily-accessible organic matter (and surface corrosion, if in an acidic environment) is likely responsible for the majority of bone mass loss during the first year of exposure for bird bones.

Importance of climate on bone mass loss. – The climatic region in which a vertebrate carcass or bone is deposited affects bone weathering. This is made clear by the work of Fernández-Jalov et al. (2010). They exposed mammal carcasses subaerially in the temperate locale of Neuadd, Wales, for 30 years and compared observed bone weathering patterns to those of mammal carcass bones exposed for 25 years in the arid climate of Amboseli National Park in Kenya (documented by Behrensmeyer [1978], Tuross et al. [1989], Trueman et al. [2004], and Western and Behrensmeyer [2009]). Fernández-Jalov and colleagues found that, compared to the Amboseli bones, the Neuadd bones did not show as much collagen degradation or surface weathering. Their results suggest that climate parameters, such as differences in solar radiation and moisture, may be partially responsible for the disparate results of the two studies (Fernández-Jalov et al. 2010). Although the climates that we performed our experiments in did not differ greatly from each other (the only major difference was that Key Largo had significantly greater humidity than any of the other sites), we were able to identify two parameters – air temperature and humidity – that influence mass loss in subaerially-exposed avian bones. For each degree increase in temperature or percent increase in humidity, there was a corresponding increase in loss of bone mass. Chemical reactions speed up as temperature rises

(Mays 2010); nitrogen (and thus protein) loss from bone increases with higher temperatures (Von Endt and Ortner 1984). Relative humidity controls the concentration of water in materials and water acts as a reactant in decay processes (Alten 1999), so higher humidity can increase bone degradation rates. Our results provide evidence of the role of climatic region on vertebrate bone weathering rates generally and they offer important implications for avian bone preservation potential during global warming. Avian bone preservation potential is likely to be decreased during such periods. This could be a substantial source of bias in the avian fossil record.

Connecting site location and depositional environment to bone mass loss. – Despite the relative lack of climate-based contrasts among the three field sites, mass loss trends at each site did differ significantly. The bones at Site 1 (Sapelo Island, Georgia) experienced significantly less mass loss than those at either Site 2 (Naples/Fort Myers, Florida) or Site 3 (Key Largo, Florida). The bones at Site 2 experienced significantly less mass loss than those at Site 3. Two variables are proposed as sources of these differences: site lithology/geochemistry and scavenger activity. Site lithology and geochemistry are important factors to consider when comparing the bone mass loss trends because lithology affects many of the physical and mineralogical attributes of soil (Chadwick and Graham 2000). The geochemistry of a soil determines its pH, moisture content, oxygen concentration, and microbial community structure (Chadwick and Graham 2000), all of which affect degradation of bone. Bones in the siliciclastic sites were exposed to slightly acidic to slightly alkaline pH, whereas bones in the carbonate site were exposed to more strongly alkaline pH. Since many strains of bacteria thrive well in alkaline environments (Nicholson 1996), we hypothesize that the bones in the carbonate site experienced greater mass loss from more intense microbial degradation, especially of the more porous epiphyses

(Nicholson 1998), due to the consistently moist conditions. The second variable, scavenger activity, is also important to consider because of resulting reductions in sample size. Site 3 was decimated by scavenging when 42 bones were removed in the first two months, whereas only 4 and 6 bones were removed during the same period at Sites 1 and 2. Scavenger activity is directly related to scavenger access to the sites, which varied depending on site location. Sapelo Island is an isolated barrier island with a comparatively small population of large scavengers like raccoons and opossums. At Rookery Bay National Estuarine Research Reserve in Naples, raccoons, rats, and other large scavengers are attracted by the food and trash left by humans visiting nearby beaches. At Florida Gulf Coast University in Fort Myers, the bones were submerged for nine months in the pond, so juvenile alligators and some fish, such as tilapia, are thought to be the likely scavengers for that site. John Pennekamp Coral Reef State Park in Key Largo is a popular tourist spot and large populations of raccoons, opossums, rats, and gulls, along with a smaller population of bobcats, have developed in response to the human activity there.

We could not discern any significant differences among the absolute mass loss trends in the three depositional environments (terrestrial, marine, and freshwater). This is most likely due to substantial bone removal by scavengers in Sites 2 and 3. Overall, bones that were fully submerged for at least 6 continuous months in the freshwater pond environments were in the best condition after a year of exposure. This provides further support for the idea that bacterial and fungal activity is slowed by waterlogging and submersion in relatively anoxic water environments (Nicholson 1996). The bones that survived the scavenging in the terrestrial environments were also in fairly good condition primarily because, compared to the marsh/mangrove environments, the dune, beach, and rock barren areas remained relatively dry (although the rock barren at Site 3 was much more damp than the dune at Site 1 or the vegetated beach at Site 2). Our results indicate that microbial activity is slowed in dry settings and that desiccation may promote preservation (Child 1995). Bones recovered from the marsh and mangrove-marsh environments were in the worst taphonomic condition as a result of intense microbial attack and wet/dry cycling from tidal action. The surface corrosion and “wet rot” we observed support the findings of Nicholson (1996), who reported that alternate wetting and drying of bone accelerates degradation.

Age and sex as taphonomic factors influencing bone mass loss and preservation potential. – In mammals, juvenile bone has been shown to be more porous and to weather more rapidly than adult bone (Robinson et al. 2003). Our results indicate that this is true for birds as well. In two of the three field sites, the juvenile bird bones experienced greater absolute mean mass loss than the adult bird bones. Since the juvenile bones were bigger than the adult bones at the start of the experiment, one might postulate that the juveniles’ greater mass loss is just a function of size. However, proportionally speaking, the juvenile bones at all sites lost more mass than the adult bones. This means that, despite the size difference, the bone mass loss trends were correlated with an age-related factor. In *Branta canadensis* (Canada goose), long bones show a regular pattern of decreasing porosity from juvenile to adult (Tumarkin-Deratzian, 2003). Similarly, the leg bones of juvenile broiler chickens are known for being porous and subject to fracture, due to genetic selection for fast growth (Rawlinson et al. 2009). Thus, using juvenile broiler chicken bones enabled us to test our hypothesis that certain microstructural bone characteristics, such as high porosity, increase avian bone mass loss and weathering. More experimental studies comparing weathering rates of adult and juvenile bones from a variety of avian species are needed to confirm this pattern. Nevertheless, it seems reasonable to interpret our results as supporting the idea that juvenile bird bones' increased porosity makes them more susceptible to weathering and loss from the fossil record than adult bird bones.

Sexual size dimorphism, typically seen as larger males, is common in avian species (see Winker et al. 1996; Kissner et al. 2003; Kalmbach and Benito 2007; Alonso et al. 2009; Hallgrimsson et al. 2011), although there are some groups (e.g., raptors, owls, moas) that exhibit reversed sexual size dimorphism. Domestic chickens exhibit male-biased size dimorphism (Mignon-Grasteau et al. 1998), but to a slightly lesser extent when compared with wild jungle fowl populations (Remeš and Székely 2010). Differences in body size affect avian bone microstructure, as do reproductive hormones (discussed earlier). Although bone density does not appear to vary between male and female birds (Zulauf-Fischer et al. 2006; Almeida Paz et al. 2008), cortical thickness and lipid content do, with females having thinner cortical bone and higher lipid (fat) content (Oviedo-Rondón and Ferket 2005; Suchý et al. 2009). It is important to note that in juvenile broiler chickens, the cortical bone of males is more porous than that of females (Rose et al. 1996). Our results on the relationship between sex and weathering-related bone mass loss were complicated. Overall, they indicate that male and female bird bones tend to lose similar relative amounts of mass and that bigger bones lose more absolute mass over time than smaller bones, regardless of sex. However, some of the observed trend can be explained by the fact that many of the biggest male bones were from juvenile broilers. Since their bones had more porous cortical tissue, they underwent more intense weathering. Male bird bones were recovered in better taphonomic condition than female bird bones at all sites, which suggests that the greater bone fat content in females may be related to increased bone weathering. Thus, for male-biased sexually dimorphic bird species, there could be a preservational bias toward adult males in the avian fossil record.

Scavenging effects on avian bone preservation potential. – Scavenging is a well known taphonomic factor that decreases the preservation potential of vertebrate carcasses and bones (Lyman 1994). Avian carcasses are especially subject to intense carnivore-related scavenging (Oliver and Graham 1994). Since our experimental arrays were deployed in close proximity to the bird carcasses, many scavenging organisms were attracted to the sites and large numbers of individual array bones were removed when carcasses were scavenged. Our results indicate that avian bones deposited in more remote locations, like isolated barrier islands, are less likely to undergo the extensive scavenging of more accessible locations. Avian bones in pond environments are less subject to scavenging than bones in terrestrial and tidal environments. Our results also indicate that bigger avian bones (here, juvenile bones) are more frequently subject to scavenging than smaller bones, suggesting that, in events such as mass die-offs, carnivorous scavengers may preferentially target larger avian carcasses and bones. Additionally, we found that scavenger activity on avian bones tended to taper off after four months of exposure. This is in contrast with scavenger patterns on mammal bones documented by Janjua and Rogers (2008), who found that animal activity was not limited to a specific time period after death. Differences in avian and mammalian bone microstructure may account for this: compared to mammals, bird bone is denser and contains less trabecular bone tissue (Dumont 2010), which is spongy and fairly easy to chew. Early opossum-like mammals have been traced back to the late Cretaceous (Horovitz et al. 2009), so scavenger-related bias in the avian fossil record is likely.

Micro-level evidence of bone alteration. – Wave-dispersive spectrometry analyses did not show any significant compositional differences in the percent of Ca, P, Na, or Mg among the test groups of avian bones. This is not surprising because chemical recrystallization of hydroxyapatite progresses at an extremely slow rate, although it starts at the same time as collagen degradation (Trueman and Tuross 2002). Bacterially-mediated precipitation of minerals in bone may happen at a much faster rate (Carpenter 2005; Daniel and Chin 2010), but this has not been demonstrated in the field and the bones examined in this study did not show evidence of bacterially-mediated mineralogical changes. One year of exposure is unlikely to be long enough to detect significant changes in mineral composition. Despite this, the WDS analyses did indicate an interesting pattern in the Ca/P ratios of male and female bone areas. Male bones displayed highest Ca/P ratios in the periosteal layer, but females had highest Ca/P ratios in the endosteal layer. These differences could potentially influence recrystallization rates, since carbonate replaces phosphate in the hydroxyapatite crystal lattice during life via dissolved bicarbonate in the blood (Krueger and Sullivan 1984), and an increased presence of carbonate in bone leads to increased chemical reactivity in taphonomic settings (i.e., dissolution) (Jackes et al. 2001). Although these bone area differences most likely vary by diet and reproductive cycle timing, it is possible that other galliform birds, such as quails, turkeys, and pheasants, might show similar Ca/P ratio bone area distributions. X-ray diffraction analyses would help in quantifying the carbonate content of the bones and shed light on the potential for differential recrystallization in male versus female avian bones.

The backscattered electron images showed that subperiosteal bone was lost across the board. No differences in mineralization were detected among the test groups, but cracking and microbial bioerosion were evident, especially in the tidal environments. Bacterial attack was limited to the periosteal and endosteal bone layers; this is similar to the type and degree of microbial alteration seen in modern mammal bones (Fernández-Jalov et al. 2010). The presence of medullary tissue in female bones seemed to protect their endosteal layer from microbial attack. This suggests that histological study of archaeological and paleontological avian remains could provide a rough estimation of the number of reproducing females in an assemblage. Medullary tissue itself has been documented in avian remains at several archaeological sites (Rick 1975; Driver 1982; Lentacker and Van Neer 1996), as well as in the fossils of theropod dinosaurs (Schweitzer et al. 2005). Thus, by looking inside the long bones of ancient birds, it may be possible to develop a better understanding of avian paleoecology.

Modified weathering profile for avian bones in hot, humid coastal environments. – Coastal environments in warm temperate, subtropical, and tropical regions have provided habitats for birds since the Jurassic. Conducting actualistic experiments in these areas is crucial for developing a better understanding of avian taphonomy and potential biases in the fossil record. Our experiments indicated that avian bones in these types of environments weather at a slightly more rapid rate than avian bones in arid savanna environments, although bones at both locations peaked in WS 1 (Behrensmeyer et al. 2003). Biological (both scavenging and microbial) and physiochemical processes (i.e., UV radiation, cyclical wetting/drying, humidity) play important roles in the breakdown of the collagen and lipid content of the bones and in the degradation of inorganic bone mineral. Surface corrosion and wet rot, linked with bacterial attack, are major sources of degradation in tidal environments. Our results suggest that subaerially-exposed avian bones in these types of environments have a fairly low preservation potential, although adult male bones were frequently recovered in good taphonomic condition. Similarly, Behrensmeyer et al. (2003) found that bones from adult birds of larger body size experienced less surface weathering than bones from birds of smaller body size. The Behrensmeyer et al. (2003) study did not examine sexual size dimorphism; nevertheless, since larger bones were overrepresented generally, and many of the species (e.g., crane, stork, ostrich) are known to exhibit male-biased sexual size dimorphism in life, it seems likely that the

Amboseli assemblage was biased toward adult male bones. The potential for future investigation is great, comparing avian bone weathering rates across a broad range of climate regimes and depositional environments, potential scavengers and microbes, as well as investigating the male-biased pattern identified here over multiple species, including those that exhibit reverse sexual size dimorphism.

Conclusions

1. Avian bones undergo slightly more rapid subaerial weathering in hot, humid coastal settings compared to arid savanna environments. Scavengers, microbes (especially bacteria), and localized conditions influenced by climatic region heavily impact the preservation potential of avian remains. Wet rot and surface corrosion in tidal environments are especially destructive. Bones in freshwater environments undergo little physical or chemical taphonomic change, which suggests that continuous submersion in oxygen-depleted environments is best for preservation of avian remains. Overall, paleoecological interpretations may be less reliable from humid coastal environments.

2. Age and sex are important sources of bias in the avian record. Juvenile bones lose more bone mass and typically weather twice as quickly as adult bones due to differences in porosity. In species exhibiting male-biased sexual size dimorphism, female bones experience greater surface weathering compared to male bones, despite the fact that both sexes undergo similar relative mass loss over time. Medullary tissue may protect the endosteal layer of female bones from microbial attack and it

has potential as an indicator of sex in ancient deposits, so its presence should be investigated in the archaeological and paleontological records.

3. WDS analyses identified higher Ca/P ratios in the periosteal cortical layer in males and higher Ca/P ratios in the endosteal cortical layer in females. These differences indicate that diet-derived carbonate has substituted for phosphate in the hydroxyapatite crystal lattice in these areas, which could be important for (much) later dissolution and recrystallization. XRD analyses should be utilized to quantify the amount of carbonate present.

