SPECIAL REVIEW

HOW MANY BIRDS BELONG IN AFRICA?

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The bird faunas of Africa and its islands.—R. E. Moreau. 1966. New York and London, Academic Press. 424 pages, 62 figs., 40 tables. $18.00.—Of the 8,600 species of birds in the world, about 17 per cent occur in the Ethiopian Region, the 8 million square miles of Africa south of the Sahara. The 1,481 species might seem quite enough, until comparisons are made with other tropical lands. In South America 7 million square miles probably harbor more than 2,000 species, an enrichment one might attribute to more and wetter tropical forest than is found in Africa. Yet 600,000 square miles of Congo forest are said to contain only about as many forest birds as Slud recorded in 2 square miles of Atlantic slope rain forest in Costa Rica. Surely Africa, so rich in great mammals and the evolutionary home of the world's greatest mammal, should have more birds than it does.

That it does not Moreau regards as a legacy of the Pleistocene, an ironic twist when one recalls that some zoologists have been sufficiently impressed with the diversity of African ungulates to attribute it to the lack of any appreciable climatic change during the glacial period. When other continents suffered their climatic and geologic ups and downs over the last several million years, the African environment escaped unscathed. Or so we were told. Proceeding from a different set of facts, botanists put matters the other way round. According to Richards the relatively small number of rain forest trees means that Africa suffered more, not less, Pleistocene upset than other parts of the tropics.

Any notion of tranquility can now be discounted. C^{14} dated pollen profiles from East African mountains unveiled by Coetzee, Livingstone, and van Zinderen Bakker reflect an appreciable drop in montane vegetation zones, perhaps as much as 1,200 meters. The downward displacement was on a par with that recently unearthed at the same latitude in the Pleistocene of South America. The glacial-age pollen records must give sweet satisfaction to Moreau, who has long regarded the remarkable similarity between isolated montane avifaunas in East and West Africa as the outcome of a Pleistocene drop in the montane forest and its distinctive birds. Moreau would use the same biogeographic argument—full-glacial descent and expansion of cool montane forest at the expense of lowland forest—to account for impoverishment generally of the African avifauna and that of the lowland rain forest in particular.

At the same time while palynologists have scarcely scratched the surface of the African Pleistocene, enough work has been done to generate a rumble among the experts. In a recent (1967) issue of *Ecological Monographs* D. A. Livingstone presents the most detailed and authoritative equatorial African pollen profiles yet seen in print. But he refuses to correlate them with optimism in the style of the Bloemfontein School in which each zone of the European chronology appears, magically, out of the mud of the African bogs. Nor is Livingstone sure that the combinations of late-glacial pollen percentages he finds on Ruwenzori represent any extant African plant community. The specter of nonuniformitar-

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ianism which sometimes haunts palynologists elsewhere lurks in the African profiles. Finally, while Moreau would take the majority position that tropical interglacials were hot and dry with perhaps a 400-meter rise in the position of vegetation zones 5,000 years ago, Livingstone would not. At the 1965 Boulder Congress of the International Quaternary Association he summarized evidence to support the view that nonglacial times in Africa were wetter and thus more pluvial than the times of continental glaciation. Brackish Lake Rudolph in the driest part of Kenya is a case in point. A spectacular 4,500-year-old beach containing Mesolithic harpoons, human skeletons, abundant fossil molluscs, and fish bones stands more than 100 feet above present lake level, the position of fossil beaches of glacio-pluvial age in other parts of the world.

Moreau is by no means alone in making bold, interesting generalizations about the past vegetation and fauna of Africa. For this reason it might be helpful to consider the state of the art in better studied areas. In Europe paleogeographers have been drawing their late Pleistocene (Full-Wurm) vegetation maps with the Mediterranean Basin shown supporting deciduous forest and cool birch and pine forest. Moreau reproduces one of these on p. 273. From innumerable pollen records we know that deciduous forest of oak, elm, hazel, and alder occupied central Europe for the last 8,000 years, a region that over 12,000 years ago supported open tundra. At that time deciduous forest must have been forced south of the Alps. It seemed that the Mediterranean shores should have been about the right distance and without protest the maps were drawn accordingly. But when *fossil evidence of the right age* finally emerged from Spain, Italy, and Greece not only was there no appreciable pollen of oaks and other deciduous species, there was no appreciable amount of forest tree pollen of any sort. The full-glacial vegetation along the northern Mediterranean evidently was a cold dry steppe dominated by *Artemisia* (see Bonatti, *Nature*, 209: 984, 1966). The full-glacial refuge of deciduous forest remains undiscovered. If such a paleogeographic gaff can be made in Europe, what about the tropics?

