

Taphonomy and ecology of modern avifaunal remains from Amboseli Park, Kenya

Anna K. Behrensmeyer, C. Tristan Stayton, and Ralph E. Chapman

Abstract.—Avian skeletal remains occur in many fossil assemblages, and in spite of small sample sizes and incomplete preservation, they may be a source of valuable paleoecological information. In this paper, we examine the taphonomy of a modern avian bone assemblage and test the relationship between ecological data based on avifaunal skeletal remains and known ecological attributes of a living bird community. A total of 54 modern skeletal occurrences and a sample of 126 identifiable bones from Amboseli Park, Kenya, were analyzed for weathering features and skeletal part preservation in order to characterize preservation features and taphonomic biases. Avian remains, with the exception of ostrich, decay more rapidly than adult mammal bones and rarely reach advanced stages of weathering. Breakage and the percentage of anterior limb elements serve as indicators of taphonomic overprinting that may affect paleoecological signals. Using ecomorphic categories including body weight, diet, and habitat, we compared species in the bone assemblage with the living Amboseli avifauna. The documented bone sample is biased toward large body size, representation of open grassland habitats, and grazing or scavenging diets. In spite of this, multidimensional scaling analysis shows that the small faunal sample (16 out of 364 species) in the pre-fossil bone assemblage accurately represents general features of avian ecospace in Amboseli. This provides a measure of the potential fidelity of paleoecological reconstructions based on small samples of avian remains. In the Cenozoic, the utility of avian fossils is enhanced because bird ecomorphology is relatively well known and conservative through time, allowing back-extrapolations of habitat preferences, diet, etc. based on modern taxa.

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Introduction

Avian fossil remains are scarce in comparison to those of other continental vertebrates, although the avian fossil record is an important source of evidence for evolution and late Cenozoic ecological change (Olson 1985, 1999), especially on islands (Steadman 1989, articles in Olson 1999). Studies of the taphonomy and paleoecology of avian fossil assemblages historically have been limited by two factors: (1) the taxonomic focus on typically rare and fragmentary bird fossils, with minimal reporting of contextual or taphonomic features, and (2) concern that the small numbers of avian species usually found in bone-bearing deposits may not constitute an adequate sample for paleoecological analysis. Most research in vertebrate taphonomy has focused on mammals, dinosaurs, and fish, although there are some notable studies of fossil

and modern avian remains (e.g., Hill and Walker 1979; Rich 1980; Olson and Pregill 1982; Bickart 1984; Jefferson 1985; Oliver and Graham 1994; Emslie et al. 1996; Davis and Briggs 1998), including a number reported within the context of archaeological studies (e.g., Steadman 1984; Ericson 1987; Livingston 1989; Steadman and Intoh 1994). The work reported below provides a test of the quality of paleoecological information that is available in avifaunal assemblages and suggests that even small assemblages have untapped potential for paleoenvironmental reconstruction and information about the synecology of the organisms they represent.

To evaluate the paleoecological potential of avian remains, we conducted a study of the taphonomic and ecological features of modern avian bones that were collected during a broader research project to document weathering, destruction and burial of bones from re-

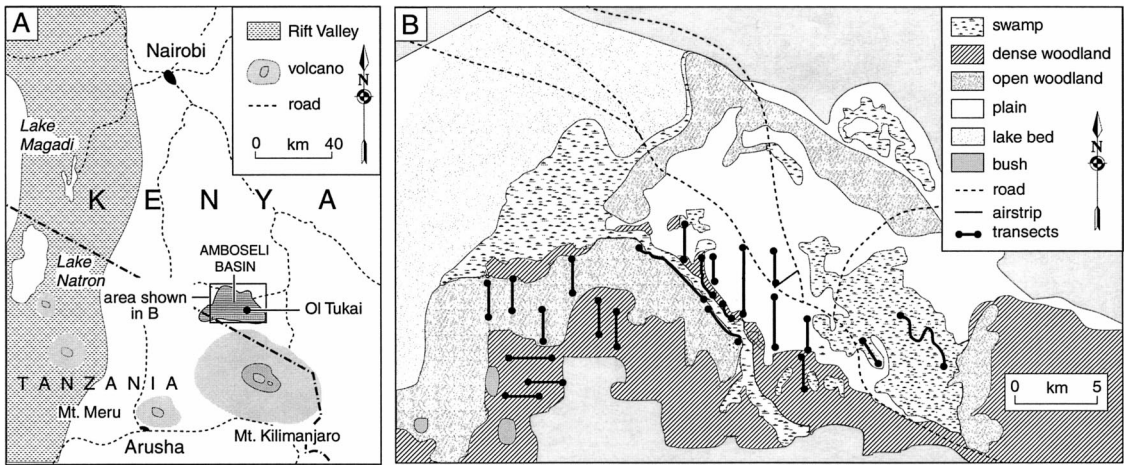


FIGURE 1. A, Map of Amboseli, showing the major habitats as they were in the late 1960's and early 1970's (Western 1973). B, The transect lines where the avifaunal bones were collected.

cent vertebrates in Amboseli National Park, Kenya (see Behrensmeyer 1978, 1991, 1993; Behrensmeyer et al. 1979; Behrensmeyer and Dechant Boaz 1980; Behrensmeyer and Chapman 1993). We use these data to examine the following: (1) taphonomic features of a pre-burial avian bone assemblage that could indicate biases in species representation, as a basis for determining how similar features in fossil assemblages might be used as evidence of bias, and (2) the extent to which species represented in the avian bone sample represent the ecology of the living avifauna of the Amboseli ecosystem, as an indicator of potential ecological fidelity in fossil avifaunas. The latter approach includes ecomorphic comparisons of species in the bone assemblage with the living avifauna to determine ecological biases that are introduced in the transition from the living bird community to the skeletal assemblage. Finally, we compare the Amboseli assemblage with examples from the fossil record to demonstrate how our taphonomic findings might be applied to paleoecological interpretations.

Amboseli National Park lies in a depression along the border between Kenya and Tanzania (Fig. 1) and includes habitats ranging from swamp to woodlands to open grasslands and thornbush (Behrensmeyer and Dechant Boaz 1980; Behrensmeyer 1993). Permanent springs feed many swamps along the park's southern borders. A large lake bed occurs on the west-

ern side of the basin, but it is dry for most of the year except in a few marshy areas fed by the springs. The climate is semiarid, with average monthly temperatures ranging from 26° to 34°C and average rainfall of 350–400 mm/yr. From the 1960s through the 1990s, an ecological shift has transformed a large part of Amboseli's woodlands to open grasslands. The causes of this shift are complex and appear to represent a combination of climate, ground water, and biotic processes, which in turn have led to a change in populations, relative abundances, and distribution of the large herbivores in Amboseli (Western and von Praet 1973; Western 1975; Behrensmeyer 1993). It is reasonable to assume that such a large change has modified the population of birds living in Amboseli as well, though data are not available to test this assumption.

Materials and Methods

We applied the same overall taphonomic approach used for mammals (Behrensmeyer 1978, 1991, 1993; Behrensmeyer and Dechant Boaz 1980), with some modifications to accommodate the different physiologies and lifestyles of African birds. The steps in analyzing the Amboseli avifaunal remains consisted of (1) identifying all specimens to body part and species, if possible; (2) describing weathering, skeletal part representation, and other evidence of postmortem modification followed by comparisons with similar features

in mammal bones; (3) characterizing ecomorphic features of the living avifauna and testing the relationship between the ecospace represented in the bone assemblage versus the living avifauna; (4) comparing taphonomic and ecological features of the Amboseli bone assemblage with two examples from the African fossil record, the Pliocene Langebaanweg avifauna from South Africa and the late Eocene avifauna from the Jebel Qatrani Formation, Fayum, Egypt.