4. More studies examining the taphonomy of subaerially-exposed, buried, and submerged avian remains are needed. Information from a wide variety of species, climates, and environments will help to shed light on our understanding of avian taphonomy and its utility in the fields of paleoecology and paleoenvironmental reconstruction.

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Figure 3.1 – Tibiotarsus (A, B) and femur (C, D) halves before deployment and array (E) setup. Scale in centimeters.

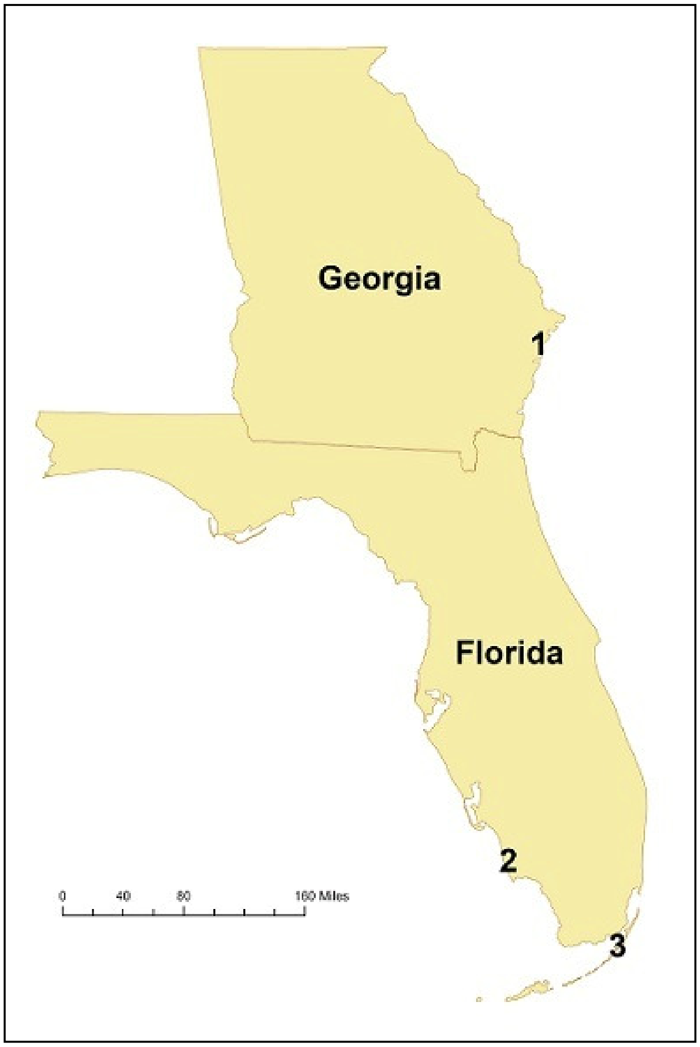

Figure 3.2 - Schematic of the field sites. The sites are indicated by number. Site 1 (siliciclastic) was at the University of Georgia's Marine Institute at Sapelo Island, Georgia. Site 2 (siliciclastic) was in Naples, Florida, at Rookery Bay National Estuarine Research Reserve and in Fort Myers, Florida, at Florida Gulf Coast University. Site 3 (carbonate) was at John Pennekamp Coral Reef State Park in Key Largo, Florida. Modified from Digital Vector Maps (2006).

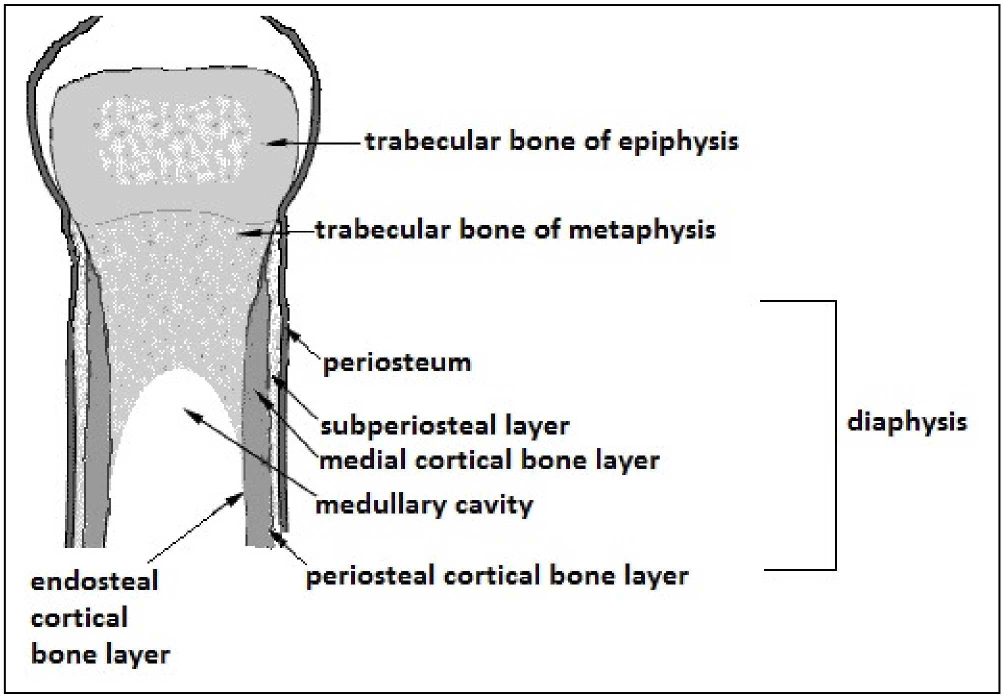

Figure 3.3 - Schematic of the different bone areas and nomenclature used in Chapter 3. Modified from Ladd et al. (2003).

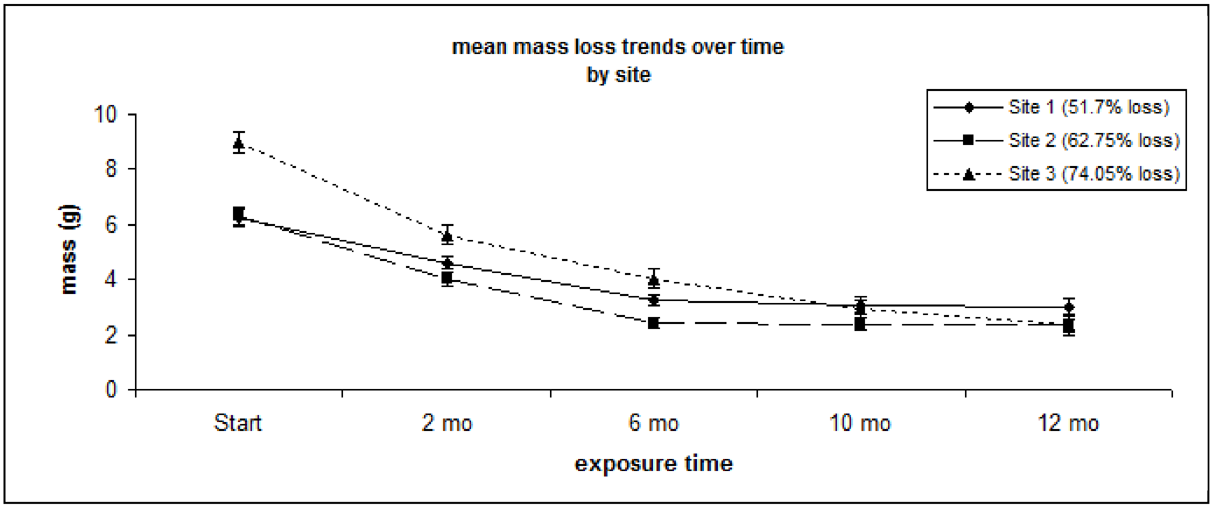

Figure 3.4 – Overall bone mass loss trends at each site. This includes absolute mean mass loss trends and relative mass loss. The mass-loss trend at Site 3 (carbonate) was steepest. The trends begin to stabilize after six months, indicating that the first six months of exposure are crucial in determining preservation potential. See Appendix C for bone count information per unit time.

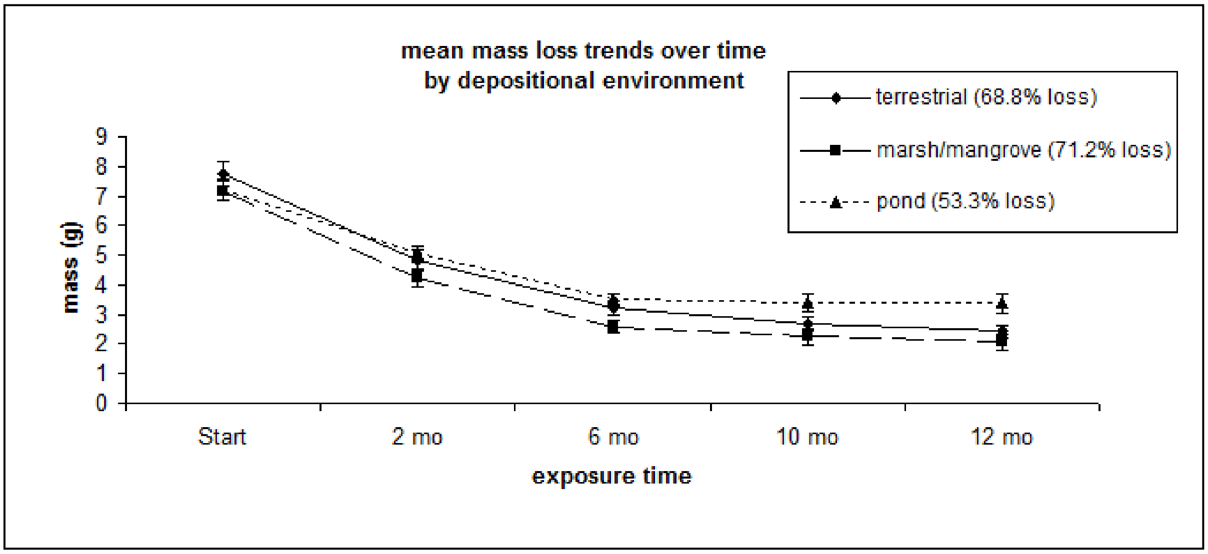

Figure 3.5 - Overall bone mass loss trends in each environment. This includes absolute mean bone mass loss trends and relative mass loss. The trends were not significantly different from each other. See Appendix D for bone count information per unit time.

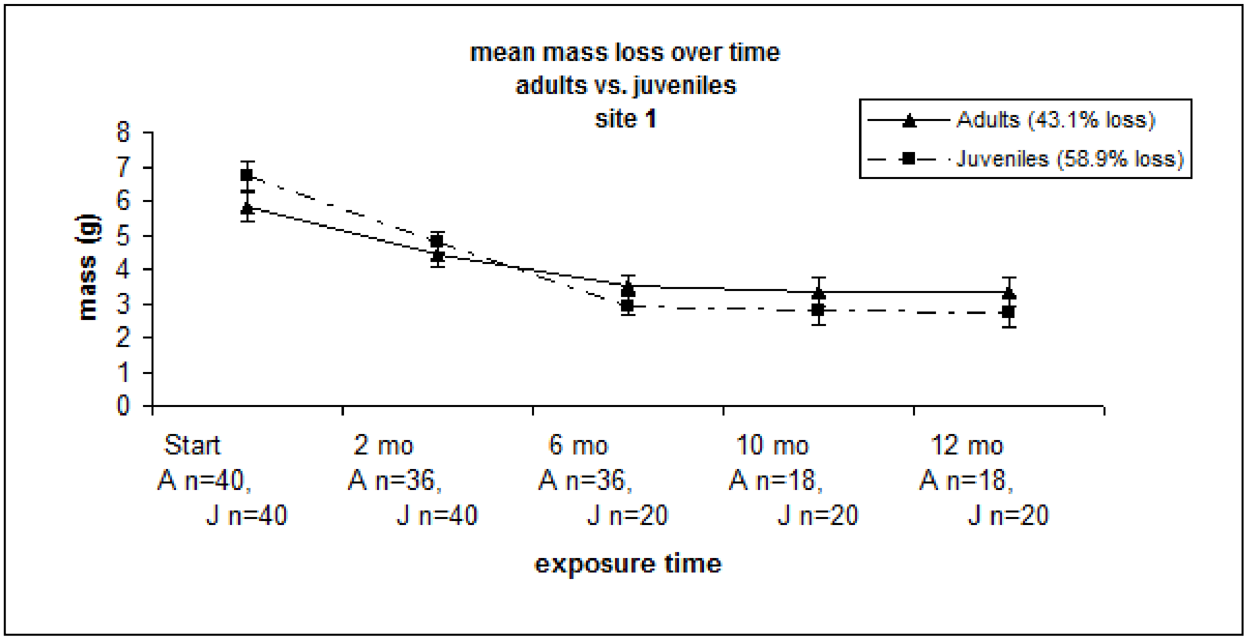

Figure 3.6 – Bone mass loss for juvenile and adult bones at Sapelo Island, Georgia. This includes absolute bone mass loss trends and relative mass loss. Juvenile bones lost significantly more mass than adult bones (p-value of 0.0125). Bone counts for each age, per unit time, are indicated by the letters “A” and “J.”

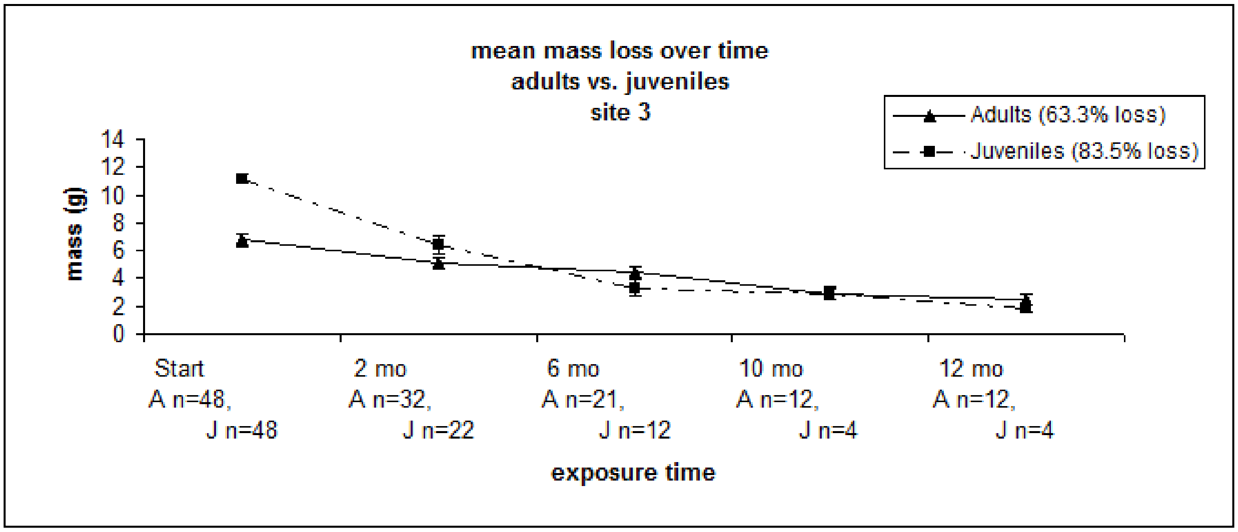

Figure 3.7 – Bone mass loss for juvenile and adult bones at Kay Largo, Florida. This includes mean absolute bone mass loss trends and relative mass loss. Juvenile bones lost significantly more mass than adult bones (p-value of 0.0001). Bone counts for each age, per unit time, are indicated by the letters "A" and "J."

