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2 Palaeoclimate, environmental factors, and bird body size: a multivariable analysis
3 of avian fossil preservation
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Abstract

For this study, we abstracted data on 693 avian fossil specimens from 398 publications to determine preservation biases in the avian fossil record. Our results show that dissociated wing and leg bones are the most commonly preserved avian skeletal elements and they are preferentially preserved in environments of high erosion and reworking potential—notably continental shelf marine environments. Using bivariate descriptive displays and multivariable regression analyses, we investigated the trends and associations between well-preserved avian specimens (i.e., fully- or partially-articulated) and a variety of taphonomic factors, including depositional environment, body size, and palaeoclimate. The regression model shows that well-preserved specimens are independently associated with depositional environments of low reworking potential commensurate with low energy systems, warm and humid climates, and smaller bird body size. Our results also indicate that fossils of smaller birds are less common than those of larger birds, but they are more often well-preserved. Bivariate analyses revealed that five times as many articulated specimens are found in warm and humid climates as in cool or dry climates, and this association persists in the multivariable regression model. Warm climates, the strongest predictor of better skeletal preservation, may be underestimated as a source of taphonomic bias in the avian fossil record, possibly because of the indirect nature of climate effects. Rapid burial events, such as volcanic ash accumulations and mudflows, are recognised for their influence on preservation, but climate-related storm events may be more important to avian taphonomy than previously understood. Our analyses indicate that geologic processes leading to high quality preservation of avian fossils are closely associated with climate. Additional studies, based both on fossils and modern taphonomic experiments, with improved collection of climate-related data, are needed to advance our understanding of avian taphonomy.

1. 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). Bickart (1984) also reports the perception among previous investigators (Matthew and Granger, 1917; Van Tyne and Berger, 1959; Ricklefs and Gill, 1980) that the fragility of bird bones limits their potential utility in detailed study of the fossil record. Olson (1985) and Bickart (1984) emphasised that avian remains make up a substantial portion of some fossil assemblages and are frequently quite well-preserved. Other researchers have pointed out that bird bones, although often pneumatic, are relatively hearty: they are frequently heavier and denser than the bones of similarly-sized mammals (Proctor and Lynch, 1993; Dumont, 2010).

In the past twenty years, there has been a surge of publications reporting new or better preserved avian fossils, yet the taphonomic factors that affect avian preservation in the fossil record remain little studied. A tendency exists among researchers to focus more on the unique taphonomic history associated with one particular kind of depositional environment at one location (exemplified by *Archaeopteryx* in the Solnhofen Limestone, Germany) than on the full range of depositional environments and taphonomic forces impacting avian fossil preservation. One environmental factor receiving relatively scant attention thus far in avian studies is palaeoclimate. Although recent neotaphonomic findings indicate that physical weathering of exposed specimens is important (Behrensmeyer et al., 2003; Cruz, 2008; Prassack, 2011), the extent to which palaeoclimate plays a role in fossil preservation has not been thoroughly evaluated.

1.1. Modern avian taphonomic studies

Several investigators have laid the groundwork for the field of modern avian taphonomy, from documenting avian carcass decay and disarticulation in marine, terrestrial, ice, and brackish settings (Schäfer, 1972; Bickart, 1984; Oliver and Graham, 1994; Davis and Briggs, 1998; Brand et al., 2003; Cruz, 2008; Cambra-Moo et al., 2008) to developing weathering profiles for avian remains (Behrensmeyer et al., 2003; Prassack, 2011). Schäfer (1972) conducted studies comparing the disarticulation of a variety of marine vertebrates, including drifting dead seabirds, finding that bones of larger birds and mammals often spread over vast distances along the seafloor. Oliver and Graham (1994) reported on the death, scavenging, and disarticulation of a flock of coots trapped in a frozen lake, enabling development of a scavenger-specific disarticulation sequence. Davis and Briggs (1998) examined taphonomic processes affecting bird carcasses in both swamp and shallow marine settings in south Florida, USA; their observations led them to establish an 11-stage idealised disarticulation sequence for bird carcasses, which they then applied to famous avian fossil deposits to judge the level of degradation. Bickart (1984) and Brand et al. (2003) explored the disarticulation sequences of doves (and other vertebrates) in diverse environments, with widely varying results. Substantial variation in disarticulation rates within and across birds and mammals was identified by Brand et al. (2003), suggesting that actualistic studies need large sample sizes to be most meaningful.

For their 2003 paper, Behrensmeyer and her colleagues analysed weathering stages and palaeoecological signatures in subaerially-exposed bird and mammal bones in Amboseli National Park, Kenya, concluding that larger bird species (body weight 1 to 10 kg) have greater preservation potential than smaller bird species. The Amboseli results suggest that robust skeletal elements may be over-represented in the fossil record as compared to smaller bird bones.

Contrastingly, an examination of the Mesozoic avian fossil record by Fountaine et al. (2005) led to different conclusions on the preservation potential of larger vs. smaller skeletons. Their analysis indicates that smaller skeletons are as likely to be preserved as larger ones, but other researchers suggest that this would only be true because of bias from a “Lagerstätten effect” (Brocklehurst et al., 2012).

Cruz (2008) compared the taphonomy of a modern avian and mammal bone assemblage from southern Patagonia 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, unlike Amboseli, the Patagonian bird assemblage was biased toward smaller bird skeletons. Prassack (2011), following Behrensmeyer et al. (2003), examined the effects of physical weathering on avian bones exposed to a saline-alkaline lake environment in northern Tanzania. She found that the bones displayed rapid, unique weathering patterns related to the saline-alkaline setting. She also attributed variations in the degree of weathering among individual skeletal elements (e.g., humerus vs. phalanx) to differences in bone structure and function.

Further experimental work on environmental and bird-specific factors was carried out by Cambra-Moo et al. (2008), who examined the initial and late stages of decay in the red junglefowl, *Gallus gallus domesticus*, under controlled laboratory conditions. Adult carcasses were found to decompose more rapidly in the first six days of exposure than juvenile carcasses, but from day seven on, the juvenile carcasses decayed more rapidly than the adult carcasses. The decay rate was much faster for subaerially exposed carcasses compared to buried carcasses; subaerially exposed carcasses also decayed faster than those in water. Further, bird age and size were found to be strongly correlated, which also impacted preservation potential. These results

highlight the need for robust field and laboratory experiments on avian preservation in a variety of environmental settings.

Overall, modern studies have reported differing rates of avian decay, skeletal disarticulation, and bone loss in disparate environments, but they have not clearly compared their experimental results with the avian fossil record for either climate or body size factors. Nor have there been enough modern studies to assess how climate factors have contributed to taphonomic differences. Although systematic comparisons across different climate regimes have not been made, the following factors are suggested to accelerate bone decomposition: stresses from repeated heating and cooling, cyclical wetting and drying, and exposure to highly acidic soils in humid settings (Behrensmeyer, 1978; Fernández-Jalvo et al., 2010; Prassack, 2011).

1.2. Developmental influences on avian fossilisation

Microstructural characteristics of bird bones may also be an important factor in their decay and weathering: avian bones vary in structure by the age and sex of the bird, as well as by individual skeletal elements (Schufeldt, 1902). It is likely, then, that particular bones are more prone than others to be preserved in the fossil record. For instance, which elements are pneumatic and their degrees of pneumaticity vary markedly among taxa (Schufeldt, 1902; Prassack, 2011), potentially affecting avian preservation. Further, avian bones have different densities and porosities that could also affect preservation. Lastly, 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). Mallard duck humeri, for example, grow extremely fast, with high accretion rates, and are completely fibrolamellar for much of the duck's life; alternatively, its

phalanges always appear to have low accretion rates and never display fibrolamellar bone structure (Castanet et al., 1996; Currey, 2002). These differences in avian bone type likely cause differential preservation. Indeed, 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, particularly in adult specimens.

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 may render female bird bones less likely to survive in the fossil record than adult male bird bones.

1.3. Taphonomic importance of climate regime, bird body size, depositional environment, sediment transport energy, and sediment type

The influences of climate and bird body size on preservation potential are much less well-studied in the avian fossil record than aspects of the depositional environment, such as sediment type and sediment transport energy. Lyman (1994) proposed an hypothesis tying a region's climate characteristics—air temperature, humidity, precipitation, and resulting unique soil attributes—with fossilisation and suggested that these characteristics could strongly impact vertebrate diagenetic processes. Climate as an indirect factor, meaning how it affects sedimentary events that in turn control the quality of fossil preservation, is not well known, especially the frequency of storm reworking (Behrensmeyer et al., 2000). Better vertebrate fossil preservation tied to relatively infrequent sedimentary events, such as rapid burial via storms,

could be climate related (Behrensmeyer and Miller, 2012). Additionally, avian body size is a promising area for avian taphonomy. Brocklehurst et al. (2012) hypothesised that “small delicate vertebrate skeletons,” like those of many passerine bird species, are more prone to be preserved as complete skeletons in low energy environments than larger avian species. Unfortunately, their hypothesis still remains to be fully tested.