The collection used in this study consists of 126 bones from 54 occurrences, with an occurrence defined as a cluster of one or more skeletal parts belonging to a single individual. These skeletal samples were collected from 7 habitats (open plains, lakebed, open wood, dense wood, open bush, dense bush, and swamp, as defined in Western 1973). The assemblage is dominated by 25 occurrences of ostrich (*Struthio camelus*), including 6 eggshells and 1 nest, from the same 7 habitats plus a hyena den (Hill 1989). All specimens were recorded using transect surveys (Behrensmeyer and Dechant-Boaz 1980; Behrensmeyer 1993), and all bird specimens except ostrich were collected for later identification. Some specimens were found partially buried but none were completely subsurface. The skeletal sample thus represents a subset of the total avian bone assemblage that was easily visible on the ground surface, which should be comparable to fossils collected from surface surveys or excavations (as opposed to screen-washing). Additional collections of very small avian remains from owl pellets, carnivore feces, and bone concentrations under isolated trees are not included in this study, which contributes to a size bias against small species discussed in the following analysis.

We used the synoptic collection of the Field Museum of Natural History, Chicago, to identify bones to species level. Remains from three of the skeletal occurrences could not be identified to species, and these are used in the analysis of bone weathering patterns but not in ecomorphic comparisons. Criteria used in the evaluation of avian weathering stages are based on the method of Behrensmeyer (1978). For the purpose of comparing the skeletal and living fauna, we have used the species list

compiled by Williams (1967), plus species with ranges that included Amboseli from Brown et al. (1982–1997). Information on the ecomorphic characteristics of Amboseli bird species is from Williams and Arlott (1963), Brown et al. (1982–1997), and Newman (1988).

Ecomorphic characteristics are used to define a species' niche, including body size measures as well as habitat and diet (Andrews et al. 1979; Andrews 1995; Damuth 1992). We use characteristics as defined in the ETE Database Manual (Damuth 1997), including weight, length (tip of beak to end of longest tail feather), activity time, general habitat, feeding habitat, diet, shelter habitat, and social structure (Table 1). For the weight and length parameters, we computed average values per species and assigned each to a numerical category based upon a logarithmic scale. For the habitat and diet categories, each general habitat, shelter habitat, or feeding habitat was assigned its own category, and species were rated 0 (does not appear, feed, shelter in this habitat) or 1 (does appear, feed, shelter) for these categories. In the activity category, species were given 0 or 1 for each of the three activity times. For the social structure parameter, species were assigned a ranking from 0 to 3 based on their typical social habits (Table 1).

Complete ecomorphic information is available for 364 of the 420 avian species that are recorded in Amboseli. Most species not fully described in terms of ecological attributes are passerines; thus the ecomorphic data under-represent this order. However, this bias should not seriously affect our results, because passerines still make up about one-third of the described species that we use. Avian species can occupy more than one habitat or a number of the diet categories; therefore we counted some species in more than one category, and the total n for these categories consequently is larger than 364. However, the weight, length, and social structure parameters are exclusive, and $n = 364$ for these three parameters.

To test how well the surface pre-fossil bone assemblage represents the ecological diversity of the entire Amboseli avifauna, we used non-metric multidimensional scaling (MDS) analysis, an ordination method that starts with a distance matrix and provides the optimal two-

TABLE 1. Ecomorphic parameters and categories used for analysis of the Amboseli avifauna and for comparison with the fossil avifaunas of Langebaanweg. These parameters are based on categories described in the ETE Database Manual (Damuth 1997), and values for species recorded in Amboseli are derived from information provided in Brown et al. 1982–1997, and Newman 1988.

Body weight (kg):	Length (m): Length of the animal from tip of beak to end of longest tail feather
(0) <0.01	(0) <0.01
(1) 0.01–0.1	(1) 0.01–0.1
(2) 0.1–1.0	(2) 0.1–1.0
(3) 1.0–10	(3) >1.0
(4) >10	
Activity time:	Social structure: The social organization of the species' population
Nocturnal	(0) Solitary
Diurnal	(1) Family (congregates in small family groups, usually ~4–6 individuals)
Crepuscular	(2) Occasionally social (e.g., usually solitary, but may migrate in flocks)
General habitat: Habitat in which the species is most typically found.	(3) Gregarious
Aquatic	Diet:
Terrestrial aquatic (marshes, swamps)	Insects
Grass (plains, open grasslands)	Invertebrates (non-insect)
Savanna	Fish
Bush/Scrub	Vertebrates (non-piscine, or general)
Wood	Carriion
Forest	Omnivore
Desert	Plants (general herbivore)
Vertical (cliffs)	Seeds
Shelter habitat: Where the species rests (roosts) or escapes from predators.	Fruit
Aquatic (rests on or under the water's surface)	Leaves (browser or grazer)
Terrestrial aquatic (on banks or in reeds; bush/scrub near water edge)	Feeding habitat: Where the species locates its food.
Surface (on the ground surface)	Aquatic (on or below the water surface)
Arboreal/Surface (on the surface, in forest foliage or the lower canopy of trees)	Terrestrial aquatic (on the banks/shore of water body)
Canopy (in the upper canopy of trees)	Surface (on the ground surface)
Vertical (cliffs, rocks, or banks)	Arboreal/Surface (either on the surface, in foliage, or in the lower canopy of trees)
Subsurface	Canopy (in the upper canopy of trees)
	Terrestrial aerial (picks up food from the ground while flying)
	Aerial (catches food mid-flight)
	Subsurface

or three- (here, three) dimensional representation of the data. This is accomplished by minimizing stress, the difference in monotonicity between the original distance matrix and the inferred distances in the new space. MDS uses ranked distances to do this and is especially effective at analyzing distance matrices derived from non-normal or discontinuous data, such as we used here (McCune and Mefford 1999). A simple-matching distance matrix was calculated on the basis of 37 ecomorphic characters from five separate categories (Table 1), excluding size (weight and length; see discussion below) and social structure. Each species was given a score of 1 or 0 in these categories (diet, feeding habitat, shel-

ter habitat, general habitat, activity time), based on ecological descriptions in the available literature. These characters were developed as non-exclusive binary variables where a species could, theoretically, occupy any combination of them. Thus, species with broad versus narrow ranges of ecological characteristics also are represented in terms of niche breadth in the ecomorphic analysis by the number of 1's they exhibit in the matrix—ecologically broad taxa have more 1's than ecologically narrow taxa. The resulting binary matrix for each species versus each ecomorphic character was then used to generate the distance matrix used in MDS ordination.