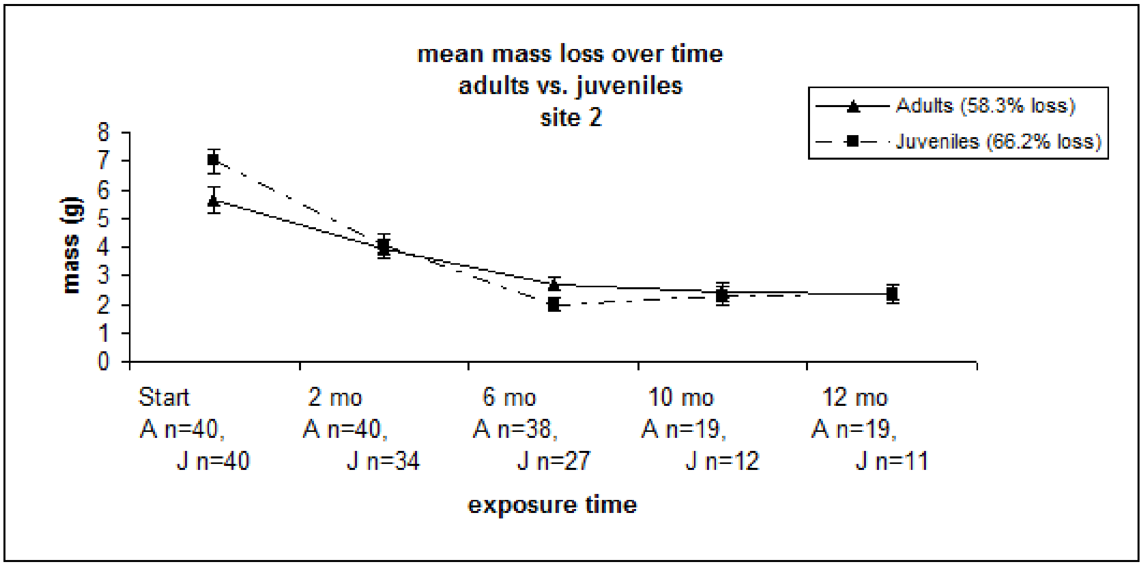

Figure 3.8 – Bone mass loss for juvenile and adult bones at Naples/Fort Myers, Florida. This includes mean absolute bone mass loss trends and relative mass loss. There was no difference between the mass-loss trends for juvenile and adult bones. Bone counts for each age, per unit time, are indicated by the letters “A” and “J.”

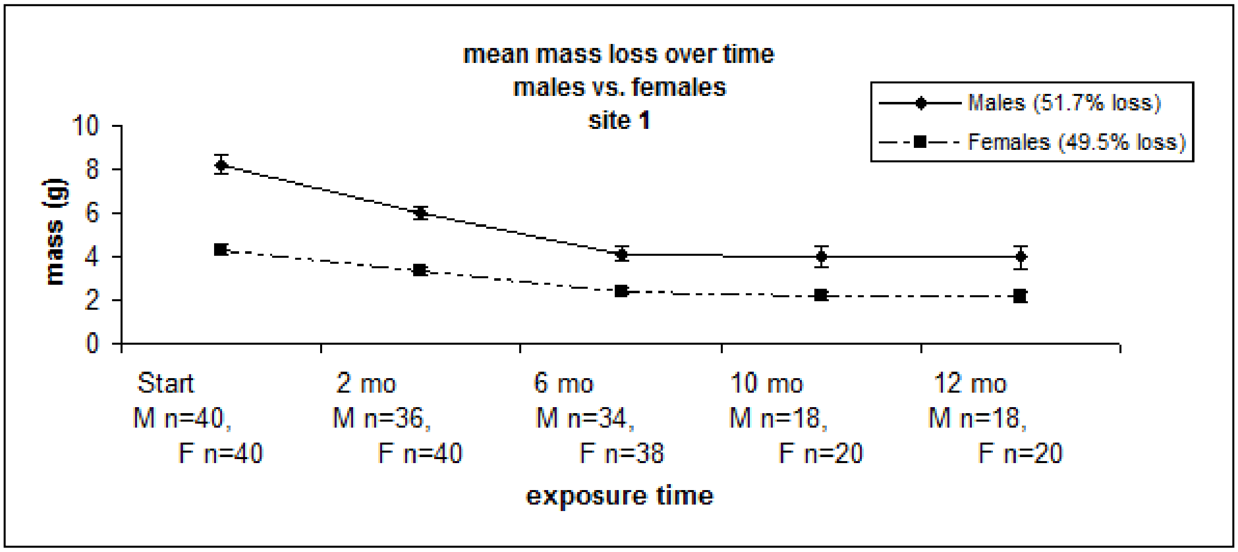

Figure 3.9 – Bone mass loss for male and femalebones at Sapelo Island, Georgia. This includes mean absolute mass loss trends and relative mass loss. Male bones lost significantly more mass than female bones (p-value of 0.0123). Bone counts for each sex, per unit time, are indicated by the letters "M" and "F."

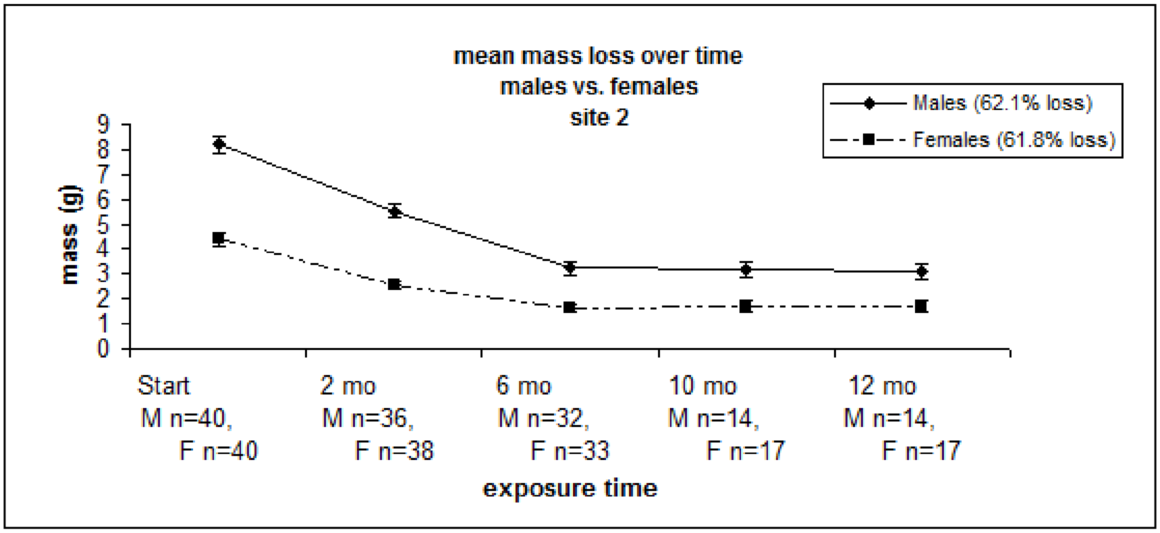

Figure 3.10 – Bone mass loss for male and female bones at Naples/Fort Myers, Florida. This includes mean absolute mass loss trends and relative mass loss. Male bones lost significantly more mass than female bones (p-value of 0.0002). Bone counts for each sex, per unit time, are indicated by the letters "M" and "F."

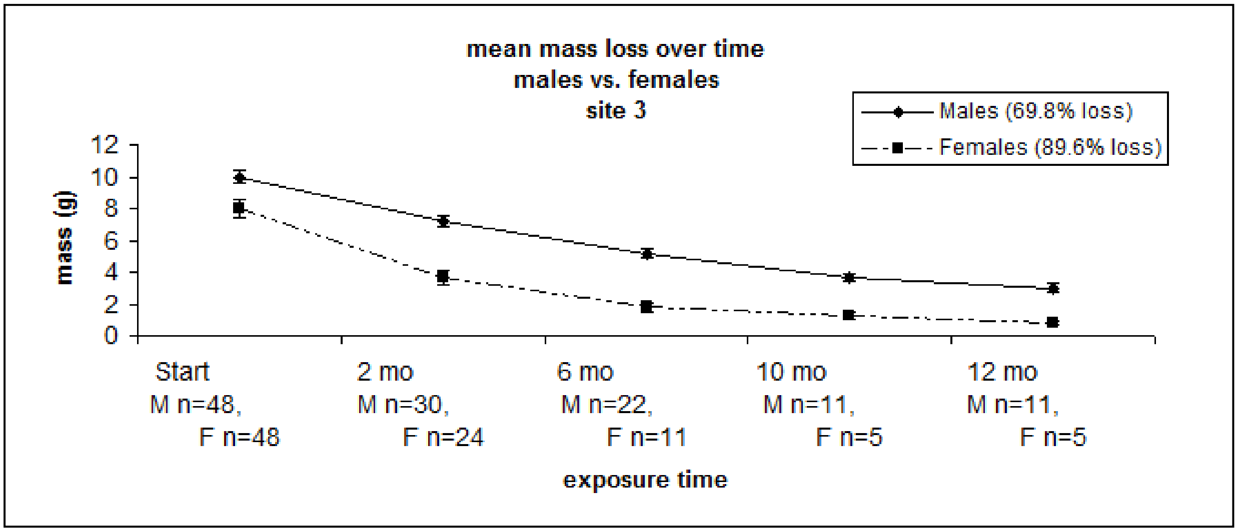

Figure 3.11 – Bone mass loss for male and female bones in Key Largo, Florida. This includes mean absolute mass loss trends and relative mass loss. There was no significant difference between the trends at this site, suggesting that mass loss was widespread across both sex groups. Bone counts for each sex, per unit time, are indicated with the letters "M" and "F."

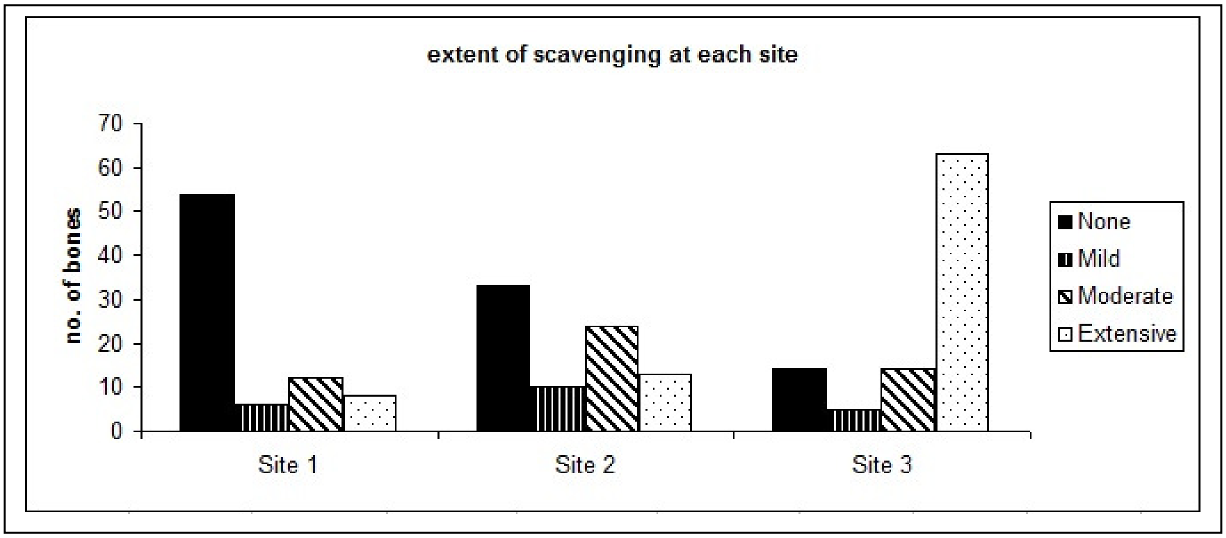

Figure 3.12 - Number of bones that experienced mild, moderate, extensive, or no scavenging at each field site. Extent of scavenging is based on classification by Janjua and Rogers (2008) for carnivores, with addition of invertebrate-related scavenging. Site 1 = Sapelo Island, Georgia (80 bone halves total deployed); Site 2 = Naples/Fort Myers, Florida (80 bone halves total deployed); Site 3 = Key Largo, Florida (96 bone halves total deployed).

Figure 3.13 - Extent of scavenging on experimental bones. (A) No scavenging – the entire bone half is present, although weathered. (B) Mild scavenging – only one side of the epiphysis has been chewed off. (C) Moderate scavenging – the entire epiphysis has been removed. (D) Extensive scavenging – the majority of the bone is gone, leaving only a small fragment plus cartilage. Scale in centimeters. Scavenging classification based on Janjua and Rogers (2008).

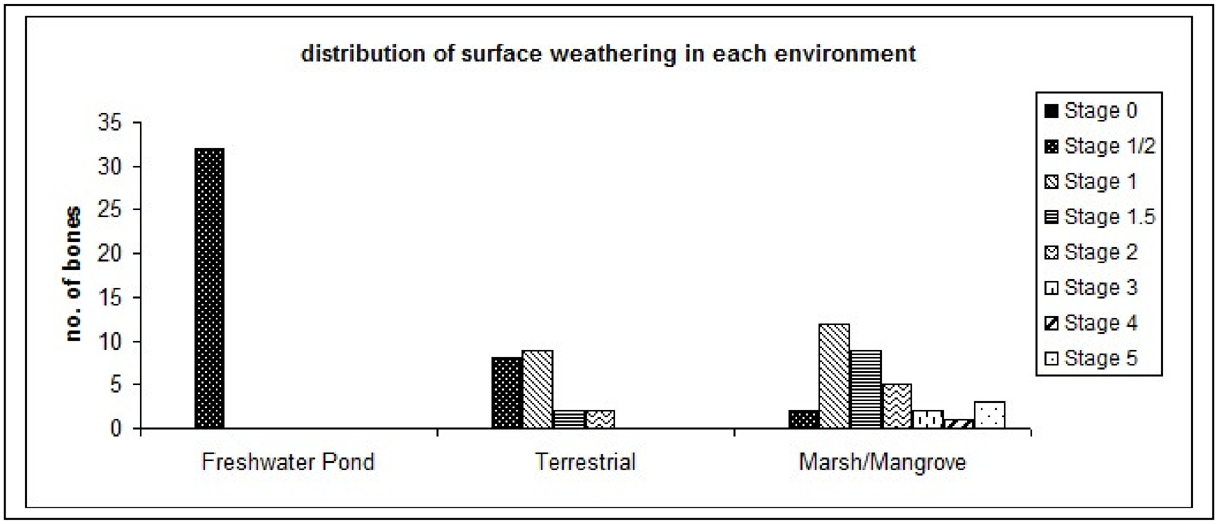

Figure 3.14 - Distribution of bones exhibiting each surface weathering stage. The bones were exposed for 12 months and are sorted by depositional environment. Of the three environments, marshes/mangroves showed the greatest range of exhibited surface bone weathering stages. Freshwater Pond = 32 bones; Terrestrial = 21 bones; Marsh/Mangrove = 34 bones. Weathering stages based on classification by Behrensmeyer (1978) and Behrensmeyer et al. (2003).