Researchers often focus on Lagerstätten that have high-quality avian preservation in specific depositional environments. Many of these Lagerstätten have carbonate sediments, leading to an assumption that well-preserved avian remains are tied to carbonate marine environments. Well-preserved avian fossils do occur in carbonate Lagerstätten, such as the Solnhofen lagoonal limestone in Germany (Owen, 1862); the Las Hoyas lacustrine limestone in Spain (Sanz and Buscalioni, 1992); or the Nammoura marine limestone deposits in Lebanon (Cau and Arduini, 2008). Nevertheless, equally notable avian preservation exists in Lagerstätten with other sediment types. The siliciclastic lacustrine mudstones of Liaoning, China, yield exceptionally preserved specimens of the Early Cretaceous bird *Jeholornis prima*, along with numerous other birds and feathered dinosaurs (Zhou and Zhang, 2002). Exceptionally preserved and articulated avian skeletons from the Eocene occur in siliciclastic beds of the Grube Messel in Germany (Mayr, 1999a, 1999b) and biosilica diatomites of the Fur Formation in Denmark (Dyke et al., 2004; Leonard et al., 2005). In addition, mixed siliciclastic-carbonate lacustrine settings can have exceptional preservation; for example, the Eocene Green River Formation in Wyoming, Utah, and Colorado, which is a renowned Lagerstätte for avian remains (Eastman, 1900; Mayr and Daniels, 2001; Wetmore, 1926). Also notable are asphalt pits like those at Rancho La Brea, where high-quality preservation of thousands of individual bird bones occurred (Howard, 1933).

181 Saturation of the bones with asphalt inhibited biological decay and decomposition, so many are
182 in near-original condition (Akersten et al., 1983).

183 Low-energy environments preferentially yield exceptional fossil preservation. In
184 particular, the Liaoning Lagerstätte in China had slow bacterial decay rates resulting from bones
185 buried in clays that were episodically covered in volcanic ash (Hou et al., 1995). The Las Hoyas
186 limestones of Cuenca, Spain, also have excellently preserved avian fossils resulting from the
187 accumulation of fine-grained carbonate sediments in anoxic bottom waters, which precluded
188 disarticulation and bacterial decay (Sanz et al., 1988). More recently, investigations at the Las
189 Hoyas site have highlighted the importance of microbial mats in delaying decay and enabling
190 exceptional preservation (Gupta et al., 2008; Iniesto et al., 2013). Contrary to the Lagerstätten
191 examples, the majority of avian fossils are not preserved under ideal circumstances, and often
192 endure scavenging, disarticulation, decay, and surface weathering before burial and
193 mineralization. Consequently, pre-burial processes that are compared across a variety of
194 depositional environments are an important area for future research in avian taphonomy.

195 Another promising area of research concerns the proposed connection between post-
196 mortem events with the initial stages of fossilisation. Such links include the bird's death position
197 and its pre-burial environment. Studies of photographs and illustrations of avian specimens from
198 fossil Lagerstätten indicate that those specimens exhibiting lateral skeletal overlapping (left-right
199 folding) and that were rapidly buried in environments with low oxygen levels have significantly
200 higher rates of skeletal completeness (Cambra-Moo and Buscalioni, 2003). This work indicates
201 that a favourable combination of environmental, biological (i.e., reduced microbial attack), and
202 orientation of the specimen at death may contribute to high preservation rates of articulated avian
203 fossils.

Physical energy within the depositional environment is a critical factor contributing to avian skeletal completeness. Though proxies for environmental energy have long been used by geologists to characterise sediments (Nichols, 2009), and invertebrates such as bivalves and gastropods are frequently used as environmental proxies (Daley, 1999; Leighton et al., 2016), such proxies have not been completely incorporated in avian taphonomic studies. Comparisons of degrees of skeletal preservation with bird size may prove useful, because larger, more robust elements may better resist energetic forces (Voorhies, 1969). Debates are ongoing as to the correct ways to measure fossil skeletal completeness and whether to use species size for ascertaining the quality of the fossil record (Brocklehurst et al., 2012; Fara and Benton, 2000; Fountaine et al., 2005; Mannion and Upchurch, 2010). These debates are beyond the scope of our study, but the quality of skeletal elements and specimen size are both essential factors that impact avian taphonomic processes.

1.4. Questions addressed

We address the following seven areas of inquiry on how climate, depositional environment, and bird size affect avian taphonomy:

- (1) Are certain depositional environments, such as the carbonate lagoons of *Archaeopteryx*, crucial in bird fossil preservation, or have other environments also proved important?
- (2) Which depositional settings and which sediment types appear to best facilitate fossilisation of avian remains?
- (3) Do sediment transport energy and bird size affect the quality of skeletal preservation?
- (4) Are dissociated bones more likely to occur in depositional environments with a high potential for erosion and reworking?

- (5) Which avian taxa and skeletal elements are found most often in the fossil record?
- (6) How do sex (i.e., male vs. female) and age (i.e., adult vs. juvenile) affect the avian fossil record?
- (7) What effects are attributable to climate (temperature, humidity, rainfall, storms), and has climate substantially affected the avian fossil record?

2. Data Sources and Methods

2.1. Search strategy

We downloaded 2,935 references from the Paleobiology Database/Fossilworks (<http://paleobiodb.org> and <http://fossilworks.org>) using the keywords of ‘aves’, ‘avian,’ and ‘bird,’ and then refined the references to 398 peer-reviewed journal articles meeting the criteria outlined in Fig. 1. We included journal articles entered into the Paleobiology Database by December 31, 2012 (demands of abstracting and analysis precluded adding later years). We added an additional 64 papers not found in the Paleobiology Database; these 64 also met the criteria listed in Fig. 1. This process yielded 398 publications (from years 1841-2012) which were abstracted into a three-level database.

2.2. Database of three levels created to address the research questions

Fig. 2 shows the three levels derived from the 398 publications and the type of data presented at each level. The 398 publications are listed in Appendix A. They yielded 445 reports from distinct locations. In 27 papers, authors reported data from more than one location or formation; for those papers, each location or formation described was counted as a separate report. From the 445 reports, we abstracted 693 *database-specimen records* with a single

specimen per taxon. If the taxonomic order of the specimen was reported or could be obtained from published literature, we listed it. When an author reported data for multiple taxa, we counted each taxon as a separate database-specimen record. In some cases the author reported fossil specimens from different genera and species of a single order; we included the different genera and species as records reported under the name of the order. The third level comprised *total bones* representing 7,209 bones recorded from all specimens in the 445 location-specific reports. For the total bone counts, when an author reported bone elements from multiple specimens of the same taxon in the same location, all of the bones were counted. We grouped the total bones by habitat (marine birds, freshwater birds, terrestrial birds, and unclassified birds when habitat was not listed by the author) and by depositional environment.

We conducted analyses listed in Fig. 2 on the following characteristics: (1) avian taxonomy, (2) habitat, (3) skeletal elements, (4) size of bird, (5) skeletal completeness index (SCI), (6) geographic locality, (7) geologic age, (8) sediment type, (9) depositional environment, (10) sediment transport energy level, (11) age and sex, and (12) climate. Environmental characteristics and bird size were treated in a regression model as potentially independent correlates of fossil skeletal integrity. Lagerstätten, defined by exceptional quality or very high densities of fossils, are presented for descriptive purposes.

2.3. Depositional environment, sediment type, sediment transport energy, habitat, and climate regime

Depositional environment data fell into three major environments (continental, transitional, marine) and were further subdivided into 18 different sub-environments. Marine sub-environments are coastal plain, continental shelf, continental slope, and deep (abyssal) marine areas. Transitional sub-environments are deltaic and swamp-marsh. Continental sub-

environments are alluvial, floodplain, fluvial, fluvio-lacustrine, glacio-fluvio-lacustrine, karst, lacustrine, eolian, palaeosol, asphalt, volcanic, and playa lake. Because more than half of the papers did not report depositional environment, other published sources for the fossil site locality were used to determine geologic age, member/formation, and depositional environment. For statistical analyses, we assigned the 18 sub-environments to four levels of *reworking potential* (hereafter, just *reworking*) as follows: low reworking (asphalt, swamp-marsh, deep marine, and lacustrine); medium reworking (floodplain, karst, palaeosol, and playa lake); moderately high reworking (marine continental slope, alluvial, volcanic, eolian, fluvio-lacustrine, and glacio-fluvio-lacustrine), and highest reworking (marine continental shelf, coastal plain, deltaic, and fluvial). It is important to note that there are exceptions to these assigned levels, such as when volcanic ash or eolian sand gently cover a carcass without reworking, or when a storm churns an otherwise low-energy swamp. In general, however, these levels are reflective of increasing erosion and reworking potential.