Of special interest in this study was the ef-

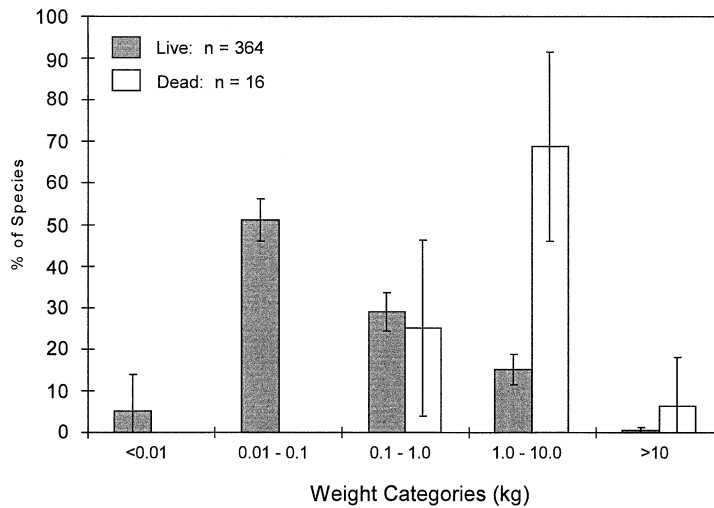


FIGURE 2. Body size distribution in the living avian fauna and the bone assemblage, showing the strong size bias toward survival and recovery of avian remains in the higher weight categories. Error bars indicate binomial confidence intervals (2 SD).

fect of size in preservation and documentation, resulting in overrepresentation of the larger taxa in the sample of avian skeletal remains from Amboseli. The size variables listed in Table 1 were not used in the MDS ordination, however, for the following reasons. The ecomorphic characters used in the MDS are direct measures of the interaction of each taxon with its environment, whereas size is an indirect measure of such interactions; it affects a broad range of organism-environment relationships, including many of the ecomorphic categories we used. Further, the size measures each included four or five categories (Table 1) and this predisposed them to overwhelming the other ecomorphic characters in the analysis, which had only two options each. Instead, we analyzed size as a separate variable (Fig. 2), and took its effects into account in interpreting preservational and ecological aspects of the avian remains.

Results and Discussion

Bone Weathering and Other Modification.—Avian bones weather in a manner similar to that of mammalian bones, and the collection shows the full range of weathering stages (WS) from 0 to 5, 0 being fresh and 5 highly cracked and fragmented by weathering (Behrensmeyer 1978) (Fig. 3). In contrast to mammal bones of comparable size, trabeculae in

the avian bone sample often are open and exposed on distal and proximal surfaces of long bones in WS 1 or 2. Most of the cracking and flaking of the external cortical bone appears to occur simultaneously, thus differing from mammalian bone in which initial weathering (WS 1) is characterized by fine cracks without flaking. Large avian limb elements may develop cracks through the cortical bone before surface cracking and flaking begins, but smaller elements generally remain intact and robust until WS 2 or 3. All of these features appear to relate to the structural composition of avian bone, with its thin but strong external cortical components supported by internal struts and pneumatic bone rather than thicker cortical bone supported by spongy cancellous bone of mammals.

Both avian and mammalian bone assemblages show unimodal distributions in terms of weathering stages (Fig. 4), but a peak in WS 2 characterizes the Amboseli mammalian assemblage, whereas the avian assemblage peaks at WS 1. The dominant weathering stage is a function of (1) the amount of time that bones spend in each stage, which can be affected by size and fragility or exposed versus protective environmental conditions, and (2) the timing of any unusual pulses of bone input to the system. There is no evidence for an increase in the number of fresh avian bones



FIGURE 3. Examples of weathering stages for the avian bones from Amboseli, following Behrensmeyer's (1978) descriptive criteria for mammals. Scale in cm.

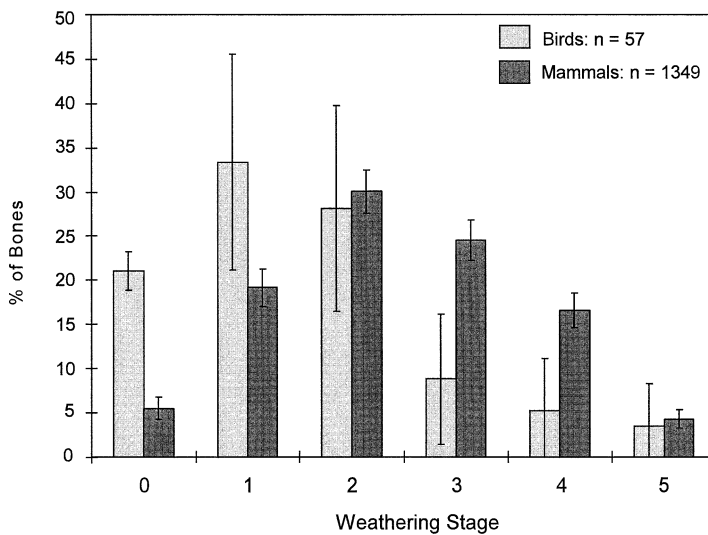


FIGURE 4. Comparison of proportions of bones in different weathering stages for birds and mammals in the 1975 samples from Amboseli. Data for mammals from Behrensmeyer (1978). The average Weathering Stage for ostrich bones is 2.1 compared with 1.2 for non-ostrich avian bones, indicating the effects of larger body size on weathering rates.

entering the system a year or two prior to the 1975 collecting effort. More bones may occur in WS 1 simply because they disintegrate quickly after this stage, relative to mammal bones in the comparative sample, which generally are larger and more robust. A dominance of WS 1 is comparable to the pattern for the bones of juvenile mammals, which are thin walled and highly porous (Lyman 1994). In carcass-monitoring experiments, bones of juveniles weather faster than those of adult mammals and do not survive into later weathering stages (Behrensmeyer unpublished data). The dominance of WS 1 in the Amboseli avian bone sample also is similar to that of mammalian bones in swamp or dense woodland habitats, where weathering proceeds more slowly than in other habitats and may even be arrested indefinitely in WS 1–2, because thick vegetation and shade decrease the effects of destructive environmental processes (Behrensmeyer 1978). However, the avian remains were collected from all habitats and for the most part were fully exposed to weathering processes, hence shade-retarded weathering rates should cause only minor inflation of the numbers of bones in WS 1.

After considering the alternatives above, we conclude that the dominance of WS 1 in avian bones results from their tendency to weather more rapidly than bones of adult mammals. It appears that after reaching WS 2, weathering of avian bones accelerates, rendering examples of WS 4 and 5 relatively rare (only 9% of avian bones, as opposed to 21% of mammal). This is consistent with the structure of avian bone, which lacks the thick cortical layer underneath the outer lamellar bone that is typical of adult mammals. Dates of death are not available for the avian remains, and it is not possible to determine the years since death for avian weathering stages as was done for the mammals (Behrensmeyer 1978). However, if these rates are comparable to the minimum time required for mammal bones to reach each stage, then for birds WS 1 = 0–1 year and WS 2 = 2–3 years. This implies that most of the Amboseli avifaunal remains represent the three-year period prior to collection, i.e., 1972–75.

Avian remains not only weather in a manner similar to mammalian bones but also are

subject to similar preburial modifications and damage. Some of the bones bear evidence of being gnawed by predators (Fig. 5A) and marked by humans (Fig. 5B). In addition, a well-fossilized distal humerus from an Egyptian Goose (*Alopochen aegyptiaca*) was collected on the Amboseli land surface (Fig. 6) along with modern specimens of the same species, attesting to the potential for avian bones to be reworked and contribute to assemblage time-averaging. None of these taphonomic features is particularly surprising, but they underscore an overall similarity between avian and mammalian bone modification and preservation.