Figure 3.15 - Bone exhibiting weathering stage ½ (Fort Myers pond). White fungus is present in the marrow cavity. This bone remained submerged for nine months in the freshwater pond at FGCU in Fort Myers, Florida. Scale in centimeters.

Figure 3.16 - Bone exhibiting weathering stage 2 (Sapelo Island dune). Weathering stage 2 includes exfoliation, flaking, and cracking. This bone was deployed in the sandy dune environment on Sapelo Island, Georgia. Scale in centimeters; round hole was manmade at start of experiment to enable attachment to array.

Figure 3.17 - Bone exhibiting weathering stage 2 (Sapelo Island marsh). This bone was deployed in the tidal marsh at Sapelo Island, Georgia. Scale in centimeters; round hole is manmade to enable attachment to array.

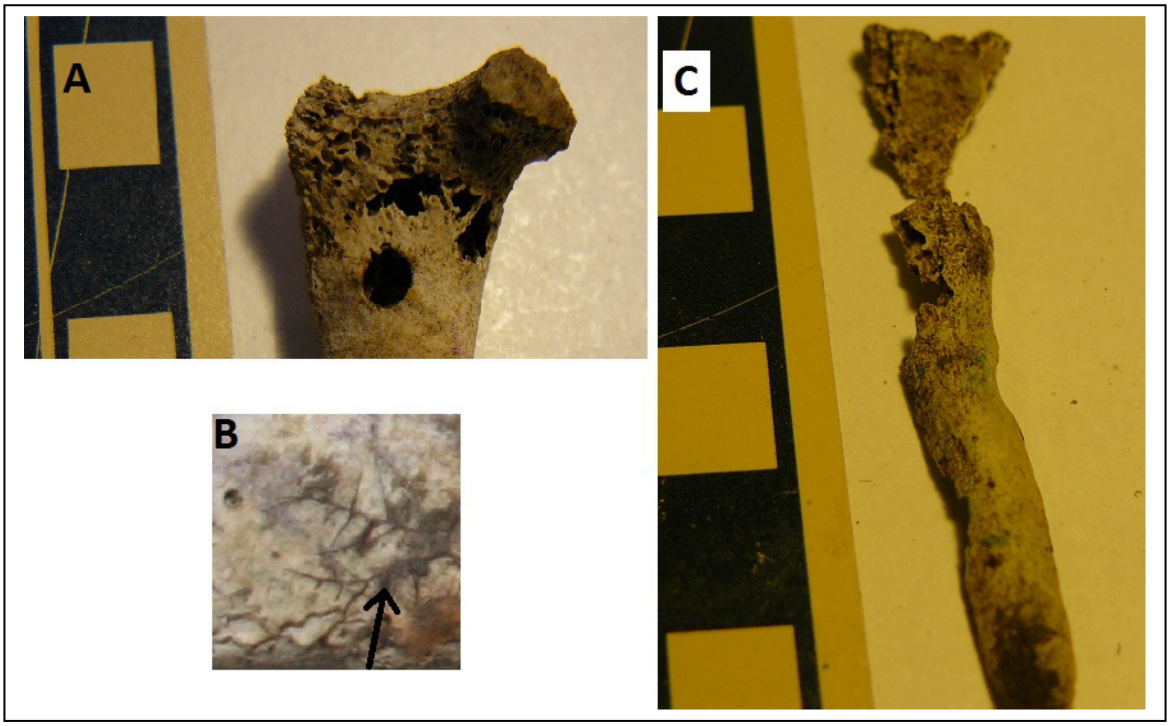

Figure 3.18 - Surface weathering and degradation of experimental bones in the Naples marsh. (A) Corrosion of bone surface (round hole is manmade). (B) Branching fungal hyphae (arrow) on surface of bone. (C) Extensive disintegration of bone (weathering stage 5). Scale in cm.

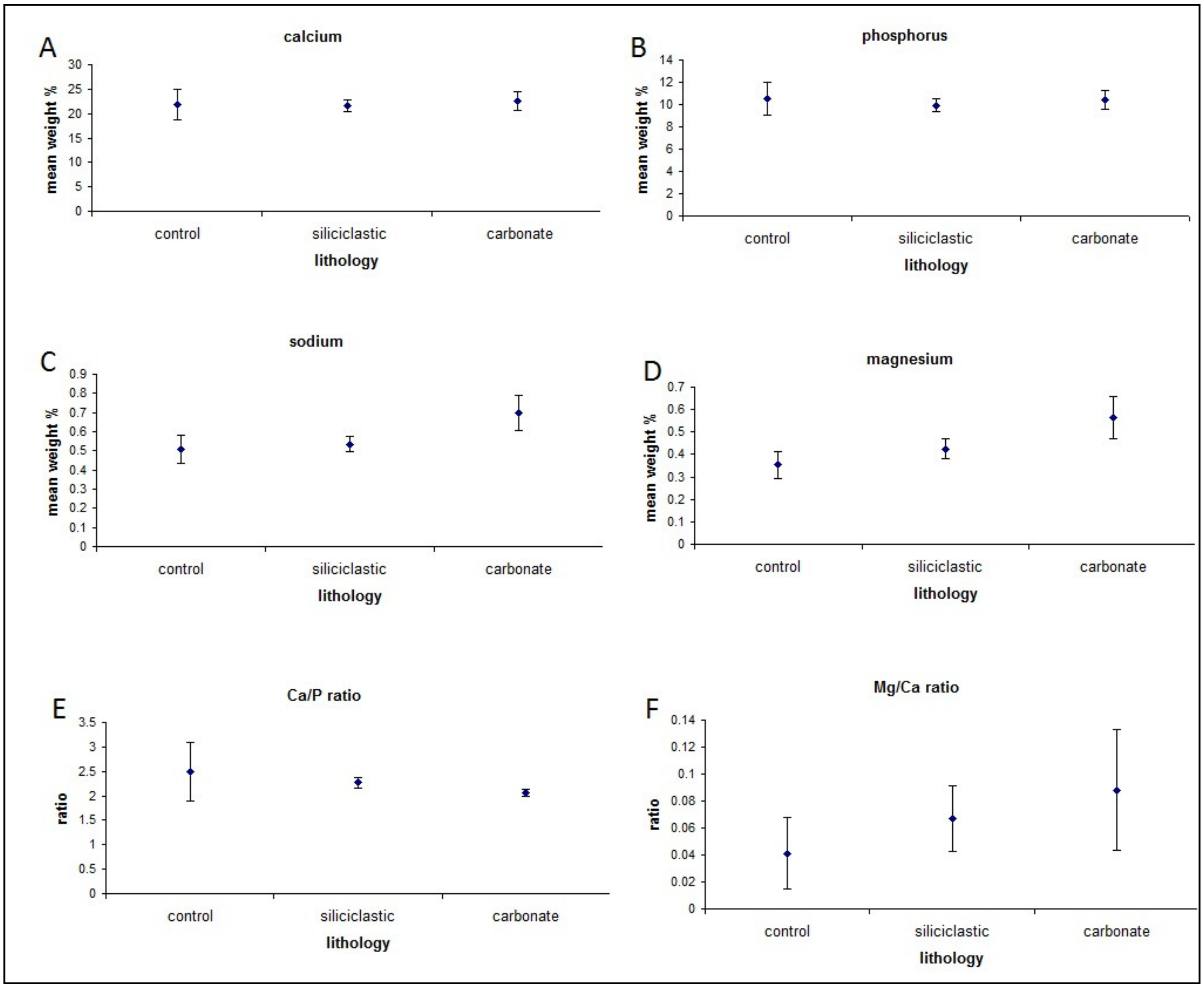

Figure 3.19 - Mineral element content of control bones and experimental bones. The bones are sorted by lithologic setting. Mean elemental weight percentages or ratios with corresponding standard errors are given. (A) Calcium; (B) phosphorus; (C) sodium; (D) magnesium; (E) Ca/P ratio; (F) Mg/Ca ratio. GEE statistical models showed no differences among the groups for elemental percentages or ratios.

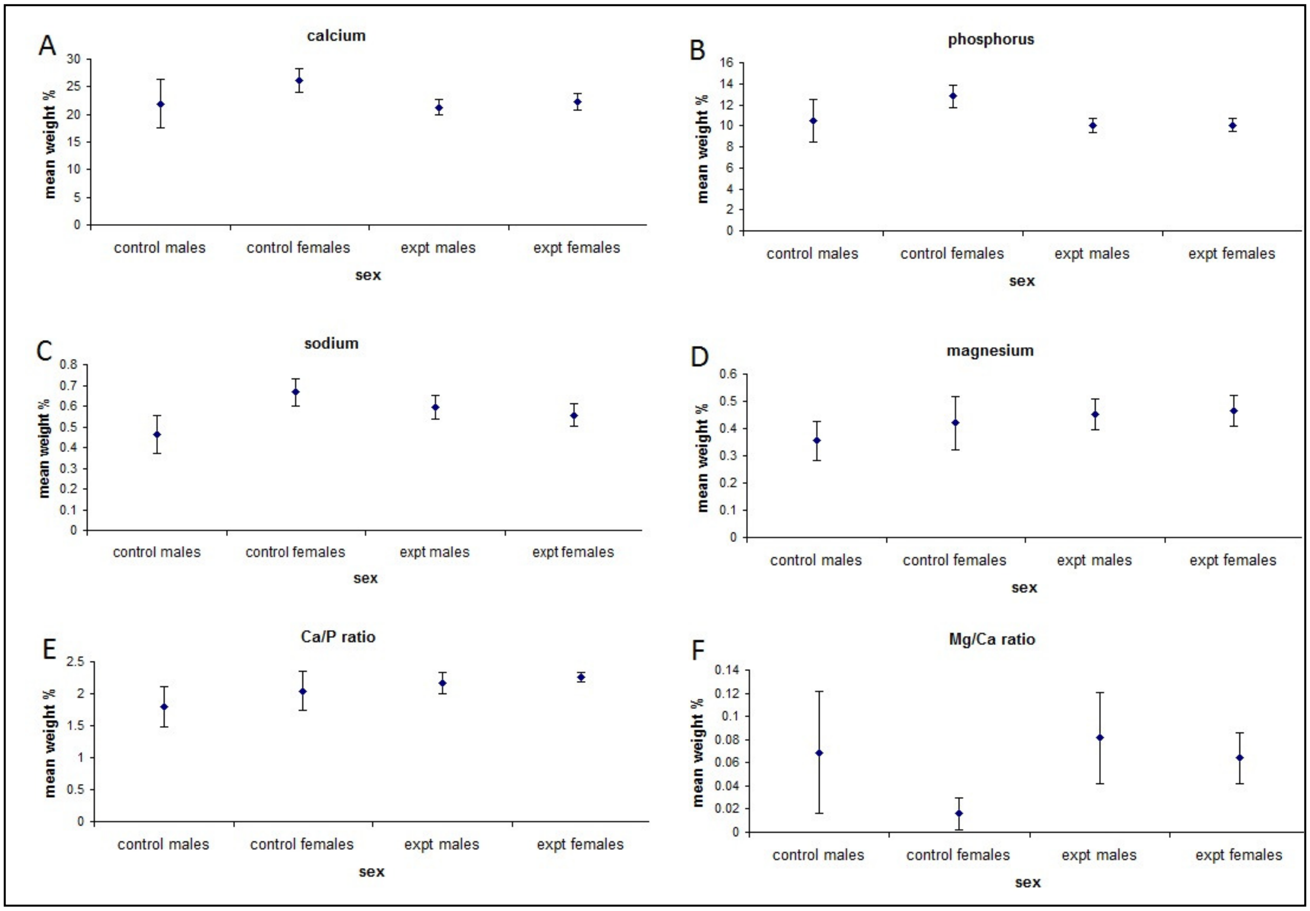

Figure 3.20 - Mineral element content of sexed control and experimental bones. Mean elemental weight percentages or ratios with corresponding standard errors are given. (A) Calcium; (B) phosphorus; (C) sodium; (D) magnesium; (E) Ca/P ratio; (F) Mg/Ca ratio; “expt” = experiment. GEE statistical models showed no differences among the groups for elemental percentages or ratios.

