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Invited review

Palaeoclimate, environmental factors, and bird body size: A multivariable analysis 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.

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1. Introduction

Storrs Olson, in the second chapter of *Avian Biology*, Volume VIII, 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; Rickleffs 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 a given 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.