The Amboseli assemblage (excluding *Ostrich*) showed a breakage level of 44% (44/99), which is low relative to examples of avian fossil assemblages (Table 3). This in part reflects the completeness of bones in several vulture and stork skeletons, which experienced relatively low levels of postmortem scavenging in Amboseli in the 1970s. Skeletal part survivorship can be expressed in the percentages of anterior elements (% A) relative to the total number of anterior (A) and posterior (P) elements. Following Ericson (1987), A = ulna + carpometacarpus + humerus, and P = femur + tibiotarsus + tarsometatarsus. The radius and fibula are excluded because they are relatively fragile and difficult to identify, thus making the number of bones from both fore- and hindlimbs equal in a complete specimen. If $\%A = A/(A + P)$, then we expect $\%A = 50\%$ if no taphonomic or sampling biases have resulted in differential preservation of any of the six skeletal parts. Amboseli's $\%A$ of 54% is not significantly different from the expected 50% (G-test; $G = .248, p < 0.25$) indicating that early postmortem processes such as carnivore and scavenger activity did not affect this ratio.

All of the features examined above—weathering, bone surface modification, breakage and survival of different skeletal parts, and evidence of time averaging—are indicators of postmortem taphonomic processes that could affect taxonomic representation and identification. The more evidence there is of postmortem damage, the more likely that species representation and other paleoecological information derived from these bones are biased relative to the original community (Behrens-



FIGURE 5. Bone modification features on avian bones. A, V-shaped mark interpreted as caused by a glancing blow from a predator or scavenger tooth. B, Semi-parallel marks interpreted as cutmarks by humans, probably from a steel knife. Scale in cm.

meyer et al. 2000). The Amboseli avifaunal remains provide an example of moderate levels of postmortem modification and destruction in an untransported assemblage that was subjected primarily to biological taphonomic processes. The following section shows how such an assemblage represents the structure of the living avifauna.

Comparison of Living and Dead Avifaunas.—The list of species identified from the Amboseli avifaunal bone assemblage (Table 2) documents a fairly broad taxonomic range of species, with 11 families represented by 54 skeletal occurrences and a minimum of 51 individuals (MNI). Struthionidae (Ostrich, *Struthio camelus*) dominates, constituting nearly 50% of the total number of records or specimens. This is consistent with the fact that ostrich is relatively common in Amboseli, as well as large in body size, which makes its bones more likely to be

spotted in a visual survey and also more resistant to weathering and other types of early postmortem destruction.

Species represented in the bone assemblage (the “dead” avifauna) were compared with all bird species present in Amboseli (the “live” avifauna) in terms of four ecomorphic characters: body size (weight), diet, general habitat, and social structure (Figs. 2, 7–9, respectively). Biases are defined as deviations of ecological information derived from the skeletal assemblage relative to that in the living avifauna. Only 4% of all species recorded from Amboseli are present in the bone sample, and one might logically assume that any ecological information retained in such a small sample would be seriously biased. Relative to the living avifauna, the death assemblage represents intermediate-sized species fairly accurately but overrepresents larger size categories (≥ 1



FIGURE 6. Comparison of recent humerus of an Egyptian Goose (*Alopochen aegyptiacus*) (bottom) with a distal fossil humerus from the same species that was found on the Amboseli land surface (top) along with the non-fossil bone assemblage. Scale in cm.

TABLE 2. Species represented in the Amboseli surface bone assemblage, with weight category and number of individuals (MNI) per species.

Family	Species	Weight category	MNI
Anatidae	Egyptian Goose (<i>Alopochen aegyptiacus</i>)	3	2
	Spur-winged Goose (<i>Plectropterus gambensis</i>)	3	1
Ardeidae	Little Egret (<i>Egretta garzetta</i>)	2	2
Ciconiidae	Yellow-Billed Stork (<i>Mycteria ibis</i>)	3	2
	Marabou Stork (<i>Leptoptilos crumeniferus</i>)	3	2
Accipitridae	White-backed Vulture (<i>Gyps africanus</i>)	3	6
	Lappet-faced Vulture (<i>Aegypius tracheliotus</i>)	3	1
Gruidae	Crowned Crane (<i>Balearica regulorum</i>)	3	1
Musophagidae	White-bellied Go-away-bird (<i>Corythaixoides leucogaster</i>)	2	2
Numididae	Helmeted Guineafowl (<i>Numida meleagris</i>)	3	2
	Vulturine Guineafowl (<i>Acryllium vulturinum</i>)	3	1
Otididae	Kori Bustard (<i>Ardeotis kori</i>)	3	1
	Red-crested Bustard (<i>Eupodotis ruficrista</i>)	2	1
Strigidae	African Marsh Owl (<i>Asio capensis</i>)	2	1
Struthionidae	Ostrich (<i>Struthio camelus</i>)	4	25
Threskiornithidae	African Spoonbill (<i>Platalea alba</i>)	3	1

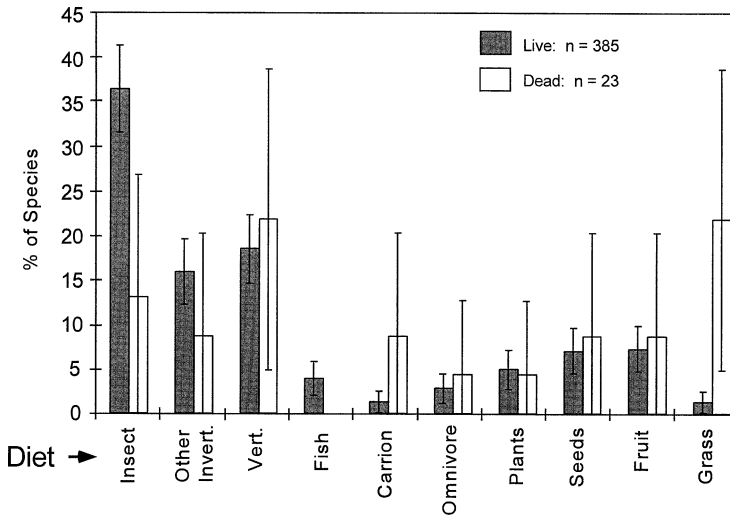


FIGURE 7. Differences in the dietary categories represented by the living avifauna and species in the avian bone assemblage, showing biases toward grass- and carrion-eating forms and against insectivores in the dead sample. Totals reflect the fact that some species had positive scores in more than one dietary category (see text and Table 1).

kg) and underrepresents smaller size categories (Fig. 2). This indicates a bias toward the survival and collection of the bones of larger animals, similar to that previously documented for mammal assemblages (Behrensmeyer et al. 1979; Behrensmeyer and Dechant Boaz 1980). All other ecological attributes of the Amboseli avifaunal remains are affected to some extent by this size bias, in that attributes of larger species tend to dominate results for diet, habitat, and social structure. In terms of diet (Fig. 7), the bone assemblage is biased toward grazers and against insectivores. The live-dead difference for carrion also suggests that there is a bias toward scavengers (vultures and Marabou Stork). These biases are partly size-related because most insectivorous birds are relatively small, but overrepresentation of scavengers could also be due to the gregarious and often competitive behavior of scavenging birds around a kill (Kruuk 1967), which can lead to death and bone scatters of these species close to other large carcasses, hence more likely documentation in the bone surveys.