We divided sediment type into seven groups: siliciclastic, carbonate, mixed siliciclastic-carbonate, asphalt, peat, phosphate, and unclassified. We created a variable representing the sediment energy that the fossil was subjected to by ranking sediment grain size into three classes: fine (low energy, represented by mostly clay- and silt-sized grains; medium (medium energy, represented by mostly sand-sized grains, although minor amounts of silt or clay can be present); and coarse (high energy, represented by mostly coarse sands or gravels). Asphalt did not have a grain type or size, yet is a substance associated with very low transport energy, thus placing it in the low energy group. It is important to note that depositional environments can be mixtures of grain types, and so we used the most commonly reported grain type. Also, these general grain size groupings were applied to all sediment types for the purpose of allowing statistical

comparisons. Because the habitat classification for the order, clade, or family of birds was reported in only a few of the papers, we used the Cornell Laboratory of Ornithology (2014) or other published sources for this information.

Climate was generally not specified in the reviewed papers. Where it was not, a climate classification for each geographic region during the specified geologic time interval was determined using information from the PALEOMAP Project (Scotese, 2002) or relevant publications. Climatically-sensitive deposits (e.g., coals, evaporites, calcretes, tillites, bauxites) were the primary source of data for the maps generated from the PALEOMAP Project (Boucot et al., 2013).

2.4. Skeletal completeness indices

Skeletal completeness indices (SCI) for the 693 specimens were based on descriptions, photographs, and figures supplied in each article and were classified into three levels. Level 0 indicates one or several isolated bones. Level 1 indicates a partially-articulated, but incomplete, skeleton or associated bones from a single specimen found together. A partially-articulated skeleton has much of the bird intact, but may be missing the upper or lower girdle and limbs or the skull. Level 2 indicates a complete or nearly complete articulated skeleton. Specimens we categorised at Level 1 contained 59% partially-articulated skeletons and 41% associated bones. Because a majority of SCI Level 1 specimens were partially-articulated, Level 1 and Level 2 specimens were combined and referred to as ‘well-preserved’ specimens for the final database-specimen analyses.

2.5. *Estimating avian body size*

Body size was generally estimated using skeletal element lengths. If these size parameters were missing from the publications, we estimated weight from extant birds where applicable; however, the majority of specimens were classified based on limb lengths. Sixteen reports were of bones that were too fragmentary and were not compared to an extant species in the description, making them unclassifiable. Skeletal element lengths were put into broad size categories based on the long axis lengths of the skull, humerus, femur, carpometacarpus, tibiotarsus, and tarsometatarsus. Size categories were designated as small (<30 mm), medium (30 to 74 mm), large (75 to 299 mm), and giant (> 299 mm). When there were multiple bones from a single specimen, we averaged the lengths. The categories are similar in concept to the tetrapod size measure of Fara and Benton (2000), but calibrated to distinguish sizes within birds. Calibration data relating bone length to body mass (weight) are presented in Appendix B. Appendix C explains why the bird body size and SCI measures we used were more suitable than measures proposed by other authors.

When bone lengths were unavailable and the fossil specimen was reported to be “the same as” or “most similar in size” to a named extant species, we used weight of the extant bird as our body size measure. Using available weight information on the extant species (Cornell Laboratory of Ornithology, 2014), we took the midpoint of the range of average weights to create four weight classes: small (< 0.45 kg.), medium (0.45 to 1.36 kg), large (1.37 to 13.6 kg), and giant (>13.6 kg). It was not possible to use a standard allometric equation (see Hone et al., 2008) to predict body mass because specific long bones were often not available. The humeral articulation facet (Field et al., 2013) was not used because relevant papers either had no photograph or the photographs were not oriented to show this facet.

2.6. Statistical analyses

Associations observed between or among categorical variables were quantified by two-tailed Chi-square tests for independence. For trends, two-tailed Cochran-Armitage Z-statistic-based trend tests for categorical data were used. To eliminate sparse data cells for the analyses of database-specimen counts, fully- and partially-articulated skeletons were pooled; large and giant size birds were also pooled. The 18 depositional sub-environments were allocated to four categories of varying reworking potential as described in Section 2.3. To prevent uninformative analyses from sparse cell sizes, the ten climate zones were collapsed into two broad categories: those warmer and more humid (hereafter referred to as “warm and humid”) versus cool, cold, or arid (hereafter referred to as “cool or dry”). Many PALEOMAP arid belts were close enough to the equator to have been warm, but since it was important to assess climate effects via rainfall and storms (see climate classifications in Belda et al., 2014), we elected to combine all dry, arid, and semi-arid zones with the cool and cold climate zones. This allowed for maximum separation between ancient climate zones with a higher likelihood of rainfall and storms versus those with a lower probability of rainfall and storms.

In the model analyses of environmental and body size independent variables, we estimated their associations with a (1, 0) dependent variable as follows: fully- or partially-articulated (1) vs. dissociated bones (0). We used a binary Poisson regression model with a sandwich estimator of standard errors to calculate multivariable-adjusted risk ratios (McNutt, 2003). Unadjusted and adjusted risk ratios from the model display the relative effect (e.g., of siliciclastic sediments, or of small bird size) with respect to a reference group. For a variable to be retained in the multivariable model required a Chi-square significance level (for the entire

variable) of $p \leq 0.20$. An alpha level of 0.05 was assumed for statistical significance. All analyses were done with Statistical Analysis Software (SAS), version 9.3 (SAS Institute, Inc., Cary, N.C.)

3. Results

The 693 database-specimens (Table 1) comprise 57 taxa from the Late Jurassic to the Recent (Table 2). These taxa represent specimens from 53 countries on all continents, including Antarctica. Through 1997, the majority of the 398 publications described avian fossils found in the northern hemisphere, with most reports representing North America and northern Europe (66%). However, the North American/European bias has lessened over the last 15 years, with a significant upward trend in reports of avian fossils from other geographic regions (Fig. 3). By 2012, the North America/northern Europe locations (51%) had a similar overall number and percentage of fossil locations as the rest of the world (49%). Much of the recent increase in reports from regions other than North America and northern Europe is due to the sharp increase in fossil discoveries in Mongolia and China.

3.1. Database-specimens: Common taxa

The database-specimen fossils are a mixture of extant and extinct taxa, with the majority representing modern birds, subclass Neornithes (Table 1). Of the neornithines, Anseriformes (duck-like, 7.6%) and Charadriiformes (e.g., waders, gulls, auks, 8.7%) had the highest representation, while the Enantiornithes (a diverse group of Cretaceous waders, swimmers, fishers, and raptors, 7.6%) made up the largest number of extinct birds. As a whole, these three groups were most often reported from lacustrine (27%), shallow marine (32%), and fluvio-lacustrine (11%) depositional environments. Anseriform fossils were most often found in

shallow marine (23%), lacustrine (19%), and fluvio-lacustrine (11%) environments, while charadriiform fossils occurred more in shallow marine environments (62%) than in either lacustrine (15%) or fluvio-lacustrine (3%) settings. Enantiornithines were more likely to be reported from lacustrine environments (48%) and less often from fluvio-lacustrine (19%) or marine continental shelf environments (7%).

3.2. Total bones: Skeletal element counts by depositional environment and bird habitat

We grouped the fossil bones by the major depositional environment (continental, marine, or transitional) in which they were found (Table 3). Marine environments contained 57% of the 7,209 total bones. Marine continental-shelf environments contributed ~47% of the total bones, along with the second highest number of partially-articulated or associated bone skeletons. Continental environments contributed 39% of the total bones. Within continental environments, lacustrine environments contributed ~11% of the bones, but had most of the well-preserved fossils (49 fully- and 24 partially-articulated skeletons or associated bones). The transitional environments of deltaic and swamp-marsh were rare, contributing only ~2% of the total bones. Marine and freshwater taxa together comprised 73% of total bones data (Fig. 4). Bird habitat strongly parallels where the fossils were found: of the marine and freshwater habitat bird bone fossils, 83.2% were found in marine depositional environments, 14.3% in continental environments, and 2.5% in transitional environments. Thus, we see a very strong bias in the fossil record toward aquatic avian taxa.

3.3. Total bones: Differential preservation of avian skeletal elements

Wing bones (humerus, ulna, carpometacarpus, and carpal phalanges) comprised 41.2% of the total bones, and leg bones (femur, fibula, tibiotarsus, tarsometatarsus, and tarsal phalanges)

made up 32.7% of the total bones (Fig. 5). The remaining 24.3% and 1.7% of the total bones were, respectively, axial elements (cranial, thorax, and pelvic bones) and associated bones/articulated skeletons (Fig. 5). The five most commonly preserved individual skeletal elements across all depositional environments were, in order of abundance, the humerus, the tarsometatarsus, the ulna, the coracoids, and the tibiotarsus (Fig. 6).