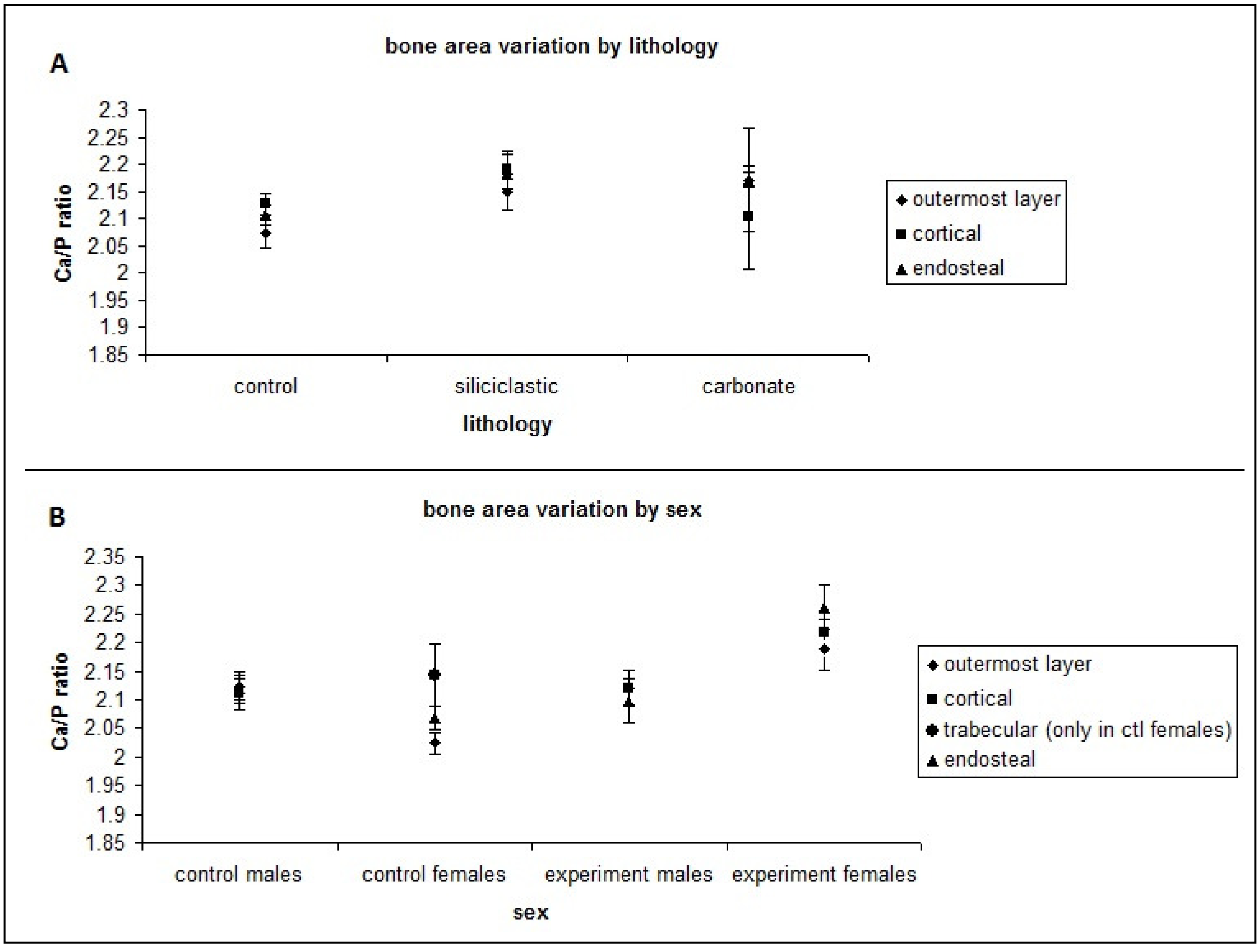

Figure 3.21 – Mean bone Ca/P ratios for different measurement sites. Mean Ca/P ratio and corresponding standard errors are given. (A) Ca/P variation in different bone areas in control, siliciclastic-, and carbonate-exposed bones. (B) Ca/P variation in different bone areas in sexed control and experimental bones. Lithology does not appear to affect bone area variation, but sex might. "Outermost layer" = subperiosteal layer in controls and periosteal cortical layer in experimental bones.

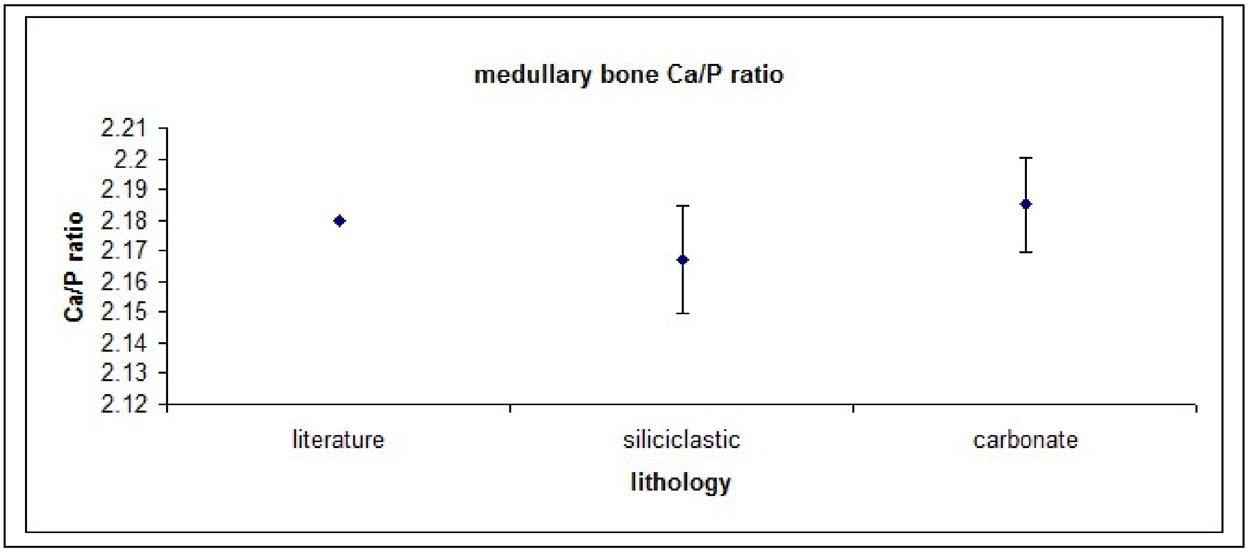

Figure 3.22 - Mean bone Ca/P ratios for medullary tissue. The experimental female bones were exposed to siliciclastic and carbonate lithologies and the literature-reported value was 2.18. There was no difference, indicating that twelve months of exposure may not be long enough to see detectable mineralogical changes.

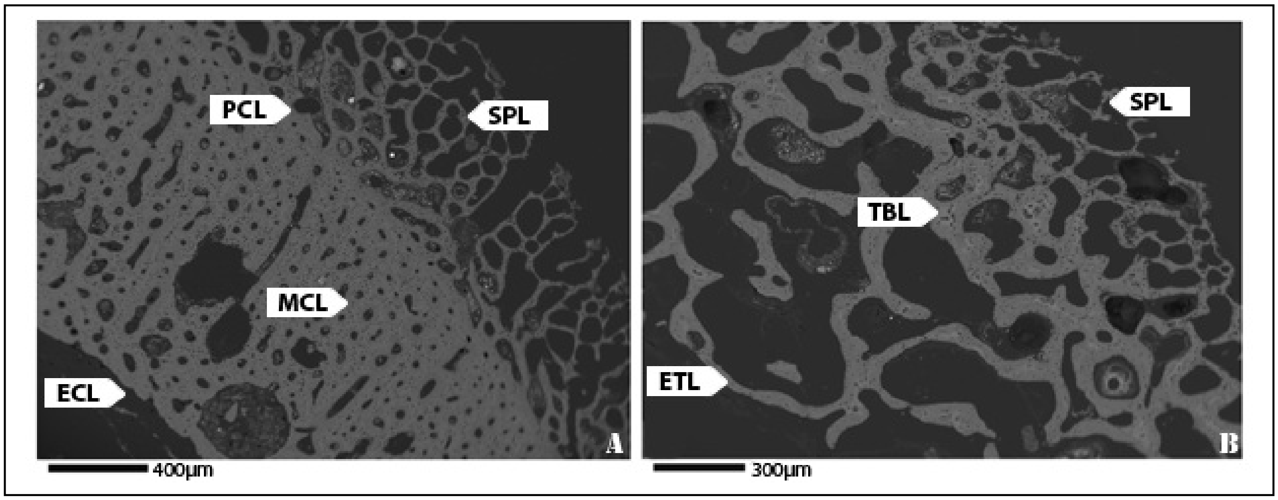

Figure 3.23 - Backscattered electron images of control bone cross sections. (A) Male control tibia diaphyseal (shaft) cross section, showing intact subperiosteal bone (SPL) and cortical bone layers. (B) Female control tibia metaphyseal (below the epiphysis) cross section, showing intact subperiosteal bone layer (SPL), as well as the trabecular bone layer (TBL) and endosteal trabecular layer (ETL).

Figure 3.24 - Backscattered electron images of experimental adult male bone cross section samples. Bones were exposed for twelve months in one of three environment types: terrestrial (A-C), freshwater (D-E), or marine-influenced (F-H2), from three different field sites. (A) Adult male tibia from sandy dune on Sapelo Island, Georgia. Longitudinal and vertical cracks are apparent in periosteal cortical layer (PCL) and endosteal cortical layer (ECL), but bone is otherwise in good condition. (B) Adult male femur from vegetated beach in Naples, Florida. Cracks surround osteons in medial cortical layer (MCL). (C) Adult male tibia from rock barren in Key Largo, Florida. Cracks are evident in PCL. (D) Adult male tibia from freshwater pond in Sapelo Island. Cracking is limited. (E) Adult male femur from freshwater pond in Fort Myers, Florida. Cracking is limited. No bones were recovered from the pond in Key Largo. (F) Adult male femur from tidal marsh in Sapelo Island. Destructive foci from bacterial attack are concentrated along the ECL. (G) Adult male tibia from mangrove marsh in Naples. Destructive foci indicate bacterial attack on both the ECL and PCL. MCL was not reached by bacterial action. (H1, H2) Adult male femur from mangrove marsh in Key Largo. H1 shows concentrated bacterial attack in PCL; H2 shows attack on ECL; MCL was not reached.

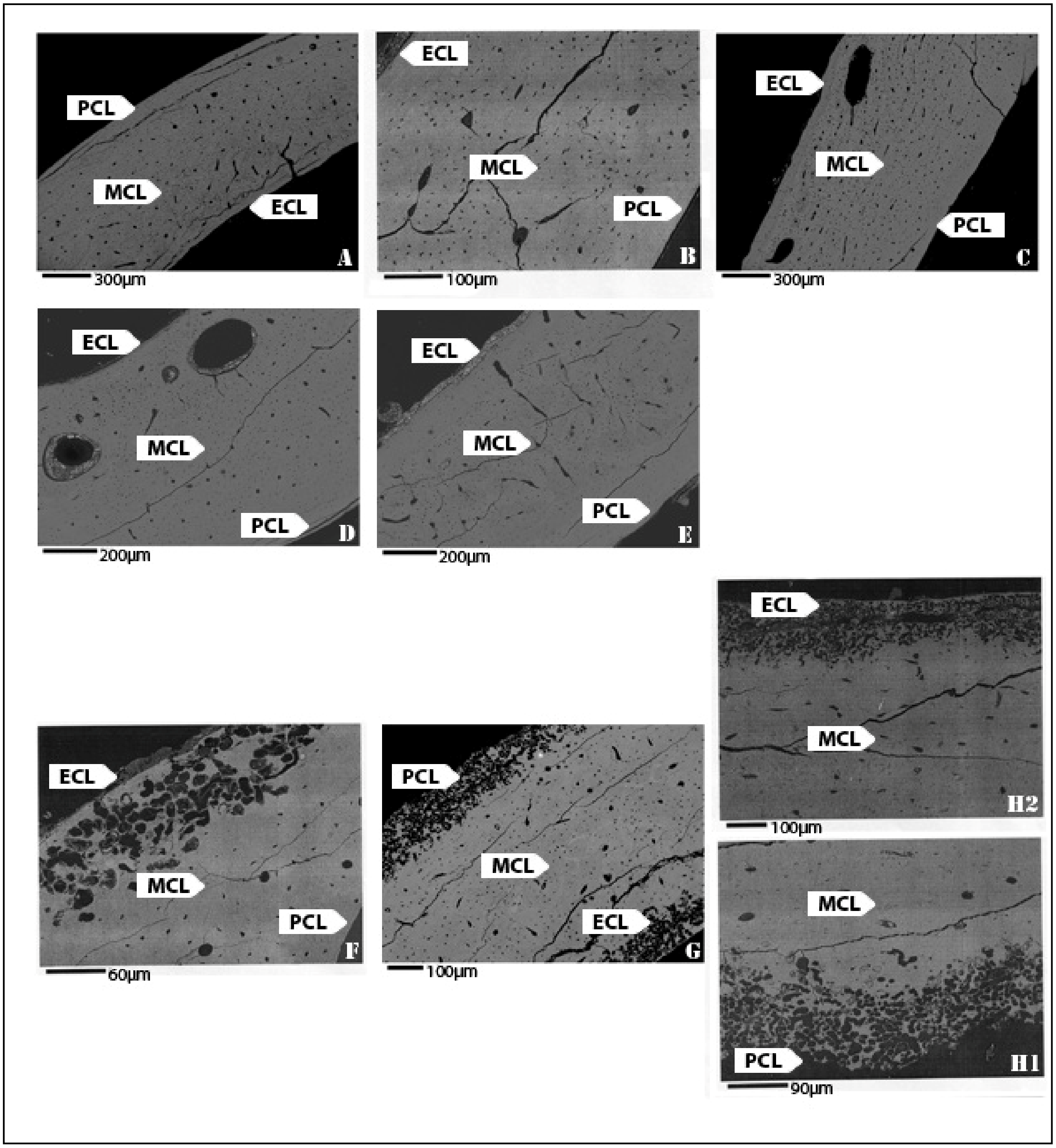
PCL
MCL
ECL
A
300µm
ECL
MCL
PCL
B
100µm
ECL
MCL
PCL
C
300µm
ECL
MCL
PCL
D
200µm
ECL
MCL
PCL
E
200µm
ECL
MCL
H2
100µm
ECL
MCL
PCL
F
60µm
PCL
MCL
ECL
G
100µm
MCL
PCL
H1
90µm

Figure 3.25 - Backscattered electron images of experimental adult female bone cross section samples. Bones were exposed for twelve months in one of three environment types: terrestrial (A-C), freshwater (D-E), or marine-influenced (F-H), from three different field sites. (A) Adult female tibia from sandy dune on Sapelo Island, Georgia. No physical or bioerosional damage is apparent. Medullary tissue (MT) is extensive. (B) Adult female femur from vegetated beach in Naples, Florida. Cracking is limited. (C) Adult female tibia from rock barren in Key Largo, Florida. Cracks are present in the medial cortical layer (MCL); the outer edge of the periosteal cortical layer (PCL) shows the initial stages of flaking. MT is extensive. (D) Adult female femur from freshwater pond in Sapelo Island. Cracking is seen in the PCL and MCL, but otherwise in good condition. (E) Adult female femur from freshwater pond in Fort Myers, Florida. Estrogen-influenced breakdown of the MCL is obvious and MT is extensive. Very little physical damage is apparent. No bones were recovered from the freshwater pond in Key Largo. (F) Adult female tibia from tidal marsh on Sapelo Island. The outermost edge of the PCL is lined by a thin region of destructive foci (bacterial attack) and substantial cracking is present in the MCL. (G) Adult female femur from mangrove marsh in Naples. PCL (not pictured) and ECL show destructive foci from bacterial action. MT was not present in this bone, suggesting that MT protects the ECL from bacterial attack. (H) Adult female femur from rock barren in Key Largo. A thick region of destructive foci line the PCL and cracks are apparent in the MCL. MT is present, although to a lesser extent than in other samples.