Comparison of live-dead habitat representation (Fig. 8) suggests a bias in the bone assemblage toward open grassland, and against species of the woodland habitat. Again, this is affected by post-death survival and collection of bones from larger-bodied species, because

grassland dwellers are often larger in body size and may also be more vulnerable to predation than species living in areas with thick cover and many refuges. The decline of woodland and forest habitat in Amboseli prior to 1975 probably contributes to this habitat bias. There is no significant difference in social structure representation in the bone assemblage and the living avifauna (Fig. 9), although the data suggest a slight bias toward bones of gregarious species.

Nonmetric multidimensional scaling (MDS) analysis provides a more comprehensive quantitative assessment of the relationship between the ecological attributes of the living avifauna and the small sample of species in the bone assemblage. A view of axis 1 versus axis 2 is shown in Figure 10, and views from all other axes are similar. The proportion of variance (RSQ) for the final configuration is 0.78581. The graph shows that the 16 species in the Amboseli assemblage are spread across most of the total ecospace defined by the 364 species in living avifauna. Further analysis of radial sectors of the scatter of points provided a test for the significance of apparent gaps in the distribution of species in the bone assemblage in MDS space (e.g., in the right middle area). Simulations ($n > 1000$) of the distribution of samples of 16 species drawn at random from the living avifauna showed that the plot

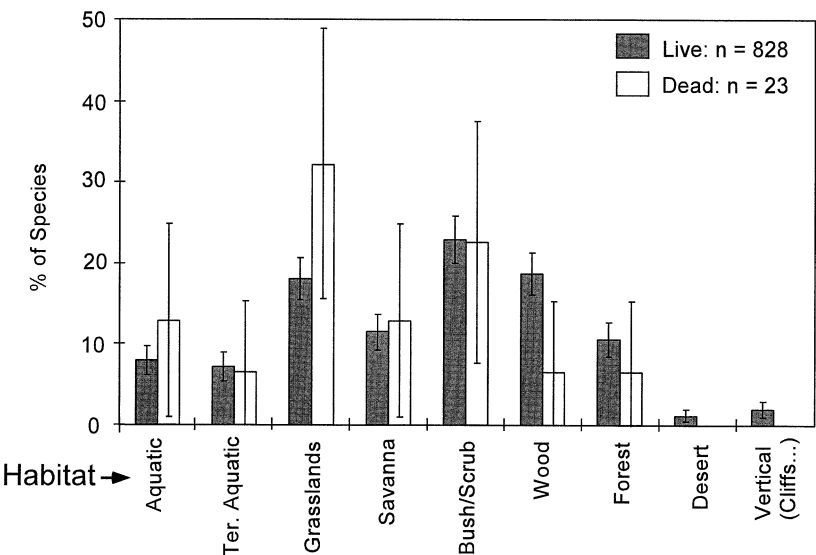


FIGURE 8. Differences in the general habitat categories represented by the living avifauna and species in the avian bone assemblage, indicating biases toward grasslands dwelling and against woodland forms in the dead sample. Totals reflect the fact that some species had positive scores in more than one habitat category (see text and Table 1). Note: Savanna habitats represent a combination of trees and grass, as contrasted with the more continuous open grasslands.

of bone assemblage species does not differ significantly from random and has no unexpected level of “gappiness” for this sample size. This indicates that the surface bone assemblage in Amboseli, although biased toward body sizes ≥ 1 kg, provides a random sample of other ecological attributes of the living avifauna (Table 1).

Although taxonomic diversity typically is vastly underrepresented in avian fossil assemblages, our results suggest that even a small sample of identifiable species (4% of the living avifauna in Amboseli) can represent overall ecological diversity and paleoenvironmental setting with a reasonable degree of accuracy. It is intriguing that the small and seriously

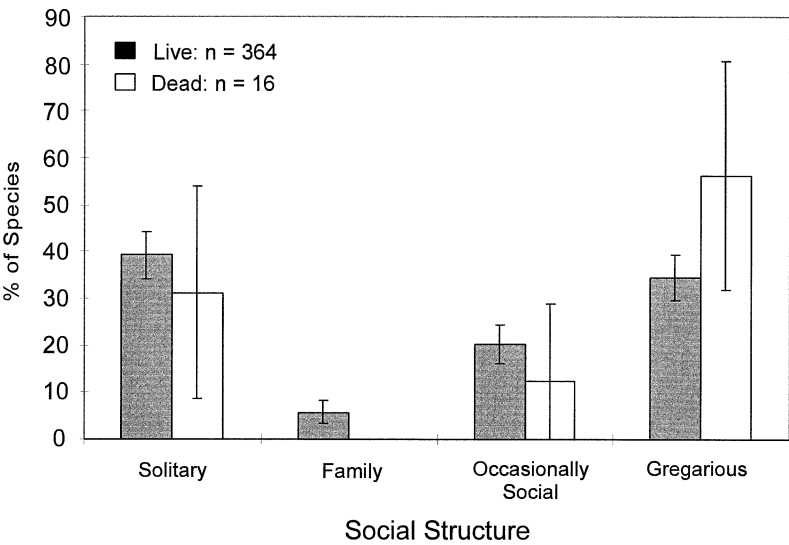


FIGURE 9. Comparison of social structure as represented in the living avifauna and the avian bone assemblage, suggesting a bias toward gregarious species in the latter. Species were scored in only one of the four categories.

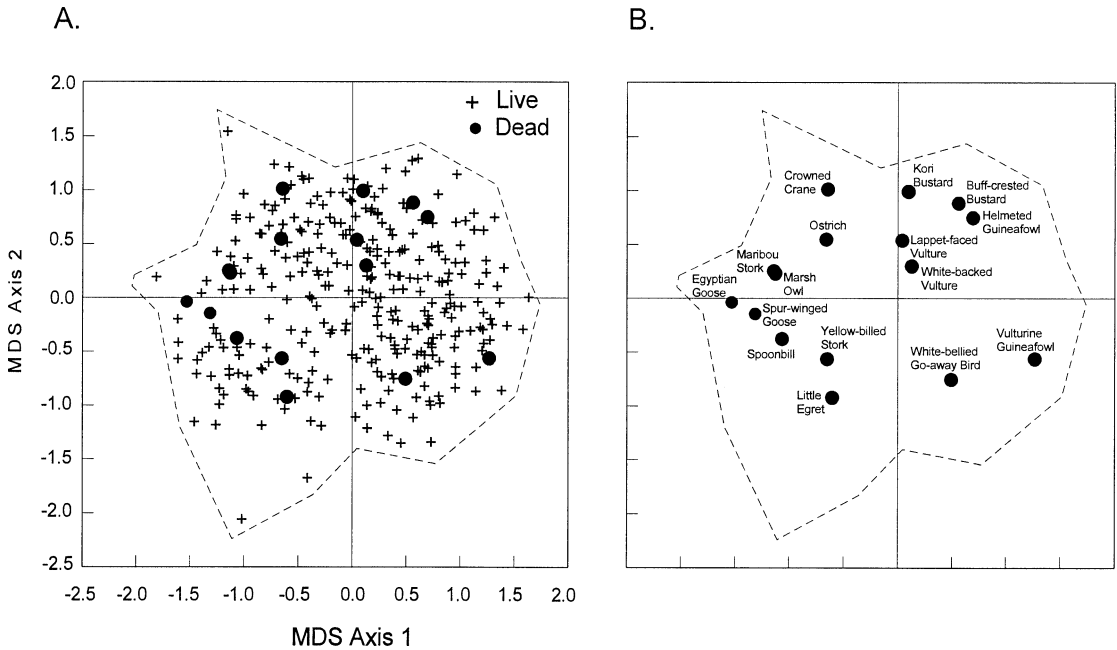


FIGURE 10. A, Results of a multidimensional scaling (MDS) analysis using 37 ecomorphic characters described in Table 1. Body size measures and social structure were excluded from this analysis (see text). The distribution of 364 living species in MDS space is indicated by the crosses and dashed line, and black dots represent the 16 species that occur in both the living avifauna and the bone assemblage. B, Key to positions of species represented in the bone sample; more-aquatic species tend to occur to the lower left and large terrestrial species toward the upper part of the distribution, although there are species >1 kg in all quadrants.

size-biased sample recovered from Amboseli retains the observed level of paleoecological fidelity. This could indicate an underlying aspect of ecosystem structuring, i.e., that there are relatively large species in all the major areas of Amboseli's avian ecospace. The fact that species over 1 kg in body weight occur in all quadrants of the MDS space (Fig. 10) supports this hypothesis.