3.4. Measures of potential for reworking of specimens

Fossils frequently experience reworking through erosion and re-deposition (e.g., via fluvial transport, storm surges, tidal currents, mass movements) and bioturbation. Although reworking of significantly older fossils into younger strata is not typically considered an issue (Martin, 1999; Kidwell and Flessa, 1995), it can be problematic especially when reworking of fossils occurs near an important stratigraphic boundary, such as the Cretaceous-Palaeogene. Classifying sediments according to their potential for being eroded, and thus reworking of fossils, is one way to approximate these effects when no direct measurement has been made. The papers included in this dataset seldom reported whether fossils showed evidence of reworking: only 10 (2.5%) of the 398 papers included any mention of reworking. Certain marine and terrestrial environments have more erosive activity: a higher level of dissociated (separate) bones occur in marine continental shelf and slope environments, both of which contained <1% well-preserved specimens (Table 3). Similarly, the fluvial and fluvio-lacustrine environments contained <1% well-preserved specimens. These sub-environments exemplify the high erosion rates and concomitant physical activity (e.g., abrasion, crushing) that contributes to skeletal degradation and reworking. In the database-specimen analyses, we used the measure of reworking potential to classify depositional environments. These data, in Fig. 7, reveal that low

reworking environments have five times the percentage of well-preserved specimens compared to moderately-high and high reworking environments.

3.5. Specimen preservation: Depositional environment, sediment type, sediment transport energy, and bird body size

3.5.1. Depositional environment and sediment type

Well-preserved specimens tended to be found more often in low reworking and lacustrine environments (Table 3 and Fig. 7). Lacustrine environments contained 91% of the specimens in low reworking potential settings, and thus dominated this category. Of all the sub-environmental categories, most of the SCI Level 1 and 2 database-specimens (44%) were preserved in lacustrine settings, a result well beyond that expected for the total number of specimens from lacustrine settings. Although low reworking settings contained only 23% of 678 database specimens, they contributed twice the percentage of well-preserved specimens than expected based on the numbers of specimens (Fig. 7).

For sediment type, the largest number and percentage of the 693 database-specimens were found in siliciclastic environments (323 or 47%), followed by mixed siliciclastic-carbonate (182 or 26%), and carbonate (86 or 12%). The 102 (or 15%) remaining types were grouped together; of the 102, there were 3 asphalt, 7 biosilica, one peat bog, 25 phosphate, and 66 unclassified. Carbonate settings did not have more well-preserved specimens than siliciclastic settings; the siliciclastic settings had 57% more well-preserved specimens than the carbonate settings (22% vs. 14%, $p=0.10$), which was not significantly different by Chi-square. (Fig. 8). Mixed siliciclastic-carbonate settings had a slightly lower percentage of well-preserved specimens (9.9%) than either the carbonate or the siliciclastic settings. The siliciclastic

environments contained significantly more SCI Level 1 and 2 specimens than did asphalt, peat, phosphate, biosilica, or unclassified environments (22% vs. 7.8%, Chi-square $p=0.001$).

3.5.2. Sediment transport energy (grain sizes)

More avian fossils occurred in high energy systems than medium or low transport energy systems (Table 4). For all avian fossils, there was considerable variation in transport energy and degree of reworking (Fig. 9). In general, low energy systems had the least amount of reworking, while moderate to high energy systems had the most amount of reworking. Low transport energy environments were approximately three to four times as likely to contain well-preserved avian fossils as were medium or high energy environments (Fig. 10). Additionally, there was a significant trend of decreasing proportions of well-preserved specimens as transport energy increased.

3.5.3. Bird body size

Most specimens were of medium (33.2%) or large (47.9%) body size, while a minority were of small body size (18.9%, Fig. 11a). However, far more small birds were well-preserved (28%) compared to medium or large and giant birds (18% and 10%, respectively, Fig. 11b). In fact, there was a significant decrease in high quality preservation as body size increased (Fig. 11b).

To better understand the bird size vs. well-preserved specimen trend, a further analysis with sediment transport energy was done. We stratified the bird size data by the three sediment transport energy levels (Fig. 12a) and found that the bird size distributions were quite different. In the lowest energy sediments, numbers of small, medium, and large birds were comparable (all

between 26 to 42%); in the medium and high energy sediments, large and giant birds made up 50 to 56% of the specimens. We next examined whether the trend for bird size vs. preservation remained significant after controlling for sediment transport energy. Smaller bird size remained strongly associated with skeletal completeness: at every energy level, as bird size increased, fewer specimens were well-preserved (Fig. 12b).

3.6. Specimen preservation: Climate regimes

Avian fossils represent a wide variety of climates (Fig. 13). In particular, most avian fossils represent warm temperate climates (252), followed by subtropical (105), arid (81) or semi-arid (81), and cool temperate (71) climates (Fig. 13). Based on these data, slightly more of the database-specimens represent warm and humid climates (55%) than cool or dry climates (45%).

Well-preserved avian fossils were more common in warm and humid climates, compared to cool or dry climates (Fig. 14a). In fact, the percentage of well-preserved specimens was five times higher in warm and humid compared to cool or dry climate zones. However, as bird size increased in warm and humid climates, fewer specimens were well-preserved; this trend was not present in cool or dry climates (Fig. 14b).

3.6.1. Lagerstätten and climate

Avian fossil specimens from Lagerstätten were much more likely to represent locations and time periods with warm and humid climates. Ninety-three of the 100 Lagerstätten specimens were associated with a warm and humid climate, and only 7 with a cool or dry climate. When restricting analysis of skeletal completeness to the 100 specimens from

Lagerstätten, we found 82.4% high-quality preservation in small birds, 76.7% in medium birds, and 34.8% in large and giant birds (Fig. 15a). Virtually all of this bird size trend came from locations or time periods with warm and humid climates; there is not enough data (7 specimens) in the Lagerstätten with cool or dry climates to make out a trend. These data show that small birds were significantly better preserved than medium or large/giant birds in fossil Lagerstätten.

Small bird body size fossils were found better preserved than medium or large/giant birds in the 278 non-Lagerstätten sites in warm and humid climate locations (Fig. 15b), although the Chi-square was not significant at $p=0.137$. In the data from 299 cool or dry non-Lagerstätten sites, small bird specimens were *less often* well-preserved than medium or large birds. Based on small numbers of well-preserved specimens, these 299 specimens indicate that small bird preservation fared much less well in non-Lagerstätten with cool or dry climates than did preservation of larger birds (Fig. 15c, trend test $p=0.08$).

3.7. *Multivariable model for correlates of preservation quality*

Adjusted risk ratios indicate that bird body size, climate, sediment transport energy, and reworking potential were all significant predictors of well-preserved avian fossils (SCI Level 1 and 2; Table 5), confirming the results of the univariate and bivariate analyses. They provide evidence that palaeoenvironmental factors (climate, sediment transport energy, depositional environment), as well as bird body size, are independently correlated with the percentage of specimens that are well-preserved, and that the bird size association is true only for warm and humid climates. The stratified results in Fig. 14b and the large risk ratio of the climate effect support the interpretation that climate is directly or indirectly tied to preservational factors that favour more complete skeletal integrity.

4. Discussion

These data show that avian fossil reports originate from all continents and that reports were dominated by northern Europe and North America until late in the 20th century, when avian fossils started to become widely discovered in central and eastern Asia. This geographic trend agrees with Benton et al. (2011), who commented on the 2000-2010 increase in new fossil tetrapod taxa reported from continents other than Europe and North America. It also agrees with Fountaine et al. (2005), who noted the extended geographic range of reports of Mesozoic birds. Our data indicate that the extended geographic range is not only true for publications on Mesozoic birds, but also for those on Cenozoic to Recent birds.

4.1. Total bone counts differ by depositional environment

The 398 published papers contributed 7,209 individual skeletal elements to our analysis. Marine environments, specifically continental shelf sites, contained 57% of the total bones, but they were poorly preserved, representing <1% of SCI Level 1 and 2 specimens. Coastal plain environments preserved a substantial number of bird fossils, but also <1% well-preserved specimens. Similarly, <1% of the bones in the fluvio-lacustrine and floodplain environments were well-preserved. Therefore, it appears that environments with enhanced erosion and reworking have less well-preserved avian fossils. The total bone data substantiate a clear bias toward continental shelf marine environments, such that birds which forage in shelf waters make up the bulk of the avian fossil record, but furnish a very small proportion of well-preserved skeletons. The wide range of depositional settings in shelf environments and the increased erosion in upshelf settings undoubtedly contribute to this phenomenon. The great diversity of

marine bird species that comprise water-loving shore- and seabird communities is also a strong contributing factor.

4.2. Counts of discrete skeletal elements

Quantity of skeletal elements preserved, as opposed to quality of preservation, provides clues as to why certain bones are more commonly preserved. The humerus, tarsometatarsus, ulna, and tibiotarsus were the first, second, third, and fifth most common bones in our avian fossil database. These elements were largely dissociated and were more commonly found in near-shore marine environments, which tend to be high energy so bones are exposed to weathering and erosion before burial. These four skeletal elements correspond closely to the frequency of sub-fossil lesser flamingo bones found in a taphonomic survey of subaerial environments (Prassack, 2011). That survey located 395 bones, with frequency in decreasing order: humerus, ulna, tibiotarsus, and tarsometatarsus. The close correspondence between our total fossilised bone counts and Prassack's findings suggests that certain avian skeletal elements consistently survive exposure much better than others.