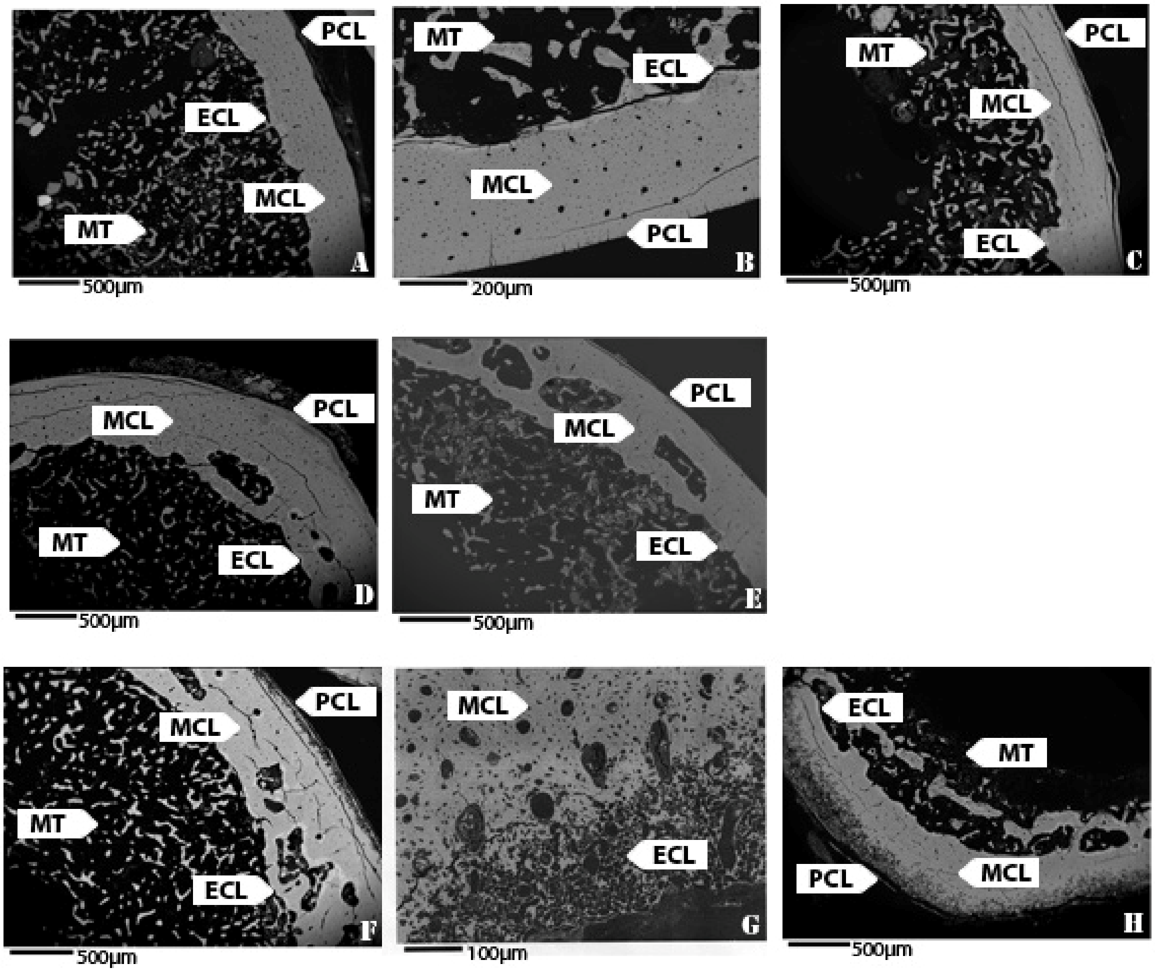
PCL
ECL
MCL
MT
A
500µm
MT
ECL
MCL
PCL
B
200µm
PCL
MT
MCL
ECL
C
500µm
MCL
PCL
MT
ECL
D
500µm
PCL
MCL
MT
ECL
E
500µm
PCL
MCL
MT
ECL
F
500µm
MCL
ECL
G
100µm
ECL
MT
MCL
PCL
H
500µm

Table 3.1 - Daily diet of chickens at the University of Georgia Poultry Farm.

Amount (cal/lb)	*Food Item*	*Percent of Daily Diet*
1189.68	Ground Corn	59.48
680	Soy Meal	34
68.3924	Vegetable Oil	3.42
34.324	Defluorinated Phosphate	1.71
9.7802	Limestone	0.49
6.9004	Salt	0.35
5	Vitamin Mixture	0.25
4.3219	Methionine (Amino Acid)	0.22
1.6	Trace Minerals (Mn, Zn, Fe)	0.08
2000 cals		100%

Table 3.2 – Monthly climate data for each experimental field site. Data were collected from the National Climatic Data Center and National Weather Service databases. "Hot days" are defined as days where the air temperature reached 90^0F or warmer.

	May08	Jun08	Jul08	Aug08	Sept08	Oct08	Nov08	Dec08	Jan08	Feb08	Mar08	Apr08	May09
Sapelo Island, Georgia													
Mean Month. Temp (^{0}F)	73.6	82.1	80.9	81.9	75.0	69.4	57.2	57.9	53.0	51.3	60.1	66.2	74.9
Total Month. Precip. (in.)	4.58	2.31	7.27	6.66	1.87	11.41	0.24	1.15	1.70	1.14	3.84	9.35	8.50
Mean Month. Humid. (%)	68.4	71.7	76.3	77.7	75.4	74.8	71.9	76.7	70.9	69.3	75.4	70.5	75.4
Total No. of Hot Days	4	15	8	11	3	0	0	0	0	0	0	0	5
Naples, Florida													
Mean Month. Temp (^{0}F)	78.7	82.0	82.1	83.3	82.6	76.3	66.8	67.5	63.6	63.5	69.8	74.3	79.2
Total Month. Precip. (in.)	0.56	10.15	13.32	11.42	6.96	4.40	0.19	1.77	0.60	0.40	0.28	0.83	6.42
Mean Month. Humid. (%)	68.5	74.6	77.7	79.9	81.6	74.4	69.2	74.7	70.1	66.7	68.3	69.6	71.9
Total No. of Hot Days	12	28	26	26	21	8	0	0	0	0	0	5	21
Fort Myers, Florida													
Mean Month. Temp (^{0}F)	80.5	82.7	82.5	84.0	82.0	75.8	67.3	67.5	63.2	64.1	70.3	74.7	79.9
Total Month. Precip. (in.)	0.81	7.14	13.19	10.33	14.86	3.43	0.09	2.07	0.3	0.27	0.65	0.29	6.42
Mean Month. Humid. (%)	63.2	72.1	75.1	73.8	77.7	74.9	68.8	73.5	68.8	64.2	64.9	65.2	67.9
Total No. of Hot Days	20	25	26	25	19	3	0	0	0	0	0	5	17

	May09	Jun09	Jul09	Aug09	Sept09	Oct09	Nov09	Dec09	Jan10	Feb10	Mar10	Apr10	May10
Key Largo, Florida													
Mean Month. Temp (^{0}F)	79.4	82.2	84.6	84.2	83.0	82.1	76.3	73.8	63.0	66.3	67.3	74.9	81.5
Total Month. Precip. (in.)	6.79	6.64	3.99	3.57	8.88	0.20	4.72	1.08	1.23	1.40	1.01	10.16	0.60
Mean Month. Humid. (%)	81.6	80.1	78.6	77.9	81.4	78.8	76.1	82.6	73.7	75.8	73.9	75.9	79.7
Total No. of Hot Days	0	4	5	4	2	0	0	0	0	0	0	0	0

Table 3.3 - Mean sediment temperature and water salinity, pH, ammonia, nitrite, and nitrate based on measurements taken during periodic visits to the experimental field sites.

Location	Mean Sediment Temp.	Water: Salinity	pH	Ammonia	Nitrite	Nitrate
Sapelo Island, Georgia						
Sandy Dune:	66.71^0F	----	----	--------	-------	-------
Saltwater Marsh:	70.14^0F	25ppm	7.3	0ppm	0ppm	1ppm
Freshwater Pond:	60.14^0F	0ppm	6.8	0ppm	0ppm	0ppm
Naples, Florida						
Vegetated Beach:	68.71^0F	----	---	-------	------	------
Mangrove Marsh:	70.85^0F	32ppm	6.4	0ppm	0ppm	0ppm
Fort Myers, Florida						
Freshwater Pond:	59.85^0F	0ppm	7.0	0ppm	0ppm	0ppm
Key Largo, Florida						
Tidal Rock Barren:	75.6^0F	-----	---	------	-----	------
Mangrove Marsh:	70.4^0F	34ppm	7.8	0ppm	0ppm	0ppm
Freshwater Pond:	69.8^0F	3ppm	7.6	1ppm	0.25ppm	0.50ppm

Table 3.4 - Comparison of six and twelve month bone mass loss. Relative and mean mass loss were very similar for both exposure periods.

Exposure Time	Relative Mass Loss	Mean Mass Loss	Standard Error	p-value
6 months	58.4%	3.79g	0.343	0.0001
12 months	58.9%	3.88g	0.334	0.0001

Table 3.5 - Mean annual climate data with associated standard errors.

TEMPERATURE		
Site Locations	Mean Annual Temp.	Standard Error
Sapelo Island, Georgia	67.9^0F	3.08
Naples, Florida	74.6^0F	2.07
Fort Myers, Florida	74.9^0F	2.11
Key Largo, Florida	76.8^0F	2.03

HUMIDITY		
Site Locations	Mean Annual Humidity	Standard Error
Sapelo Island, Georgia	73.4%	0.854
Naples, Florida	72.8%	1.32
Fort Myers, Florida	70.0%	1.33
Key Largo, Florida	78.1%	0.806

PRECIPITATION		
Site Locations	Mean Annual Precip.	Standard Error
Sapelo Island, Georgia	4.62 in.	1.01
Naples, Florida	4.41 in.	1.32
Fort Myers, Florida	4.64 in.	1.47
Key Largo, Florida	3.87 in.	0.929

NUMBER OF HOT DAYS		
Site Locations	Mean Annual No. of Hot Days	Standard Error
Sapelo Island, Georgia	3.54 days	1.38
Naples, Florida	11.3 days	3.19
Fort Myers, Florida	10.8 days	3.10
Key Largo, Florida	1.15 days	0.529

Table 3.6 - Classification of carnivore-related scavenging on modern bones from Janjua and Rogers (2008).

Degree of Scavenging	Description
Mild	gnaw marks on only one end of a bone
Moderate	one epiphysis or distal/proximal end chewed off
Extensive	both ends gnawed to point where marrow cavity is exposed, or bone is entirely gone

Table 3.7 - Stages of subaerial weathering and degradation for avian bones in arid environments. Based on Behrensmeyer (1978) and Behrensmeyer et al. (2003).

Weathering Stage	Characteristics
0	fresh bone: greasy with soft tissue present
1	surface cracking and flaking of external bone layers
2	intense flaking and cracking, with loss of some external bone layers
3	splintering and deep cracks
4	rough texture; disintegrates when moved
5	falling apart *in situ*

Table 3.8 - Mean differences between bone area Ca/P ratios within control and experimental male and female bones. PCL = periosteal cortical layer, MCL = medial cortical layer, ECL = endosteal cortical layer. Controls only: SPL = subperiosteal layer, TBL = trabecular bone layer, ETL = endosteal trabecular layer. Male bones have positive mean differences between the Ca/P ratios of each bone area, whereas female bones have negative mean differences.

MALES

Group	Bone Area Comparisons	Mean Difference Between Ca/P ratios	Standard Error
Control Male	SPL: ECL	+0.0117	0.039
Control Male	SPL : MCL	+0.0010	0.022
Control Male	MCL : ECL	+0.0107	0.040
Experimental Males	PCL : ECL	+0.0220	0.046
Experimental Males	PCL : MCL	+0.0006	0.045
Experimental Males	MCL : ECL	+0.0213	0.031

FEMALES

Group	Bone Area Comparisons	Mean Difference Between Ca/P ratios	Standard Error
Control Female	SPL: ETL	-0.119	0.058
Control Female	SPL : TBL	-0.045	0.001
Control Female	TBL : ETL	-0.075	0.059
Experimental Females	PCL: ECL	-0.074	0.061
Experimental Females	PCL : MCL	-0.029	0.031
Experimental Females	MCL : ECL	-0.046	0.039

Table 3.9 - Oxford Histological Index, which classifies the degree of microscopic alteration of bone. From Hedges et al. (1995).

Histological Index Level	Percentage of Intact Bone	Description
0	≤5	No original features identifiable
1	≤15	Small areas of preserved bone present, surrounded by destructive foci
2	≤33	Clear bone structure preserved between destructive foci
3	≥67	Clear preservation of bone osteocytes
4	≥85	Well preserved; only minor amounts of destructive foci
5	≥95	Indistinguishable from fresh bone

Table 3.10 – Modified weathering profile for avian bones in humid coastal environments compared to the weathering profile for avian bones in arid savanna habitats (from Behrensmeyer et al. 2003).

Arid Savanna Avian Bone Weathering Profile			Humid Coastal Avian Bone Weathering Profile		
Exposure Time	WS	Description	Exposure Time	WS	Description
0-1year	0	fresh bone: greasy with soft tissue present	0-2months	0	Both environments: fresh bone: greasy with soft tissue present; intense scavenging
1 year	1	surface cracking and flaking of external bone layers	2 mo-1 year	½	Both environments: loss of periosteum and subperiosteal layer; no cracking or flaking; microbial activity
2-3 years	2	intense flaking and cracking, with loss of some external bone layers	6mo-1 year	1-1.5	Terrestrial: drying; bleaching; surface exfoliation; microbial activity Tidal: surface corrosion; wet rot; microbial activity
3+ years	3	splintering and deep cracks	6mo-1 year	2	Terrestrial: flaking and cracking; loss of some external bone layers Tidal: exfoliation from corrosion; wet rot; hairline cracking
3+ years	4	rough texture; disintegrates when moved	8mo-1 year	3	Tidal: fibrous texture; disintegrates when moved
3+ years	5	falling apart *in situ*	8mo-1 year	4-5	Tidal: falling apart *in situ*

CHAPTER 4

CONCLUSIONS

The overall conclusion to be drawn from this research is that the taphonomy of an avian assemblage is not simply correlated with just one factor, such as depositional environment. Rather, the preservation condition of avian remains can be biased by internal factors (sex and/or body size, age, and bone microstructure) and external factors (scavenging, microbial attack, climate, environment, and submersion versus subaerial exposure). This research highlights the range of elements acting on avian carcass disarticulation and loss and avian bone weathering and degradation, as well as their potential impacts on paleoecological, paleoenvironmental, and evolutionary interpretations.

The review of a sample of bird-fossil literature emphasizes that the avian record is dominated by preservation of disarticulated skeletal elements in mostly siliciclastic sediments, as well as in shallow marine settings and warm temperate climates. The review indicates that sex and age have been previously unstudied as sources of taphonomic bias in avian carcass and bone preservation. These results are important because they suggest that taphonomic biases can play a large role in our understanding of the avian fossil record and avian evolution. The results also lend support to the use of experimental studies for identifying the effects of a variety of taphonomic factors on avian preservation potential.