Applications to the Fossil Record.—To better assess how the Amboseli study might be used in interpreting the fossil avifaunal record, we compared taphonomic and ecologic features of the modern assemblage with two fossil avifaunas from Africa, the Pliocene (4–5 Ma) Langebaanweg assemblage from South Africa (Rich 1980) and the late Eocene-early Oligocene Fayum assemblage from the Jebel Qatrani Formation, Egypt (Olson and Rasmussen 1986; Rasmussen et al. 1987, 1992). These assemblages were chosen because they occur on the African continent, where there has been a stable avifauna for much of the Cenozoic (Rich 1979; Olson and Rasmussen 1986), and be-

cause they represent samples derived from limited areas and stratigraphic intervals. Langebaanweg also is one of the largest known pre-Pleistocene avifaunas for any continent, with over 10,000 specimens and 61 taxa, and it has been subjected to taphonomic and paleoecological as well as taxonomic analysis (Rich 1980; Olson 1985). The fossil avifauna is derived from a phosphate mine on the coast of South Africa, and the paleoenvironment of this sand-dominated deposit has been described as a near coastal floodplain adjacent to fluvial, estuarine, tidal mudflat, and pond environments (Rich 1980; Hendy 1981). The bone assemblage itself is a fluvial accumulation that probably includes both attritional and mass death components; Rich was unable to distinguish these in her analysis. For comparison with Amboseli, we used the collection from Unit 1 of the Quartzose Sand Member, E Quarry (see Rich 1980 for full description), which includes a wide range of body sizes and taxa. The Fayum Jebel Qatrani Formation is well known for its primates and other early

TABLE 3. Bone breakage and skeletal part ratios of avian bone assemblages from Amboseli and two fossil localities, Langebaanweg (Rich 1980) and the Fayum (Rasmussen et al. 1987). % Incomplete (Broken) Bones (non-ostrich) = $(I/(C + I)) \times 100\%$, with C = complete and I = incomplete. % Anterior Elements = $(A/(A + P)) \times 100\%$, with A = anterior (ulna + hum. + cmc) and P = posterior (femur + tib. + tmt).

	Amboseli		Langebaanweg		Fayum	
Total sample size	126		4350		32	
Broken bones	44/99	56%	2364/3357	70%	23/30	77%
% Anterior elements	44/82	54%	1707/2799	39%	7/23	30%
Number of species	16		61		18	

African mammals, and represents near-coastal environments including estuaries, fluvial swamps, and forested floodplains (Bown et al. 1982) similar to those of Langebaanweg, but more laterally extensive and complex.

Weathering and bone surface modification features have not been analyzed for these fossil assemblages, but published descriptions and photographs indicate that most of the fossil bones are unweathered and show variable degrees of surface erosion, from unabraded to rounded and pitted. Results for bone breakage and skeletal-part representation (Table 3) show that the fossil assemblages record considerably more damage and selective sorting than does the Amboseli assemblage. For example, although the proportion of anterior elements (%A) is close to 50% in the Amboseli sample, %A is significantly less than 50% for the Langebaanweg fossil assemblage ($G = 71.08, p \ll 0.005$, indicating a bias for posterior limb elements) and also for the Fayum, although the G-test fails to show significance for this small sample ($G = 2.34, p < 0.10$). Increased breakage and sorting in the fossil assemblages could be a simple consequence of prolonged exposure to destructive physical processes prior to burial, but these taphonomic features could also reflect more thorough early postmortem processing (predation and scavenging) of the avian remains compared with Amboseli. For Langebaanweg, Rich (1980) suggested that the bones were sorted by fluvial action, and thus elements with relatively high density, such as tarsometatarsi and tibiotarsi (posterior limb bones) as well as coracoids, are better represented than elongate bones with lower densities and high surface-to-volume ratios, such as radii, ulnae, and carpometacarpi (anterior limb bones).

Livingston (1989) attributes such anterior

versus posterior biases to underlying anatomical causes, in which bone survival is primarily determined by the lifestyle of the different species. Thus, species that are strong fliers with robust wing elements leave bone assemblages richer in forelimb elements than species that tend to be more cursorial. The Langebaanweg avifauna is dominated by cursorial species that did not fly frequently (e.g., large representation of the cursorial Phasianidae in the assemblage [Rich 1980]) (Fig. 11), which is consistent with Livingston's hypothesis. Thus, the bias of the Langebaanweg assemblage toward posterior limb elements may reflect a combination of bone robusticity relating to the dominant mode of locomotion for the most abundant taxa and predator activity or fluvial sorting. The Fayum assemblage is too small to provide a test of Livingston's prediction, but it would be expected to have robust anterior and posterior limb elements because of the dominance of semiaquatic, flying/wading species such as storks and flamingos.

A goal of taphonomic analysis is to establish biases that could affect paleoecological reconstructions based on faunal composition, and it is clear from bone completeness and skeletal part ratios that compared with Amboseli, both fossil assemblages were subject to taphonomic processes that caused greater fragmentation and selected more strongly against the fragile skeletal parts. We expect fossil assemblages to provide a limited sample of species that survived these processes; the critical question for paleoecology is whether such a sample is seriously biased with respect to the ecological attributes of the paleo-avifauna. The analysis of the Amboseli avifaunal bone assemblage suggests that small samples may be relatively faithful in representing overall ecological signals in spite of biases in