4.3. Why certain skeletal elements predominate

Because differential preservation is apparent in the avian fossil record, some studies of skeletal element distribution have suggested theories for the abundance of certain bird bones in natural assemblages (Bovy, 2002). These theories include preservation bias related to differences in bone density and skeletal biomechanics (Livingston, 1989; Lyman, 1984), damage or loss due to predation or scavenging (Oliver and Graham, 1994), morphological configurations at death that are specific to different avian taxa (Cambra-Moo and Buscalioni, 2003), and

analytical collection-based bias (Crockford et al., 1997). The bone density/biomechanics theory is particularly interesting. Dumont (2010) found that bone stiffness and strength were strongly correlated with increased bone density in pneumatic bird bones. Kirkpatrick (1994) found that the humerus experiences the greatest amount of stress in a flying bird's skeleton: the bone's pneumaticity allows for lift, and the increased stiffness and tensile strength allow it to withstand the high shear stress experienced during flight. Different bird taxa have differing degrees of bone pneumaticity across their skeletal elements, reflecting their different modes of life (Schufeldt, 1902; Prassack, 2011). The strengthening and stiffening of the humerus bone may play a critical role in its preservation potential, enabling it to resist taphonomic degradation and leading to its prevalence in the avian fossil record. The morphological configuration of specific avian taxonomic groups, as well as burial positions, appear to play critical roles in differential preservation of skeletal elements by influencing each stage of disarticulation (Cambra-Moo and Buscalioni, 2003; Cambra-Moo, 2006). More actualistic investigations of avian bone density and of bone microstructure in varying skeletal elements, as well as across varying bird orders, in combination with post-mortem factors, could yield insight into why the avian fossil record is so dominated by axial elements.

4.4. Environmental determinants of preservation quality: sediment type, depositional environment, and sediment transport energy

Approximately half of avian fossils were preserved in siliciclastic settings, with another 25% in mixed siliciclastic-carbonate settings. While it is certainly true that higher frequencies of siliciclastic sediments in these papers may be at least partly tied to the predominance of siliciclastic environments on earth (Railsback, 1993), the SCI Level 1 and 2 percentages do not

support the idea that carbonate environments chiefly produce intact or mostly intact bird skeletons, like *Archaeopteryx* from the Solnhofen limestone. Rather, higher univariate percentages of well-preserved specimens (SCI Level 1 and 2) were found for siliciclastic settings when compared to carbonate and all other sedimentary settings. Although our results do not support a significant preservation effect difference between siliciclastic and carbonate environments after multivariate adjustment, the direction of the results suggests that somewhat more well-preserved specimens occur in siliciclastic environs. The greater worldwide frequency of siliciclastic settings alone cannot explain these data, which indicate that both siliciclastic and carbonate sediments allow for high quality preservation.

The high proportion of more complete skeletons in lacustrine settings is likely due to their deposition in anoxic fine sediments. Compared to coarser-grained sediments, burial in fine-grained sediments increased the potential for higher-quality articulated fossils by reducing biological and physical degradation. When compared to medium, moderately high, and high reworking potential environments, low reworking (predominantly lacustrine and fine-grained sediments) settings were significantly more likely to preserve articulated skeletons.

4.5. Bird attributes of preservation quality: Body size

Although large and giant bird specimens were found more than twice as frequently as small birds overall (Fig. 11a), our skeletal completeness trend analyses show that smaller birds were three times as likely to be well-preserved (Fig. 11b). This result would not be expected if smaller and more delicate skeletal elements were equally exposed to energetic forces and scavenger activity before and during burial. These results indicate that, although smaller specimens are much more likely to be well-preserved compared to larger specimens in quiet low-

energy environments (see Brocklehurst et al., 2012), smaller specimens are also more likely than larger specimens to be well-preserved in less quiet and higher transport energy environments—a result not predicted before. Factors in addition to the relatively quiet environment must therefore be involved in protecting smaller-sized specimens from disruption during fossilisation. Furthermore, occurrence of more smaller birds in SCI Levels 1 and 2 was true for low, medium, and high energy levels, lacustrine environments, non-lacustrine environments, warm and humid climates, as well as fossil Lagerstätten. Only within cool or dry climates did the favourable preservation trend of smaller bird sizes fail.

The lower prevalence of small birds overall, and in non-Lagerstätten, as well as their lower prevalence in higher energy sediments could be evidence of significant destruction of small birds in more turbulent settings (Boessenecker et al., 2014). The greater overall fossil prevalence of larger versus smaller size specimens agrees with Behrensmeyer et al. (2003), whose data indicated that modern avian remains in higher weight categories had increased preservation potential. Our results highlight that a bias towards large specimens disappears in lower energy environments, while the better preservation of smaller specimens remains.

4.6. Multivariable model for correlates of preservation quality

The adjusted risk ratios from the model confirm the univariate and bivariate analyses and provide compelling evidence that the three environmental factors (climate, sediment transport energy, depositional environment) and bird body size are independently correlated with skeletal preservation, while Fig. 14b graphically shows that the superior preservation of smaller birds is only true for warm climates. The model and Figs. 14a and 14b suggest several taphonomic factors that combine to preferentially preserve smaller avian skeletons rather than just a

Lagerstätten effect. Of the environmental factors, climate is the strongest predictor of the quality of avian fossil preservation. We believe it is premature to accept the hypothesis that small delicate skeletons are more easily destroyed and more likely to be buried whole, due to a Lagerstätten effect (see Brocklehurst et al., 2012). The finding of better-preserved small avian skeletons was only partially explained in our multivariable model by low transport energy and reworking potential, the hallmarks of Lagerstätten preservation.

4.7. Climate: Can direct effects be implicated in avian taphonomy?

The climate conditions associated with the depositional environments in our dataset are necessarily at a “macro” scale based on Scotese’s PALEOMAP projections and Boucot et al. (2013). This resolution may result in higher specimen counts in the warm and humid climate zones, compared to the cool or dry climate zones, partially because of the greater worldwide land area associated with the warm and humid belts. However, the large differences in percentage of well-preserved specimens between these two broad climate categories exist despite differences in worldwide land area. The climate zone data reveal significantly greater skeletal completeness for specimens in warm and humid climates when compared to cool or dry climates. This climate association cannot be attributed simply to a higher worldwide distribution of the warmest climate zones. In addition to the main effects of climate, the association of more well-preserved skeletons for smaller bird body sizes did not occur in the cool or dry climates. The regression model and stratified results (Table 5 and Fig. 14b) indicate that warmer climate zones are tightly associated with underlying environmental factors that lead to higher levels of well-preserved skeletons, as well as with factors that favour better skeletal integrity as bird size decreases. Yet, the mechanisms that explain the warm climate effect remain unclear. Exposure to cooler local

environments during burial may expose bone to freeze/thaw cycles, subjecting it to the effects of ice crystal expansion (Todisco and Monchot, 2008). The effects of freezing, however, are likely to be swamped by the much more disruptive processes from sediments with substantial reworking potential. The direct effects of exposure to cold are unlikely to account for much of the effect of climate as seen in our results.

Warm temperature and high humidity may affect specimens directly. We found consistently better bone preservation (more elements and articulation) in the warm and humid climates, which indicate that climate and associated factors influence avian taphonomy. For example, Tappen (1994) showed that certain vertebrates undergo much slower rates of skeletal degradation in tropical rainforests than in open and drier conditions. Some authors attribute the slower rate in tropical settings to vegetation cover protecting carcasses (Madgwick and Mulville, 2012; Ross and Cunningham, 2011). Protection of the remains of smaller birds could plausibly be related to vegetation cover, where they may be protected from predators and surficial weathering more easily than the remains of larger birds. Other modern studies found that avian remains tend to weather rapidly in warmer and more humid environments (e.g., Gardner and Walker, 2009), so protection of small birds from weathering by vegetation in tropical and subtropical environments may not fully explain the trend.

Detecting direct effects of climate would be aided if local conditions at the time of fossil burial were known with greater precision, such as through estimates coming from bone mineral. Methods employing both the carbonate and phosphate portions of fossil bone could help with this problem. Analysis of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes in bone carbonate appears to correlate with aridity and with water derived from precipitation, respectively (Kohn and Law, 2006). Stable isotopic analysis of bone phosphate is another palaeoclimate indicator, as it appears to

correspond with local precipitation at the time of apatite formation (Fricke and Wing, 2004). Estimates from bone phosphate also correlate with information from soil carbonates, provided the samples come from diagenetically-resistant bone phosphate (Barrick et al., 1999). Currently, these methods have limited utility, as they require the fossil bones to be exceptionally well-preserved or quite young (Kohn and Cerling, 2002). Improving the methods for estimating palaeoclimate parameters applicable to avian remains is critical and may require multiple proxies.

4.8. Age and sex of specimens

Developmental, metabolic, and reproductive factors may affect the survival of avian remains. The porous nature of juvenile bird bones may place them at high risk for weathering and loss, while the depleted calcium content of adult female bird bones may increase their chances for taphonomic destruction. However, as only 33 (4.9%) of the 693 database-specimens documented sex and age and only 28 (4.1%) documented age, not enough samples were available for analysis. Because both sex and developmental age may have an impact on bird bone preservation, these characteristics deserve increased attention in future studies.