The field study data show that internal factors, which affect bone microstructure, can have as significant an effect on the taphonomic condition of avian remains as external ones. Juvenile bird leg bones are more porous than those of adults and this leads to rapid weathering and loss in the juveniles. The fact that age-based differences were not detected in the carcass study suggests that external factors, such as scavenging, may have overprinted the pattern, or juveniles may experience differential survivorship of skeletal elements. Sex affects the calcium content in bones from reproducing female birds and, compared to males, they have greater bone lipid content. These factors appear to cause increased female carcass and leg bone weathering and degradation. Teasing out the effect of climate on overall avian preservation potential is more difficult, but the leg bone weathering results indicate that air temperature and relative humidity are positively correlated with bone mass loss over time. This has important implications for avian preservation potential during global warming events. Lastly, compared to previously documented weathering rates in arid savanna environments, avian bones in humid coastal habitats weather slightly faster. This suggests that paleoecological interpretations from such environments may be less reliable.

Future studies using the experimental methods presented in this thesis would benefit from using a greater variety of avian species of known diet, sex, age, and living conditions (i.e., ducks, songbirds, etc.), using more "scavenger-proof" protective crates over the carcasses, and deploying experiments in more disparate climatic regions. Utilizing a variety of avian species would test whether the results reported in this study are widely applicable to different bird groups, which is vital for understanding taphonomic bias in the fossil record. It would also be useful to generally avoid species and breeds which have been genetically altered (e.g., the juvenile Ross Broiler chickens used in this study). Scavenger-proofing the protective crates would help retain more carcass and wing bone elements; one suggestion for future work is to use reinforced steel cages. Deploying experiments in climatic regions which are more strikingly different might enable better climate-based comparisons of weathering, degradation, and loss of avian bone samples. For "micro-level" analyses, recommendations for future work include increasing the sample size for both the control and experimental groups, as well as utilizing an X-ray diffractometer to estimate the amount of carbonate present in each bone sample. These method-related suggestions are important for those planning to further the field of avian taphonomy through modern field studies.

APPENDIX A

LIST OF PAPERS REVIEWED IN CHAPTER 2

Appendix A. List of papers reviewed in Chapter 2. Information regarding species, environment, lithology, and climate is presented. The list is sorted by geologic age, from Recent to Late Jurassic.

Age/Location	Birds	Depositional Environment	Lithology	Climate	Reference
Holocene					
Niue Island, South Pacific	*Nycticorax* *Megapodius* Gallirallus	karst (cave)	carbonate	tropical	Steadman et al., 2000
Late Pleistocene					
Las Breas de San Felipe, Cuba	*Ciconia* *Mycteria*	asphalt pit	siliciclastic	tropical	Suárez and Olson, 2003
Arizpe, Mexico	*Meleagris*	alluvial	siliciclastic	tropical	Cracraft, 1968
Kingdom of Tonga	*Eclectus*	karst	carbonate	subtropical	Steadman, 2006
Oklahoma, USA (above Pearlette Ash Member of Crooked Creek Form.)	*Pelecanus*	fluvial	siliciclastic	temperate	Mengel, 1952
Wyoming, USA (Lava Creek Tuff, Yellowstone Nat'l Park)	*Fulica*	hot spring	siliciclastic	dry temperate	Channing et al., 2005
Wyoming, USA (Little Box Elder Cave)	*Anas*	karst (cave)	carbonate	temperate	Emslie, 1985
Fossil Lake, Oregon, USA	*Anabernicula*	lacustrine	mixed siliciclastic-carbonate	temperate	Howard, 1964
Arizona, USA (Kartchner Caverns State, Mud Flats)	*Geococcyx*	karst (cave)	carbonate	cool arid desert	Carpenter and Mead, 2003
Kansas, USA (Jones Sink Fauna)	*Colymbus* Anatidae Charadriiformes Columbiformes Passeriformes	lacustrine	unknown	cool temperate	Downs, 1954
Late Pleistocene					
California, USA (Newport Bay)	Gaviiformes Anatidae Procellariiformes Pelecaniformes Podicipediformes Charadriiformes	marine - continental shelf	unknown	temperate	Howard, 1949

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Late Pleistocene					
Carlsbad, New Mexico, USA (Dark Canyon Cave)	*Podiceps* *Phalacrocorax* Anatidae *Gymnogyps* *Coragyps* Falconiformes Galliformes Charadriiformes Columbiformes Psittaciformes Cuculidae Strigiformes Passeriformes	karst (cave)	carbonate	cool arid desert	Howard, 1971
Ethiopia, Africa (Kibish Form.)	*Pelecanus* *Anhinga* *Ardea* *Numidinae*	fluvio-lacustrine	mixed siliciclastic-carbonate	semiarid	Louchart, 2008
Pleistocene					
Florida, USA (Ward Island)	*Grus*	fluvial	unknown	warm temperate	Olson, 1972
California, USA (Rancho La Brea)	*Strix*	asphalt pit	siliciclastic	cool temperate	Howard, 1933
California, USA (Upper San Pedro horizon)	*Chendytes*	alluvial	siliciclastic	cool temperate	Miller, 1925
Nebraska, USA (Sappa Form.)	Anatidae Galliformes Gruiformes	glacio-fluvio-lacustrine	unknown	cool temperate	Short, 1970a
California, USA (Orange, Los Angeles, & Ventura Co.)	*Chendytes*	marine - continental shelf	unknown	temperate	Howard, 1955
Karpathos, Greece	Falconiformes Gruiformes Columbiformes Strigiformes Passeriformes	karst (cave)	carbonate	arid	Weesie, 1984
Pliocene					
California, USA (Anza-Borrego Desert State Park)	Teratornithid	deltaic	siliciclastic	cool temperate	Howard, 1972

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Pliocene					
Kansas & Idaho, USA (Saw Rock Canyon & Hagerman Local Fauna)	Podicipedidae	fluvio-lacustrine	siliciclastic	temperate	Murray, 1967
Idaho, USA (Hagerman Local Fauna)	*Phalacrocorax*	lacustrine	siliciclastic	temperate	Murray, 1970
Nebraska, USA (Kimball Form.)	*Anhinga*	fluvial	siliciclastic	cool temperate	Martin and Mengel, 1975
Queensland, Australia (Allingham Form.)	*Anhinga*	fluvio-lacustrine	unknown	warm temperate	Mackness, 1995
Florida, USA ("Rhino Hole," Alachua Co.)	*Jacana*	lacustrine	carbonate	tropical	Olson, 1976
Florida, USA (Gilchrist/Columbia County line)	*Titanis*	marine - continental shelf	carbonate	tropical	Brodkorb, 1963
Kansas, USA (Rexroad and Fox Canyon Local Faunas)	*Accipiter* *Buteo* *Falco* *Bubo*	floodplain	unknown	temperate	Feduccia and Ford, 1970
Kansas, USA (Rexroad Fauna)	*Otus* *Speotyto* *Asio*	floodplain	unknown	temperate	Ford, 1966
Idaho, USA (Hagerman Local Fauna)	*Speotyto* *Asio* Strigidae	lacustrine	siliciclastic	temperate	Ford and Murray, 1967
Florida, USA (Citrus County)	*Aphelocoma*	karst (sinkhole)	carbonate	tropical	Emslie, 1996
Nebraska, USA (Devil's Gulch)	*Heterochen*	fluvial	siliciclastic	warm temperate	Short, 1970b
Cape Province, South Africa (Langebaanweg)	*Scopus*	floodplain	unknown	tropical	Olson, 1984a

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Pliocene					
California, USA (Rosamond Series of Mohave Desert)	*Branta*	fluvio-lacustrine	siliciclastic	cool arid desert	Miller, 1930
Kansas, USA (Fox Canyon Fauna)	*Mimus* *Anthus* *Zonotrichia* *Junco* *Calcarius* *Sturnella*	floodplain	unknown	dry temperate	Emslie, 2007
Kansas, Idaho, Arizona, Oregon (Rexroad, Hagerman, and Saw Rock Canyon Faunas)	Gruiformes	floodplain & lacustrine	unknown	temperate	Feduccia, 1968
Idaho and Oregon, USA (Owyhee Pliocene)	Gruiformes Ciconiiformes Anseriformes Falconiformes Pelecaniformes	floodplain	mixed siliciclastic-carbonate	cool temperate	Miller, 1944
Kansas, USA (Sherman Co.)	*Grus*	fluvial	siliciclastic	cool arid desert	Wetmore and Martin, 1930
Kansas, USA (Rexroad Form.)	*Pliogyps*	floodplain	unknown	temperate	Tordoff, 1959
Qasr as-Sahabi, Libya, Africa (Sahabi Form.)	Pelecaniformes Ciconiiformes Falconiformes Anseriformes	floodplain	mixed siliciclastic-carbonate	semiarid	Ballmann, 1987
South Dakota, USA (Ash Hollow Form.)	*Nettion*	fluvial	siliciclastic	arid	Brodkorb, 1964
Venezuela (Codore Form.)	*Jabiru*	floodplain	mixed siliciclastic-carbonate	semiarid	Walsh and Sánchez, 2008
California, USA (Kern County)	*Vultur* *Parabuteo*	fluvio-lacustrine	unknown	cool temperate	Miller, 1931

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Miocene - Pliocene					
Chile (Bahia Inglesa Form.)	Pelecaniformes	marine - continental shelf	siliciclastic	semiarid	Walsh and Hume, 2001
Peru (Pisco Form.)	*Perugyps*	fluvial	mixed siliciclastic-carbonate	cool temperate	Stucchi and Emslie, 2005
Nebraska, USA (Snake & Sheep Creek Beds)	Galliformes Falconiformes Anseriformes	fluvial	siliciclastic	semiarid	Wetmore, 1923
Miocene					
Florida, USA (Thomas Farm, Gilchrist Co.)	*Boreortalis*	karst (sinkhole)	carbonate	subtropical	Brodkorb, 1954
Florida, USA (Alachua Co.)	Momotidae	fluvial	carbonate	subtropical	Becker, 1986a
Rusinga & Makobo Islands, Kenya, Africa (Ngorora Form.)	*Anhinga* *Leakeyornis* *Nycticorax* *Ciconia*	floodplain	siliciclastic	dry temperate	Dyke and Walker, 2008
Ruwais, Abu Dhabi, United Arab Emirates (Baynunah Form.)	*Anhinga* Ardeidae	fluvial	mixed siliciclastic-carbonate	tropical	Stewart and Beech, 2006
Nebraska, USA (Sand Canyon Beds in Sheep Creek Form.)	*Ardea*	fluvial	unknown	dry temperate	Becker, 1986b
South Dakota, USA (Flint Hill Fauna)	*Paranyroca* *Palaeoborus*	floodplain	siliciclastic	dry temperate	Miller and Compton, 1939
Chubut Province, Argentina	Diomedeidae	floodplain	unknown	warm temperate	Olson, 1984b
Nebraska, USA (Sioux County)	*Geranoaëtus* *Buteonidae*	fluvial	siliciclastic	semiarid	Wetmore, 1926b
Anatolia, Turkey	*Phasianidae*	alluvial	siliciclastic	warm temperate	Harrison, 1985

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Miocene					
Florida, USA (Thomas Farm, Gilchrist Co.)	*Proictinia* *Phalacrocorax*	karst (sinkhole)	carbonate	subtropical	Brodkorb, 1956
California, USA (Round Mountain Silt)	*Hadrogyps*	deltaic	mixed siliciclastic-carbonate	semiarid	Emslie, 1988
Bavaria, Germany	Strigiformes	fissure fill	siliciclastic	warm temperate	Mlíkovský, 1998
Western Kenya, Africa	*Aegypius* *Melierax* *Accipiter* *Otus*	volcanic uplands	mixed siliciclastic-carbonate	tropical	Walker and Dyke, 2006
Allier, France	*Ameripodius*	fluvio-lacustrine	unknown	warm temperate	Mourer-Chauviré, 2000
Chad & Libya, Africa	*Afrocygynus* Cygnina	fluvio-lacustrine	unknown	tropical	Louchart et al., 2005
Nebraska, USA (Agate Springs, Lower Harrison Formation)	*Ortalis* Cracidae	fluvial	siliciclastic	semiarid	Wetmore, 1933
California, USA (Temblor Formation)	Anseriformes Pelecaniformes Procellariiformes Charadriiformes	marine - continental shelf	siliciclastic	semiarid	Miller, 1961
New Zealand (St. Bathans Fauna)	Columbidae	lacustrine	siliciclastic	arid	Worthy et al., 2009
Comallo, Argentina	Phorusrhacids	floodplain	siliciclastic	arid	Chiappe and Bertelli, 2006
Oligocene - Miocene					
Lake Eyre region, South Australia (Etadunna Form.)	*Phoenicopterus* *Phoeniconaias*	lacustrine	carbonate	semiarid	Miller, 1963
Japan & Washington, USA	Plotopteridae	marine - continental slope	unknown	warm temperate	Olson and Hasegawa, 1979

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Oligocene - Miocene					
Queensland, Australia (Riversleigh World Heritage Property)	*Eoanseranas*	lacustrine	carbonate	warm temperate	Worthy and Scanlon, 2009
Oligocene					
Chubut Province, Argentina (Patagonia Form.)	*Microdytes*	marine - continental shelf	siliciclastic	temperate	Simpson, 1981
Fayum Province, Egypt (Jebel Qatrani Form.)	*Eremopezus* *Stromeria* Musophagidae Falconiformes Pandionidae Rallidae Gruidae Jacanidae Phoenicopteridae Xenerodiopidae Ardeidae Ciconiidae Balaenicipitidae Pelecaniformes	fluvial	mixed siliciclastic-carbonate	tropical	Rasmussen et al., 1987
Luberon, France	Passeriformes	lacustrine	carbonate	warm temperate	Mayr and Manegold, 2006
Frauenweiler, Germany (“Grube Unterfeld”)	*Eurotrochilus*	marine - continental shelf	siliciclastic	warm temperate	Mayr, 2004
Frauenweiler, Germany (“Grube Unterfeld”)	Passeriformes	marine - continental shelf	siliciclastic	warm temperate	Mayr and Manegold, 2004
South Dakota, USA (Oreodon Beds)	*Buteo*	fluvio-lacustrine	siliciclastic	arid	Wetmore and Case, 1934
South Dakota, USA (Chadron Formation)	*Procrax*	fluvial	unknown	arid	Tordoff and MacDonald, 1957
Australia (Etadunna Form.)	*Emuarius*	lacustrine	unknown	warm temperate	Boles, 2001