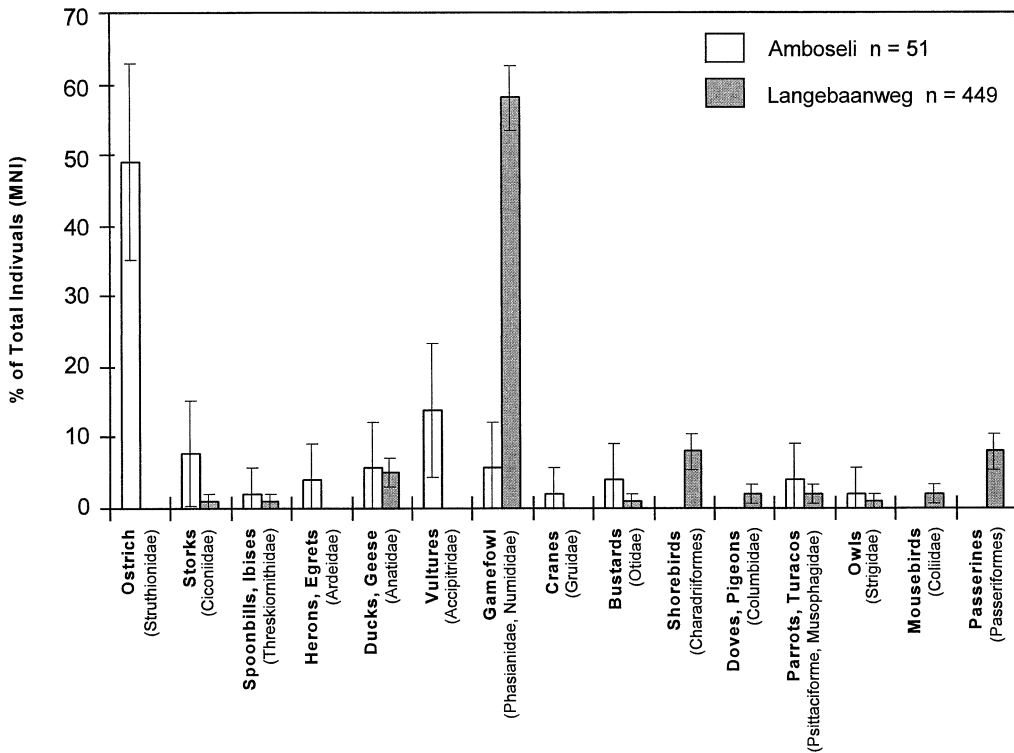


FIGURE 11. Comparison of the taxonomic compositions of bone samples from Amboseli and Langebaanweg Quarry E, based on minimum numbers of individuals (MNI) for families that are represented by more than 1% of the samples. Langebaanweg data from Rich 1980.

body size and skeletal-part preservation. This would be further supported if large and robust species occur in most of the major dietary and habitat categories in a wide spectrum of modern and ancient ecosystems. If this were true, then the loss of the smaller species (such as many of the passerines) might seriously affect paleodiversity measures but would have less effect on the overall ecological signal of the preserved avifauna.

With regard to a taphonomic indicator such as %A, an assemblage with close to 50% could indicate either minimal taphonomic overprinting, hence minimal effect on taxonomic and paleoecological signals, or overprinting that removed equal numbers of anterior and posterior limb elements. If taxa are identified primarily on the basis of appendicular skeletal parts, whether they are anterior, posterior, or both, then taphonomic biases in limb bone representation could have a strong impact on species representation. Using the Amboseli bone assemblage, we can examine how biased

limb frequencies in small samples might affect ecological signals. In Amboseli, 63% (10/16) of the species and 69% (25/36) of the individuals identified in the bone sample are represented by posterior elements (Table 4), suggesting that a fossil assemblage heavily biased toward these elements could miss about one-third of the ecomorphic information represented by the total bone assemblage. For example, species not represented by posterior elements include three semiaquatic forms, which would particularly affect the reconstruction of this component of the Amboseli ecosystem. Thus, although we have made a case for a general level of ecological fidelity in the small Amboseli avifaunal sample, it is clear that such samples can easily omit species that bear important ecological information.

In taxonomic composition (Fig. 11), the Amboseli avifauna is dominated by ostriches (*Struthio camelus*). Collecting bias increases the number of ostrich bones documented in the surface bone assemblage, but it is likely that

TABLE 4. Comparison of species represented by anterior and posterior limb elements in the Amboseli and Fayum avifaunal bone assemblages. For Amboseli, 10 (63%) out of 16 species (Table 1) are represented by either anterior or posterior limb bones. For the Fayum sample, 13 out of 18 (72%) species are represented by posterior bones and only 5 (28%) by anterior. Note: the African Spoonbill (*Platalea alba*) is not included in the list for Amboseli because it is not represented by appendicular specimens. MNI = number of individuals per species.

Amboseli species	Anterior	Posterior	MNI
African Marsh Owl (<i>Asio capensis</i>)		1	1
Buff- or Red-crested Bustard (<i>Eupodotis gindiana</i> or <i>E. ruficrista</i>)		1	1
Helmeted Guineafowl (<i>Numida meleagris</i>)		2	2
Crowned Crane (<i>Balearica regulorum</i>)	1		1
Egyptian Goose (<i>Alopochen aegyptiacus</i>)	2		2
Kori Bustard (<i>Ardeotis kori</i>)		1	1
Lappet-faced Vulture (<i>Aegypius tracheliotus</i>)	1	1	1
Little Egret (<i>Egretta garzetta</i>)		2	2
Marabou Stork (<i>Leptoptilos crumeniferus</i>)	2	1	2
Ostrich (<i>Struthio camelus</i>)	2	9	10
Spur-winged Goose (<i>Plectropterus gambensis</i>)	1		1
Vulturine Guineafowl (<i>Acryllium vulturinum</i>)	1		1
White-backed Vulture (<i>Gyps africanus</i>)	5	4	6
White-bellied Go-away-bird (<i>Corythaixoides leucogaster</i>)	1	1	1
Yellow-billed Stork (<i>Mycteria ibis</i>)	1		1
Indet.	3	2	3
TOTAL	20	25	36

Fayum species	Anterior	Posterior	MNI
<i>Eremopezus eocaenus</i>		1	1
<i>Stromeria fajumensis</i>		1	1
aff. <i>Crinifer</i>	1	1	2
aff. <i>Haliaeetus</i>		1	1
aff. <i>Pandion</i>	1		1
? <i>Pandionidae</i>	1		1
<i>Rallidae</i> indet.		1	1
<i>Gruidae</i> indet.		1	1
<i>Nupharanassa tolutaria</i>		1	1
<i>Nupharanassa bulotorum</i>		3	3
<i>Janipes nymphaeobates</i>		1	1
aff. <i>Palaelodus</i>	2	1	3
Genus indet., species 2			1
<i>Xenerodiops mycter</i>	1		1
<i>Nycteorax</i> sp.		1	1
<i>Ardeidae</i> indet.		1	1
<i>Palaeohippiorhynchus dietrichi</i>			1
? <i>Palaeohippiorhynchus dietrichi</i>		1	1
<i>Goliathia andrewsi</i>	1	1	2
Indet.			1
TOTAL	7	16	26

bones of ostriches also have a lower burial rate than those of smaller species. Their dominance in the pre-burial avifaunal assemblage probably is not a good predictor of ostrich abundance in the future fossil record of Amboseli (Fig. 11), but one still might expect some remains to be preserved, especially egg-shell fragments. Ostriches are rare or absent in the two fossil assemblages; occasional egg-shell fragments do occur rarely at Langebaanweg, but not in the fossil assemblage from the Quartzose Sand Member that was used for this analysis. This absence suggests ecological

differences that were not completely overprinted by the taphonomic effects mentioned above.