4.9. Modern experiments needed

As already noted, modern studies and our review indicate that climate factors affect the degradation of exposed avian skeletal elements. Experimental work that includes the role of climate is crucial for developing a more robust model for avian preservation. Future studies should examine the taphonomic impact of specific climate-related factors like temperature, pH, moisture/humidity, and seasonality, as well as depositional environment factors on the

713 weathering and degradation of avian bone.

714 For modern studies, weather station data that can be used to investigate climate effects
715 are now widely available (Smith et al., 2011; NCDC, 2013; RCC-CD, 2013). Some have used
716 temperature, humidity, rainfall, and other data to investigate preservational factors on exposed,
717 submerged, and buried avian bones (e.g., Bickart, 1984; Brand et al., 2003; Cambra-Moo et al.,
718 2008; Gardner and Walker, 2009; Fernández-Jalvo et al., 2010). Experimental approaches
719 similar to these studies would provide increased clarity for understanding these multi-factorial
720 preservation processes.

721
722 ***4.10. Implications: Effects of warmer climates on quality of preservation may be***
723 ***underestimated***

724 Some of the results we obtained may not be surprising as they tend to confirm that quieter
725 environments have a better potential for high-quality preservation. However, the risk ratio for
726 warm and humid climates appears somewhat larger than that of other environmental variables,
727 placing climate in the first rank of taphonomic factors associated with avian fossil preservation.
728 Climate factors (temperature, humidity, precipitation) may act directly on specimens (via
729 freezing, drying, cracking, flaking, fungal attack) or their effects may be more indirect. Our
730 study suggests that warm-climate-induced causal processes are conducive to increased
731 preservation of fully- and partially-articulated specimens. In particular, the majority of well-
732 preserved specimens were recovered from lacustrine sediments in warm and humid climate
733 regimes. Because lakes are typically in geographic depressions, they are well situated to
734 accumulate material from rapid or catastrophic burial events (e.g., mudflows and volcanic ash

eruptions), which makes them particularly conducive to high-quality preservation of fossils (Behrensmeyer et al., 2000).

Of equal, if not greater, significance may be the more frequent events where sediment is water-driven by storms. During periods of increased global temperature, the hydrologic cycle becomes more vigorous, generating frequent (relative to cooler periods) intense storms (Easterling et al., 2000). Storm rainfall intensity, rather than the amount of precipitation, has the greatest impact on soil erosion and runoff (Nearing et al., 2005). Climatological studies indicate that warming climates in the modern era have caused an increase in heavy storm events (Easterling et al., 2000). In our dataset, only 100 avian specimens were found in Lagerstätten, and of those, only seven were traceable to time periods that had cool or dry climates, while the rest represented warm and humid environments. Such an association is indicative of a potentially strong role for climate, especially warm climates, in contributing to the formation of fossil Lagerstätten. For the Las Hoyas fossil Lagerstätte, investigators concluded that an interaction of climatological, biological, and geological conditions led to excellent preservation (Gupta et al., 2008). In this instance, storms led to rapid burial without disarticulation. The Las Hoyas limestone strata formed in a subtropical wetland, with alternating wet and dry periods. The organic material containing the best-preserved fossils was transported during seasonal storms. Other studies of the Las Hoyas site have concluded that bacterial sealing (microbial mats) and anoxia, plus rapid burial, were the mechanisms that explain the quality of preservation (Buscalioni and Fregenal-Martínez, 2006).

In a warming world, increased storm events that trigger sediment flows could enhance the preservation of avian remains and potentially increase the formation of Lagerstätten. Thus, occurrence of episodic but intense storms can be viewed as an overall positive taphonomic factor

for avian skeletal preservation. Nevertheless, increases in storms and floods may lead to erosion, transport, disarticulation, and thus decreased preservation potential, so high preservational quality would likely require a “Goldilocks” succession of events: just one major storm (the depositional event) with later storms being less frequent and violent to minimize transport and abrasion (see Reif, 1982). Evidence from storm and flooding events may be difficult to discern, but careful analysis of sediments has shown that gleaned seasonal flooding events from fossil-bearing strata is possible (Buscalioni and Fregenal-Martínez, 2006). Unfortunately, this storm-related analysis is not frequently done, and as a consequence, the impact of warmer climates on the preservation of avian fossils may be greatly underestimated.

5. Conclusions

We found that marine shelf environments provided the largest number of total bones in the reviewed fossil studies. The body part distribution among the 7,209 bones revealed that wing bone elements survived best. Age and sex of specimens were not reported often enough to allow us to draw any conclusions as to their potential function in avian bone preservation. The regression model showed that well-preserved specimens were independently associated with depositional environments of low reworking potential, with low sediment transport energy, with warm and humid climates, and with smaller bird body size. Bivariate analyses indicated that five times as many articulated specimens were found in warm and humid climates as in cool or dry climates. Smaller fossil birds were less common than larger birds in these data, yet were significantly more often found well-preserved. In addition, smaller birds were more often well-preserved in association with warm and humid ancient climates. The regression model and stratified data results suggested that climate is closely associated with taphonomic factors leading

781 to better preservation in general—and smaller bird preservation in particular. The strongest
782 predictor of better skeletal preservation was warmer climate, and warm palaeoclimates may have
783 been greatly underestimated as a taphonomic factor impacting avian taphonomy. This may result
784 from the indirect effects of climate. If climate is causally associated with better avian fossil
785 preservation, it is unlikely to be through weathering, as bird bone weathering studies have
786 yielded conflicting results (Brand et al., 2003). Warmer climates are more likely to be indirectly
787 associated with better fossil preservation, through more frequent intense storms, rapid burial
788 during such storms, anoxic waters, and microbial action. Our study highlights the need for
789 additional fossil as well as modern (experimental) taphonomic studies, with improved collection
790 of climate-related data, to advance our understanding of avian taphonomy.

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Supplemental data and text is contained in Appendices A, B, C, and D.

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Titles, Legends, and Footnotes for the Figures and Tables

Figure 1. Selection of avian database publications.

The 398 publications were abstracted for depositional environment, climate, bird body size, age and sex, type and number of discrete skeletal elements, and quality of skeletal preservation.

Logos for the Paleobiology Database and Fossilworks from <https://paleobiodb.org> and <http://fossilworks.org> respectively (used under Creative Commons License CC-BY-4.0). Sieve image modified from work by Pearson Scott Foresman, (used under Creative Commons License CC-0-1.0).

Figure 2. Schematics of the avian datasets.

Of the 398 papers, 371 contained one geologic unit per paper and 27 contained two or more units, yielding 445 reports on distinct geologic units. The 693 specimens represent 57 orders, clades, or families. The specimens are one per taxa for each formation; when multiple specimens were reported per taxa in the same geologic unit, only a single specimen was used. The 7,209 bones represent all bones described for all reports.

Table 1. Order, sub-class, clade, or family of the 693 database-specimens.

FOOTNOTE:

Of the 398 papers, 341 reported a single taxon; 57 reported multiple taxa. The median number of taxa reported per paper was 1.0, the mean was 2.1. The maximum taxa reported in one paper was 16. When multiple specimens of the same taxa were reported by a paper, the first specimen with long bone measurements was included in the database-specimens.

¹ Family; ² Clade; ³ Sub-class; ⁴ controversial taxonomic assignment; ⁵ no taxon assigned.

unclassified or diverse habitats

Table 2. Geologic ages of the avian specimens in 445 geographic location-specific reports and their frequency counts.

Figure 3. Percentages of 398 papers by year published and location of fossil, contrasting North America and northern Europe with other countries.

Other countries, Cochran-Armitage Z trend statistic, 8.50, $p < 0.0001$. For years 1841-1997, 11% (7/62), and for years 1998-2012, 38% (51/134) of other countries' reports were from Mongolia or China. North America and northern Europe is defined as: U.S., Canada, Denmark, Belgium, France, Germany, U.K.

Table 3. Total bone[†] counts by depositional environment and skeletal completeness index.

FOOTNOTE:

Totals for fully- or partially-articulated skeletons & associated bones reflect duplicate specimens of the same order, genus and species that were not included in the database specimens. [†] All bones described in each of the 445 reports.

Figure 4. Percent distribution of 7,209 bones by species habitats.

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Images of seagull, wood duck, and pheasant from Wikimedia Commons
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Figure 5. Bone count distribution and percentage by skeletal body part (N=7,209 bones)
Associated bones also includes partially articulated skeletons. Cranial, thorax, wing, pelvic, and
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Figure 6. Diagram of bird skeleton with color indicating the 5 most commonly preserved bone
elements.
The five bones in order of abundance were humerus (1520), tarsometatarsus (954), the coracoids
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Skeleton image modified from Proctor and Lynch, 1993.

Figure 7. Percentages of well-preserved specimens (SCI Level 1 and 2) by environments of
varying reworking potential (N=678 database-specimens).
Cochran-Armitage trend test, 7.91, $p < 0.0001$. The sub-environments of Table 3 are allocated to
the four reworking potential categories described in Section 2.3.