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Oligocene					
Westerwald, Germany (Enspel Site)	Colymboides	lacustrine	siliciclastic	warm temperate	Mayr and Poschmann, 2009
Heidelberg, Germany ("Grube Unterfeld")	*Eurotrochilus* *Palaeotodus*	marine - continental shelf	siliciclastic	warm temperate	Mayr and Micklich, 2010
Eocene - Pleistocene					
Inner & Outer Mongolia	Falconiformes Gruiformes Galliformes	fluvial	mixed siliciclastic-carbonate	arid	Wetmore, 1934
Eocene - Oligocene					
Essex, England, UK (London Clay Form.)	Anseriformes	marine - continental shelf	siliciclastic	warm temperate	Dyke, 2001
Eocene					
Wyoming, USA (Bridger Formation)	*Amitabha*	fluvio-lacustrine	carbonate	subtropical	Gulas-Wroblewski and Wroblewski, 2003
Wyoming, USA (Bridger Form.)	*Protostrix*	fluvio-lacustrine	carbonate	subtropical	Rich, 1982
Wyoming, USA (Wind River Form.)	*Eostrix*	fluvial	unknown	subtropical	Martin and Black, 1972
Wyoming, USA (Bridger Form.)	*Minerva*	fluvio-lacustrine	carbonate	subtropical	Wetmore, 1921
Wyoming, USA (Green River Form.)	*Gallinuloides*	lacustrine	mixed carbonate-siliciclastic	subtropical	Eastman, 1900
Utah, USA (Green River Formation)	*Nautilornis* *Presbyornis*	lacustrine	mixed carbonate-siliciclastic	warm temperate	Wetmore, 1926a
Utah, USA (Myton Pocket)	*Eonessa*	deltaic	mixed carbonate-siliciclastic	warm temperate	Wetmore, 1938
Darmstadt, Germany (Messel Pit)	*Chascacocolius*	lacustrine	siliciclastic	subtropical	Mayr, 2005
Murgon, Australia	Passeriformes	fluvio-lacustrine	unknown	warm temperate	Boles, 1997

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Eocene					
California, USA (Powoy Formation)	Strigiformes Gruiformes	alluvial	mixed siliciclastic-carbonate	warm temperate	Howard, 1965
Jutland, Denmark (Fur Form.)	*Mopsitta* Pseudasturidae	marine - continental shelf	siliciclastic	warm temperate	Waterhouse et al., 2008
Hessen, Germany (Messel Pit)	*Gracilitarsus*	lacustrine	siliciclastic	warm temperate	Mayr, 2001
Hessen, Germany (Grube Messel)	*Pumiliornis*	lacustrine	siliciclastic	warm temperate	Mayr, 1999a
Hessen, Germany (Messel)	*Paraprefica* *Masillapodargus*	lacustrine	siliciclastic	warm temperate	Mayr, 1999b
Colorado, USA (Florissant Form.)	*Eocuculus*	lacustrine	siliciclastic	warm temperate	Chandler, 1999
Essex, England, UK (London Clay Form.)	*Paraortygoides*	marine - continental shelf	siliciclastic	warm temperate	Dyke and Gulas, 2002
Isle of Sheppey, England, UK (London Clay Form.)	*Lithornis*	marine - continental shelf	siliciclastic	warm temperate	Owen, 1841
Walton-on-the-Naze, England, UK (London Clay Form.)	*Pulchrapollia*	marine - continental shelf	siliciclastic	warm temperate	Dyke and Cooper, 2000
Oregon, USA (Nehalem River Basin)	*Argillornis* Pelagornithidae	marine - continental shelf	unknown	warm temperate	Goedert, 1989
Jutland, Denmark (Fur Form.)	*Lithornis*	marine - continental shelf	unknown	warm temperate	Leonard et al., 2005
Jutland, Denmark (Fur Form.)	Coliiformes Apodiformes	marine - continental shelf	unknown	warm temperate	Dyke et al., 2004

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Eocene					
Wyoming, USA (Green River Form.) &	*Fluvioviridavis*	lacustrine	mixed carbonate-siliciclastic	subtropical	Mayr and Daniels, 2001
Hessen, Germany (Messel)			siliciclastic	warm temperate	
Hessen, Germany (Messel Pit)	*Primozygodactylus*	lacustrine	siliciclastic	warm temperate	Mayr and Zelenkov, 2009
Belgium (Brussels Form.)	Pelagornithidae	marine - continental shelf	mixed siliciclastic-carbonate	warm temperate	Mayr and Smith, 2010
Isle of Sheppey, England, UK (London Clay Form.)	*Dasornis*	marine - continental shelf	siliciclastic	warm temperate	Mayr, 2008
Seymour Island, Antarctica (La Meseta Form.)	*Palaeeudyptes*	marine - continental shelf	siliciclastic	cold temperate	Myrcha et al., 1990
Quebrada Perdida, Peru (Paracas Form.)	Sphenisciformes	marine - continental shelf	siliciclastic	warm temperate	Clarke et al., 2007
Pisco Basin, Peru (Otuma Formation)	*Icadyptes*	marine - continental shelf	siliciclastic	warm temperate	Ksepka et al., 2008
Paleocene					
Maryland, USA (Aquia Formation)	Anseriformes	marine - continental slope	siliciclastic	warm temperate	Olson, 1994
Morocco, Africa (Ouled Abdoun Basin)	*Lithoptila*	marine - continental shelf	unknown	semiarid	Bourdon et al., 2005
Cretaceous					
Nammoura, Lebanon, Africa	Enantiornithes	marine - continental shelf	carbonate	semiarid	Dalla Vecchia & Chiappe, 2002
Cuenca, Spain (Las Hoyas)	*Iberomesornis*	lacustrine	carbonate	subtropical	Sanz et al., 1988

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Cretaceous					
Hebei Province, China (Yixian Form.)	*Vescornis*	lacustrine	siliciclastic	subtropical	Zhang et al., 2004
New Jersey, USA (Hornerstown Form.)	Charadriiformes Procellariiformes Graculavidae	marine - continental shelf	siliciclastic	warm temperate	Olson and Parris, 1987
Liaoning Province, China (Jiufotang Form.)	*Jeholornis*	lacustrine	siliciclastic	subtropical	Zhou and Zhang, 2002
Cuenca, Spain (Las Hoyas)	*Concornis*	lacustrine	carbonate	subtropical	Sanz and Buscalioni, 1992
Salta Province, Argentina (Lecho Form.)	Enantiornithes	fluvio-lacustrine	siliciclastic	warm temperate	Walker, 1981
Liaoning Province, China (Jiufotang Form.)	*Eocathayornis*	lacustrine	siliciclastic	subtropical	Zhou, 2002
Liaoning Province, China (Jiufotang Form.)	*Yanornis* *Yixianornis*	lacustrine	siliciclastic	subtropical	Zhou and Zhang, 2001
Chabu Sumu, China (Ordos Basin)	Enantiornithes	fluvio-lacustrine	unknown	subtropical	Dong, 1993
Umnogobi Aimak, Mongolia, China (Nemegt Form.)	*Teviornis*	deltaic	siliciclastic	warm temperate	Kurochkin et al., 2002
Montana, USA (Two Medicine Formation)	*Piksi*	floodplain	siliciclastic	warm temperate	Varricchio, 2002
Saratov Province, Russia (Rybushka Form.)	*Hesperornis*	marine - deep	mixed siliciclastic-carbonate	warm temperate	Panteleyev et al., 2004
Alabama, USA (Mooreville Chalk Formation)	*Halimornis*	marine - continental shelf	carbonate	warm temperate	Chiappe et al., 2002

APPENDIX A Continued.

Age/Location	Birds	Depositional Environment	Lithology	Climate	References
Cretaceous					
Kalasin Province, Thailand (Sao Khua Form.)	*Anas*	fluvio-lacustrine	siliciclastic	arid	Buffetaut et al., 2005
Rio Negro Province, Patagonia, Argentina (Las Alamitos Form.)	Ornithurae Hesperornithes Neornithes *Patagopteryx*	floodplain	siliciclastic	warm temperate	Agnolin and Martinelli, 2009
Liaoning Province, China (Jiufotang Form.)	*Zhongjianornis*	lacustrine	siliciclastic	subtropical	Zhou and Li, 2010
Texas, USA (Woodbine Form.)	*Flexomornis*	fluvial	siliciclastic	warm temperate	Tykoski and Fiorillo, 2010
Ellesmere Island, Canada (Kanguk Form.)	*Hesperornis*	marine - continental shelf	siliciclastic	warm temperate	Hills et al., 1999
Gansu Province, China (Xiagou Formation)	Enantiornithes	lacustrine	siliciclastic	subtropical	Hailu et al., 2005
Late Jurassic					
Liaoning Province, China (Yixian Form.)	*Confuciusornis*	lacustrine	siliciclastic	subtropical	Hou et al., 1995

APPENDIX B

NUMBER AND TYPE OF REMAINS PER DEPOSITIONAL ENVIRONMENT REVIEWED IN CHAPTER 2

Appendix B. Number and type of remains per depositional environment reviewed in Chapter 2. G/F/L = glacio-fluvio-lacustrine, V/U = volcanic uplands.

	Marine Environments		
	Continental shelf	Continental slope	Deep (abyssal)
Skeletons			
fully articulated	1	0	0
partial articulated	2	0	0
associated	4	7	0
dissociated	3	0	0
Cranial			
rostrum/bill	1	0	0
premaxilla/mandible	5	0	0
pterygoid	1	0	0
quadrate	1	0	0
skull/cranium	8	0	0
Thorax/Abdominal			
furcula	2	0	0
coracoid	40	1	0
ribs	6	0	0
sternum/keel	5	0	0
scapula	15	0	0
cervical vertebrae	47	0	0
thoracic vertebrae	9	0	0
Pelvic Girdle/Tail			
coccyx	1	0	0
sacrum	3	0	0
synsacrum	9	0	0
pelvis	5	0	0
caudal vertebrae	2	0	0
pygostyle	1	0	0
Wing			
humerus	71	3	0
ulna	26	1	0
radius	8	0	0
carpometacarpus	21	1	0
phalanges (digits)	11	2	0
Leg			
femur	58	0	0
tibiotarsus	51	1	0
fibula	3	0	0
tarsometatarsus	36	0	2
phalanges	9	0	0
Miscellaneous			
unidentified remains	0	0	0
3D body mold	0	0	0
Total	465	16	2

APPENDIX B Continued.

	Continental Environments						
	Lacustrine	Fluvial	Floodplain	Fluvio-lacustrine	Karst	Alluvial	G/F/L
Skeletons							
fully articulated	8	0	0	0	0	0	0
partial articulated	13	0	0	0	0	0	0
associated	4	0	0	1	0	0	0
dissociated	1	1	0	0	0	0	0
Cranial							
rostrum/bill	0	1	5	0	0	0	0
premaxilla/mandible	5	2	68	0	14	0	0
pterygoid	0	0	0	0	1	0	0
quadrate	1	0	1	1	1	0	0
skull/cranium	9	1	1	2	1	0	0
Thorax/Abdominal							
furcula	1	0	1	0	0	0	0
coracoid	33	8	35	20	2	0	1
ribs	0	0	0	5	0	0	0
sternum/keel	2	0	4	4	3	0	0
scapula	5	3	5	8	2	0	0
cervical vertebrae	6	1	1	14	4	1	0
thoracic vertebrae	0	0	0	0	1	0	0
Pelvic Girdle/Tail							
coccyx	0	0	0	0	0	0	0
sacrum	0	0	0	0	0	0	0
synsacrum	1	0	0	2	0	0	0
pelvis	0	0	0	3	1	0	0
caudal vertebrae	0	0	0	0	0	0	0
pygostyle	0	0	0	0	0	0	0
Wing							
humerus	40	15	37	48	10	3	1
ulna	11	9	3	24	8	0	2
radius	3	5	1	8	9	0	0
carpometacarpus	20	11	11	13	10	0	0
phalanges (digits)	3	1	0	0	0	0	0
Leg							
femur	4	4	6	19	10	0	0
tibiotarsus	26	31	26	16	9	2	0
fibula	0	0	0	0	0	0	0
tarsometatarsus	19	41	31	23	20	1	5
phalanges	10	4	7	0	7	0	0
Miscellaneous							
unidentified remains	2	0	0	23	0	0	0
3D body mold	0	0	0	0	0	0	0
Total	227	138	243	234	113	7	9

APPENDIX B Continued.

	Transitional Environments	Unclassified Environments			
	Deltaic	Asphalt Pit	Hot Spring	V/C	Fissure Fill
Skeletons					
fully articulated	0	0	0	0	0
partial articulated	0	0	0	0	0
associated	0	0	0	0	0
dissociated	0	0	0	0	0
Cranial					
rostrum/bill	0	2	0	1	0
premaxilla/mandible	1	0	0	0	0
pterygoid	0	0	0	0	0
quadrate	0	0	0	0	0
skull/cranium	0	0	0	0	0
Thorax/Abdominal					
furcula	0	0	0	0	0
coracoid	0	10	0	0	0
ribs	0	0	0	0	0
sternum/keel	0	0	0	0	0
scapula	0	8	0	0	0
cervical vertebrae	0	0	0	0	0
thoracic vertebrae	0	0	0	0	0
Pelvic Girdle/Tail					
coccyx	0	0	0	0	0
sacrum	0	0	0	0	0
synsacrum	0	0	0	0	0
pelvis	0	0	0	0	0
caudal vertebrae	0	0	0	0	0
pygostyle	0	0	0	0	0
Wing					
humerus	2	6	0	2	1
ulna	3	0	0	0	0
radius	3	0	0	0	0
carpometacarpus	2	7	0	0	0
phalanges (digits)	3	0	0	0	0
Leg					
femur	0	4	0	0	0
tibiotarsus	0	13	0	0	0
fibula	0	0	0	0	0
tarsometatarsus	2	11	0	1	0
phalanges	0	0	0	0	0
Miscellaneous					
unidentified remains	0	0	0	0	0
3D body mold	0	0	1	0	0
Total	16	61	1	4	1

APPENDIX C

TOTAL BONE COUNTS OVER TIME FOR EACH FIELD SITE DISCUSSED IN CHAPTER 3

Appendix C. Total bone counts over time for each field site discussed in Chapter 3.

Field Site	No. of Bones Deployed (Start)	Two Mo.	Six Mo.	Ten Mo.	Twelve Mo.
1: Sapelo Island, Georgia	80	76	72	38	38
2: Naples/ Fort Myers, Florida	80	74	67	33	33
3: Key Largo, Florida	96	54	33	16	16

APPENDIX D

TOTAL BONE COUNTS OVER TIME FOR EACH TYPE OF DEPOSITIONAL ENVIRONMENT DISCUSSED IN CHAPTER 3

Appendix D. Total bone counts over time for each type of depositional environment discussed in Chapter 3.

Field Site	No. of Bones Deployed (Start)	Two Mo.	Six Mo.	Ten Mo.	Twelve Mo.
1: Freshwater Pond	96	78	60	32	32
2: Terrestrial	64	49	45	21	21
3: Marsh/Mangrove	96	74	63	34	34