The Langebaanweg assemblage is dominated by Phasianidae, mostly francolins (*Francolinus* or *Pternistis*), (Rich 1980), which are gregarious ground birds ≤ 1 kg body weight. The prevalence of francolins is not a consequence of collection bias and does not appear to result from differential preservation due to body size or morphology relative to other elements in the avifauna, because a range of smaller and larger as well as similar-sized species are also

preserved. Most of the bones are adult, which Rich attributes to destruction of the more fragile juvenile bones by fluvial processes. She cites a number of possible ecological factors (following Voorhies 1969a,b, and Wolff 1973) including: (1) occurrence of francolins near the site of deposition, (2) social structure (often found in small family groups), and (3) high reproductive rate. The Amboseli avifaunal bone assemblage includes gregarious species (Fig. 9), but none have the group-based social structure of francolins, which are present in the living fauna of Amboseli but absent in the bone sample. Francolins are in Size Category 2 (Table 1), which is not well sampled in Amboseli, but in spite of this bias in the modern analog assemblage, their extraordinary abundance at Langebaanweg suggests sustained high population numbers, one or more mass mortality events, or both.

Another interesting aspect of the data is the large representation of vultures (Accipitridae) in the Amboseli assemblage (15%) and the lack of this family in the Langebaanweg assemblage. Langebaanweg includes many large mammals and at least one mass death occurrence of the giraffe *Sivatherium* , and should be somewhat similar to Amboseli in the availability of large carcasses. Rich (1980: p. 166) explained the low relative abundances of vultures and other raptorial groups as consistent with the pattern of relatively low representation in modern avifaunas. The Amboseli sample also shows a relatively large representation of Marabou Storks, a species with scavenging habits similar to vultures. The number of scavenger bones in the Amboseli sample could result partly from collecting in the proximity of mammal carcasses, but also may reflect an unusual number of scavengers (or scavenger deaths due to competition with mammal scavengers) in this ecosystem during the years covered by the bone sample. The paucity of these relatively large birds in the Langebaanweg sample is puzzling and could indicate taphonomic and/or ecological features of the Pliocene fluvial ecosystem, such as swampy grasslands and marshes where scavenging birds were uncommon.

The small sample of fossil avifauna from the Jebel Qatrani Formation has been used to sup-

port reconstructions of the late Eocene ecosystem of Egypt as swampland bordered by forest and open woodland or grassland (Olson and Rasmussen 1986). They justify this interpretation on the basis of the longevity of bird taxa in the Cenozoic, with most of the Fayum fossils referable to living families and some to living genera, plus the assumption that ecological requirements of the Eocene species were similar to those of modern close relatives with similar morphology. The taphonomy of the Fayum avifauna has not been examined in detail, and although Rasmussen et al. (1987) discuss some possible preservation biases, they assume that their limited sample is broadly representative of the Eocene-Oligocene ecosystem. Results from Amboseli support this assumption to some extent, although the taxonomic and ecological effects of the bias toward posterior limb elements in the Fayum sample should be subjected to further testing. For example, if the proportion of species represented only by anterior elements were the same for Amboseli and the pre-burial Fayum assemblage (Table 4), then 5 species could be missing from the Fayum sample simply because of the bias against anterior elements.

The degree to which species' relative abundances in the recent or fossil assemblages reflect their abundances in life is unknown. However, it is clear that the Amboseli avifaunal bone sample is biased toward large, terrestrial, grazing birds, and perhaps also toward scavengers, whereas the Langebaanweg avifauna shows a dominance of medium-sized terrestrial or shore birds with gregarious or family-based social structures and the Fayum assemblage is characterized by aquatic species. Representation of aquatic forms is an interesting point for comparison; in the case of Amboseli, which has many swamps, the low number of aquatic species likely reflects a collecting bias because aquatic birds that die in water were inaccessible to the surface transect sampling. But in the fossil record, it is often assumed that aquatic birds (and all other aquatic organisms) have a better chance of being preserved and fossilized than terrestrial forms. Langebaanweg does not show a particular abundance of aquatic species (i.e., most

Anatidae, Threskiornithidae, Ardeidae, Charadriiformes, Ciconiidae, etc.) in a paleoenvironment reconstructed as a coastal estuaries and nearshore swamps. Bird bones are relatively easily transported, and this pattern of species abundance may indicate that allochthonous fluvial input of terrestrial forms overwhelmed the more autochthonous coastal signal in the bone assemblage.

Summary and Conclusions

The results of this study indicate that fossil avifaunal remains deserve more serious attention as a source of information about taphonomy and paleoecology. As with mammalian remains, taphonomic features provide evidence for the extent of taphonomic overprinting and biases relative to the composition of the original avifauna. Avian bones weather faster than mammalian bones primarily because they disintegrate quickly after WS 2, and we interpret this to be a consequence of their internal structure, which lacks the thick cortical bone layers of mammals. Both avian and mammal bones undergo similar pre-burial taphonomic modification, and similar kinds of ecological information can be derived from both vertebrate groups. One might expect that faster rates of weathering would lead to shorter periods of time-averaging in avian versus mammalian remains. However, the reworked fossil bone in the recent surface assemblage of Amboseli indicates that avian remains can be time-averaged over ecologically long intervals and thus have no necessary advantage over mammals in this regard.

The ratio of anterior to posterior limb elements in avian bone assemblages provides evidence for taphonomic processes that may affect species representation and paleoecological information. In general, anterior/posterior ratios that deviate significantly from 50/50 indicate hydraulic sorting or destructive processes operating to remove the lighter or less robust elements. However, whether these elements belong to the wing or hindlimb can reflect the ecology of the living species, i.e., strong fliers versus cursorial or aquatic forms. Thus, it is possible for an assemblage formed by taphonomic processes that favored preservation of robust bones to accurately reflect the

ecology of the dominant species, even if these processes resulted in a small and fragmentary avifaunal sample.

Compared with the living avifauna in Amboseli, the surface bone assemblage is biased toward species of large size, terrestrial habitat, and grazing diet. This is partly a consequence of our sampling methodology, which used transect surveys to locate and record bones that were obvious on the ground surface, and partly the result of the greater durability of larger avian bones. The size bias in the bone assemblage is the most fundamental control on species presence or absence, but in spite of this bias, MDS analysis shows that the relatively small sample of avian bones provides a broadly accurate characterization of avian ecospace in Amboseli. This is apparent in spite of strong taphonomic and collection biases against species <1 kg body weight, which also suggests that large species of African birds occur in many of the available ecological niches. If the Amboseli remains were treated as a fossil assemblage, the avifauna alone would provide a reconstruction of the environment as an open grassland with lake and swamp environments inhabited by large animals whose carcasses maintained populations of scavenging species. This would be a fairly accurate representation of the actual ecology of Amboseli.

The Langebaanweg avifaunal assemblage from a Pliocene fluvial-coastal paleoenvironment is characterized by small to medium-sized species of terrestrial or ocean margin habitats and a very low representation of scavenging or raptorial species. Although the collecting bias against species <1 kg in the Amboseli assemblage affects its comparability to the Langebaanweg fossil assemblage, which preserved abundant remains of species of this size, both assemblages are characterized by numerous remains of gregarious species and relatively few of aquatic species. The Eocene Fayum avifauna, in contrast, is dominated by aquatic to semiaquatic species. These differences and similarities represent a mix of ecological signal, taphonomic overprinting, and collecting biases that is typical of the fossil record. Our study indicates, however, that because of the combination of conservative avian

ecology and morphology, the taxonomic identifiability of robust limb elements that are most often preserved as fossils, and the occurrence of large-bodied species in most avian niches, small avifaunal assemblages may provide broadly accurate paleoecological signals. To the extent that the African avifauna has been relatively stable since the Oligocene, the pattern of dead-live ecological fidelity documented in the Amboseli bone assemblage could apply more generally to the Cenozoic avifaunal fossil record in Africa and also to other continents and time periods.

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