Figure 8. Percentage of well-preserved (SCI Level 1 and 2) specimens by environments of
differing sediment type (N=693 database specimens). Overall heterogeneity Chi-square,
 $p = 0.0002$. Siliciclastic settings percentage exceeds carbonate settings percentage, Chi-square,
 $p = 0.10$. 66 unclassified reports lacked adequate information to identify sediment type.

Table 4. Grain sizes or types grouped to reflect high, medium and low energy environments.

FOOTNOTE:

See Section 2.3 for explanation of grain size usage, applied to all sediment types.

^aAsphalt, a saturated hydrocarbon, is included in the low energy group based on very low transport energy.

^b30 of the 693 database specimens were in formations missing data on grain type.

Figure 9. Transport energy distribution within environments of varying reworking potential
(N=657 database-specimens).
36 specimens were missing data on transport energy or reworking potential.

Figure 10. Percentage and trend of well-preserved (SCI Level 1 and 2) specimens by environments of differing sediment transport energy (N=663 database specimens). 30 specimens were missing data on sediment transport energy. Linear trend by Cochran-Armitage trend statistic.

Figure 11a. Percentage distribution of database-specimens by bird body size (N=677). 16 specimens were missing body size due to fragmented specimens.

Figure 11b. Percentage and trend of well-preserved (SCI Level 1 and 2) specimens by bird body size (N=677). 16 specimens were missing body size due to fragmented specimens. Linear trend by Cochran-Armitage trend statistic.

Figure 12a. Percentage distribution of database-specimens by bird body sizes within sediment transport energy classes (N=647). 46 specimens were missing data on transport energy or bird body size.

Figure 12b. Percentage and trend of well-preserved (SCI Level 1 and 2) specimens by bird body size within sediment transport energy classes (N=647 database-specimens). Low energy: Cochran-Armitage trend statistic, 3.21 $p=0.0007$. Medium energy: Cochran-Armitage trend statistic, 1.79, $p=0.037$. High energy: Cochran-Armitage trend statistic, 1.35, $p=0.088$. 46 specimens were missing data on transport energy or bird body size.

Figure 13. Frequencies of 693 database-specimens in 10 climate zones.

Figure 14a. Percentage of well-preserved (SCI Level 1 and 2) specimens by climate categories (N=677 specimens). Chi-square, 55.8, $p<0.0001$.

Figure 14b. Percentage and trends of well-preserved (SCI Level 1 and 2) specimens across bird body sizes, within climate categories (N=677 specimens). Linear trend by Cochran-Armitage trend statistic.

Figure 15a, b, and c. Percentage and trends of well-preserved (SCI Level 1 and 2) specimens by bird body size and Lagerstätten status (N=677). (a) within Lagerstätten, (b) non-Lagerstätten and warm and humid climate, (c) non-Lagerstätten and cool or dry climate. Linear trend by Cochran-Armitage trend statistic.

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Table 5. Model-adjusted estimates of specimens in SCI Level 1 and 2 for environmental and bird factors, (N= 662 database-specimens).

FOOTNOTE:
^a Z-statistic from least square means vs. referent level. C.I., confidence interval. ^b Warm and humid includes warm temperate, tropical and subtropical . ^c Cool or dry includes temperate, cool temperate, cold temperate, dry temperate, cool arid desert, semi-arid, and arid. ^d Unclassified includes 66 specimens that lacked adequate information to identify sediment type. ^e See Section 2.3 for the assignment of depositional environments to each level of the variable. Multivariable model included bird size, climate, sediment transport energy, and reworking potential of the environment as variables; sediment type did not meet the $p \leq 0.20$ criterion for inclusion. N=662 specimens with complete data; 31 specimens were missing information on the univariate estimates. An additional 21 specimens were missing data in the multivariable model due to multivariable missing value patterns.

Figure 1. Selection of avian database publications.

The 398 publications were abstracted for depositional environment, climate, bird body size, age and sex, type and number of discrete skeletal elements, and quality of skeletal preservation.

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Table 1. Order, sub-class, clade, or family of the 693 database-specimens.

Sub-class	Order, clade, or family	Habitat	Frequency (%)
Neornithes	Accipitriformes	Terrestrial	13 (1.9)
Neornithes	Aegotheliformes ⁴	Terrestrial	2 (0.3)
Neornithes	Alcediniformes	Terrestrial	1 (0.1)
Neornithes	Anseriformes	Freshwater	53 (7.6)
Neornithes	Apodiformes	Terrestrial	4 (0.6)
Incertae sedis	Archaeopterygidae	Unclassified/diverse [#]	1 (0.1)
Incertae sedis	Cariamiformes	Unclassified/diverse	6 (0.9)
Neornithes	Charadriiformes	Marine	60 (8.7)
Neornithes	Ciconiiformes	Freshwater	19 (2.7)
Neornithes	Coliiformes	Terrestrial	4 (0.6)
Neornithes	Columbiformes	Terrestrial	10 (1.4)
Incertae sedis	Confuciusornithiformes	Uncl/diverse	5 (0.7)
Neornithes	Coraciiformes	Terrestrial	6 (0.9)
Neornithes	Cuculiformes	Terrestrial	6 (0.9)
Neornithes	Cypselomorphae ²	Terrestrial	1 (0.1)
Enantiornithes	Enantiornithes ³	Unclassified/diverse	50 (7.2)
Enantiornithes	Euenantiornithes	Unclassified/diverse	1 (0.1)
Incertae sedis	Euornithes	Unclassified/diverse	1 (0.1)
Neornithes	Falconiformes	Terrestrial	24 (3.5)
Neornithes	Fluvioviridavidae ¹	Freshwater	1 (0.1)
Neornithes	Galliformes	Terrestrial	28 (4.0)
Neornithes	Gastornithiformes ⁴	Terrestrial	3 (0.4)
Neornithes	Gaviiformes	Freshwater	9 (1.3)
Enantiornithes	Gobipterygiformes	Terrestrial	2 (0.3)
Neornithes	Gruiformes	Unclassified/diverse	35 (5.1)
Hesperornithes	Hesperornithes	Marine	2 (0.3)
Hesperornithes	Hesperornithiformes	Marine	21 (3.0)
Ichthyornithes	Ichthyornithiformes	Marine	7 (1.0)
Incertae sedis	Jeholornithiformes	Terrestrial	2 (0.3)
Pygostylia	Liaoningornithiformes	Terrestrial	1 (0.1)
Neornithes	Lithornithiformes	Terrestrial	4 (0.6)
Incertae sedis	Metornithes ²	Unclassified/diverse	2 (0.3)
Enantiornithes	Mystiornithiformes	Unclassified/diverse	1 (0.1)
Neornithes	Neornithes ³	Unclassified/diverse	5 (0.7)
Neornithes	Odontopterygiformes	Marine	16 (2.3)
	Ornithothoraces ²	Unclassified/diverse	4 (0.6)
Ornithurae	Ornithurae ³	Unclassified/diverse	16 (2.3)
	Ornithuromorpha ²	Unclassified/diverse	4 (0.6)
Neornithes	Passeriformes	Terrestrial	27 (3.9)
	Patagopterygiformes	Terrestrial	2 (0.3)
Neornithes	Pelecaniformes	Marine	49 (7.1)
Neornithes	Phaethontiformes	Marine	2 (0.3)
Neornithes	Phoenicopteriformes	Freshwater	6 (0.9)

Neornithes	Piciformes	Terrestrial	2 (0.3)
Neornithes	Podicipediformes	Freshwater	9 (1.3)
Neornithes	Procellariiformes	Marine	47 (6.8)
Neornithes	Psittaciformes	Terrestrial	6 (0.9)
Pygostylia	Pygostylia ²	Unclassified/diverse	3 (0.4)
Incertae sedis	Sapeornithiformes	Unclassified/diverse	4 (0.6)
Neornithes	Sphenisciformes	Marine	54 (7.8)
Neornithes	Strigiformes	Terrestrial	18 (2.6)
Neornithes	Struthioniformes	Terrestrial	4 (0.6)
Neornithes	Suliformes	Marine	18 (2.6)
Incertae sedis	Teratornithidae ¹	Terrestrial	2 (0.3)
Neornithes	Upupiformes	Terrestrial	1 (0.1)
Ornithurae	Yanornithiformes	Terrestrial	1 (0.1)
Incertae sedis	Zygodactylidae	Terrestrial	1 (0.1)
	unassigned ⁵	Unclassified/diverse	7 (1.0)
Total	57 identified taxa		693 (100.0)

Of the 398 papers, 341 reported a single taxon; 57 reported multiple taxa. The median number of taxa reported per paper was 1.0, the mean was 2.1. The maximum taxa reported in one paper was 16. When multiple specimens of the same taxa were reported by a paper, the first specimen with long bone measurements was included in the database-specimens.

¹ Family; ² Clade; ³ Sub-class; ⁴ controversial taxonomic assignment; ⁵ no taxon assigned.

unclassified or diverse habitats

Table 2. Geologic ages of the avian specimens in 445 geographic location-specific reports and their frequency counts.

Geologic Ages	Frequency (%)
Holocene	6 (1.4)
Late Pleistocene	17 (3.8)
Pleistocene	16 (3.6)
Pliocene	61 (13.7)
Miocene	93 (20.9)
Oligocene	41 (9.2)
Eocene	74 (16.6)
Palaeocene	10 (2.3)
Cretaceous	125 (28.1)
Late Jurassic	2 (0.5)
Total	445 (100.0)

Figure 3. Percentages of 398 papers by year published and location of fossil, contrasting North America and northern Europe with other countries.

Other countries, Cochran-Armitage Z trend statistic, 8.50, $p < 0.0001$. For years 1841-1997, 11% (7/62), and for years 1998-2012, 38% (51/134) of other countries' reports were from Mongolia or China. North America and northern Europe is defined as: U.S., Canada, Denmark, Belgium, France, Germany, U.K.

Table 3. Total bone[†] counts by depositional environment and skeletal completeness index.

Depositional environment		Skeletal completeness index (SCI)				
Environment	Sub-environment	Fully-articulated	Partially-articulated or associated bones	Separate bones	Total counts	Percent
Continental 39% of total bones	alluvial	2	1	18	21	0.29
	floodplain	1	1	342	344	4.77
	fluvial	0	3	243	246	3.41
	fluvio-lacustrine	1	0	374	375	5.20
	glacio-fluvio-lacustrine	0	0	5	5	0.07
	karst	0	0	790	790	10.96
	lacustrine	49	24	740	813	11.28
	eolian	3	1	15	19	0.26
	palaeosol	0	0	184	184	2.55
	asphalt	0	0	5	5	0.07
	volcanic	0	1	3	4	0.06
	playa lake	0	0	1	1	0.01
Marine 57% of total bones	marine continental shelf	3	23	3336	3362	46.6
	marine continental slope	0	1	380	381	5.3
	coastal plain	1	3	299	303	4.2
	marine deep	1	5	78	84	1.2
Transitional 2% of total bones	deltaic	0	0	130	130	1.80
	swamp-marsh	0	0	2	2	0.03
Unreported 2% of total bones	unreported	0	1	139	140	1.94
Totals		61	64	7084	7209	100.0

Totals for fully- or partially-articulated skeletons & associated bones reflect duplicate specimens of the same order, genus and species that were not included in the database specimens. [†] All bones described in each of the 445 reports.

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Associated bones also includes partially articulated skeletons. Cranial, thorax, wing, pelvic, and leg images are adapted from work by Ruth Lawson, whose art appears on Wikimedia Commons (used under Creative Commons License CC-BY-3.0). The associated bones image and the articulated skeleton image are adapted from work by Craig Dylke, creator of <http://traumador.blogspot.com> (used under Creative Commons License CC-BY-NC-ND-3.0).

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Figure 7. Percentages of well-preserved specimens (SCI Level 1 and 2) by environments of varying reworking potential (N=678 database-specimens).

Cochran-Armitage trend test, 7.91, $p < 0.0001$. The sub-environments of Table 3 are allocated to the four reworking potential categories described in in Section 2.3.

Figure 8. Percentage of well-preserved (SCI Level 1 and 2) specimens by environments of differing sediment type (N=693 database specimens). Overall heterogeneity Chi-square, $p=0.0002$. Siliciclastic settings percentage exceeds carbonate settings percentage, Chi-square, $p=0.10$. 66 unclassified reports lacked adequate information to identify sediment type.

Table 4. Grain sizes or types grouped to reflect high, medium and low energy environments.

Sediment transport energy (coarseness of the sediment)	Grain sizes or types reported in the formation containing the database- specimen	Number of specimens
Low energy (fine) 26.9% of specimens	Clay	98
	Clay and silt	76
	Silt	1
	Asphalt ^a	3
Medium energy (medium) 32.7% of specimens	Clay, silt, and sand	138
	Silt and sand	79
High energy (coarse) 40.3% of specimens	Clay and sand	82
	Clay, sand, and gravel	30
	Crystalline	3
	Gravel and sand	21
	Sand	99
	Silt, sand, and gravel	33
Total		663 ^b

See Section 2.3 for explanation of grain size usage, applied to all sediment types.

^aAsphalt, a saturated hydrocarbon, is included in the low energy group based on very low transport energy.

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Figure 11a. Percentage distribution of database-specimens by bird body size (N=677). 16 specimens were missing body size due to fragmented specimens.

Figure 11b. Percentage and trend of well-preserved (SCI Level 1 and 2) specimens by bird body size (N=677). 16 specimens were missing body size due to fragmented specimens. Linear trend by Cochran-Armitage trend statistic.

Figure 12a. Percentage distribution of database-specimens by bird body sizes within sediment transport energy classes (N=647). 46 specimens were missing data on transport energy or bird body size.

Figure 12b. Percentage and trend of well-preserved (SCI Level 1 and 2) specimens by bird body size within sediment transport energy classes (N=647 database-specimens).

Low energy: Cochran-Armitage trend statistic, 3.21 $p=0.0007$. Medium energy: Cochran-Armitage trend statistic, 1.79, $p=0.037$. High energy: Cochran-Armitage trend statistic, 1.35, $p=0.088$. 46 specimens were missing data on transport energy or bird body size.

Figure 13. Frequencies of 693 database-specimens in 10 climate zones.

Figure 14a. Percentage of well-preserved (SCI Level 1 and 2) specimens by climate categories (N=677 specimens). Chi-square, 55.8, $p < 0.0001$.

Figure 14b. Percentage and trends of well-preserved (SCI Level 1 and 2) specimens across bird body sizes, within climate categories (N=677 specimens). Linear trend by Cochran-Armitage trend statistic.

Figure 15a, b, and c. Percentage and trends of well-preserved (SCI Level 1 and 2) specimens by bird body size and Lagerstätten status (N=677). (a) within Lagerstätten, (b) non-Lagerstätten and warm and humid climate, (c) non-Lagerstätten and cool or dry climate. Linear trend by Cochran-Armitage trend statistic.

Table 5. Model-adjusted estimates of specimens in SCI Level 1 and 2 for environmental and bird factors, (N= 662 database-specimens).

			Univariate				Multivariable			
	n	Percent SCI Level 1 and 2	Unadjusted Risk Ratio	95% C.I.	z-statistic (1 df) ^a	p-value	Adjusted Risk Ratio	95% C.I.	z-statistic (1 df)	p-value
Bird size										
Small	127	28.4	2.72	1.76, 4.21	4.5	<0.0001	1.59	1.04, 2.44	2.2	0.032
Medium	218	18.4	1.82	1.23, 2.69	3.0	0.003	1.55	0.90, 1.94	1.4	0.153
Large+giant	317	10.1	ref.				ref.			
Climate										
Warm and humid ^b	361	26.3	5.77	3.17, 10.53	5.7	<0.0001	3.02	1.48, 6.14	3.1	0.002
Cool or dry ^c	301	4.3	ref.				ref.			
Sediment type										
Siliciclastic	317	22.4	1.58	0.86, 2.90	1.5	0.139	--	--	--	--
Mixed siliciclastic+carbonate	168	10.7	0.72	0.35, 1.51	0.6	0.543	--	--		
Peat, asphalt, phosphate and Unclassified ^d	92	7.6	0.54	0.20, 1.46	0.9	0.386	--	--	--	--
Carbonate	85	14.1	ref.							
Sediment transport energy										
Low	170	37.1	3.93	2.38, 6.49	5.4	<0.0001	2.29	1.32, 3.98	2.9	0.003
Medium	213	9.9	1.10	0.57, 2.13	0.3	0.769	1.12	0.51, 2.47	0.3	0.770
High	279	8.6	ref.				ref.			
Erosion&reworking potential of depositional environment ^e										
Low reworking	156	44.2	4.58	2.78, 7.54	6.0	<0.0001	2.80	1.72, 4.54	4.2	<0.0001
Medium reworking	103	1.9	0.21	0.06, 0.79	2.3	0.021	0.20	0.05, 0.78	2.3	0.020
Moderately high reworking	110	8.2	0.83	0.36, 1.97	0.4	0.666	1.04	0.44, 2.42	0.1	0.93
High reworking	293	9.6	ref.				ref.			

^aZ-statistic from least square means vs. referent level. C.I., confidence interval. ^b Warm and humid includes warm temperate, tropical and subtropical. ^c Cool or dry includes temperate, cool temperate, cold temperate, dry temperate, cool arid desert, semi-arid, and arid. ^dUnclassified includes 66 specimens that lacked adequate information to identify sediment type. ^e See Section 2.3 for the assignment of depositional environments to each level of the variable. Multivariable model included bird size, climate, sediment transport energy, and reworking potential of the environment as variables; sediment type did not meet the $p \leq 0.20$ criterion for inclusion. N=662 specimens with complete data; 31 specimens were missing information on the univariate estimates. An additional 21 specimens were missing data in the multivariable model due to multivariable missing value patterns.