In the absence of a sufficient fossil record, as in Africa, scientists in need of a Pleistocene chronology commonly end up betting on lucky seven, the classic countdown of four glacial and three interglacial episodes. This dicy approach to the Pleistocene seems inversely correlated with distance from the ice margin. Those working within or near the glaciated regions are considerably less confident that seven is the winning number. If we grant Moreau's apparent success in predicting that the history of montane forest birds must be related to a Pleistocene depression of montane forest in Africa, it is still worth recalling that the best zoogeographic evidence can not tell us either how often or when a drop in life zones may have occurred.

For a final example of the hazards of prehistoric guesswork, even within recent millenia, what European ornithologist would have predicted on the basis of modern distributions that the pelican that once apparently inhabited Britain was the Dalmatian species, *Pelecanus crispus*, rather than the more northerly ranging White Pelican, *P. onocrotalus*? Brilliant detective work by Forbes, Joysey, and West showed that the diagnostic tarsometatarsus was of the Bronze Age, or early Subboreal in the pollen chronology (*Science in archaeology*. New York, Basic Books, Inc., 1963; pp. 197–203). Whether or not Neolithic farmers drove the bird out of the British Isles, it was gone by Roman times. What dare one say about the fossil record of Africa, at least until it approaches some similar level of stratigraphic and paleoecological sophistication?

As Moreau comments in passing, matters are worse. Where are the African ornithologists, much less ecologists of any sort, who might conceivably take an interest in the fossil record or in compiling such deficient basic data as a breeding bird census? There are about as many nonwhite resident ornithologists in Africa as Negro ornithologists in America where the science is, de facto, segregated. As much as anywhere the politics of ecology cast a long shadow in Africa. If the analysis Moreau attempts regarding African birds is of broad biological interest, and I believe that it is, then the lack of indigenous African scientists ready to pursue the subject must be viewed with alarm. One hopes, and expects, that the deficiency will gradually disappear as the current generation of African students and intellectuals fills top priority positions calling for their skills in teaching, government, medicine, engineering, and resource development.

But back to the matter of the impoverished avifauna. If not a legacy of the Pleistocene or an inherent deficiency in the African ecosystem, then what? In company with many zoogeographers Moreau pays scant attention to the effect of prehistoric man. South of the Sahara there is no impressive record of plant domestication, no long episode of intensive cultivation, and in some places no Neolithic at all. One might discount any ecologically significant anthropogenic changes. However, Africa harbors a uniquely rich material culture of the Middle and Early Stone Age, preceded by the Villafranchian Australopithecines and, ultimately, by their Miocene protypes. While the most obvious habitat simplifier available to pre-agricultural people, fire, is unknown in African archaeological sites until roughly 50,000 years ago, it is likely that ancient man started or spread fires long before. The African climax was gradually reduced with ecological side effects that could well include the constriction of niches for passerines, the group Moreau finds most illuminating ecologically. By the same token the African avifauna must be rigorously selected for camp followers and disturbance species, accounting for the present global success of certain Ploceidae and Sturnidae and the peculiar behavior of the Indicatoridae.

Turning to Madagascar Moreau observes another kind of passerine deficiency. There the group comprises only 34 per cent as opposed to 44–51 per cent of the total African avifauna. Again the possibility of prehistoric habitat upset seems a promising explanation, as 80 per cent of the 240,000 square mile island is secondary vegetation, notably fire-resistant grassland in place of the natural dry forest. From 8,000 feet in a DC-3 between Tananarive and Morondava I was struck by the ungrazed, uncultivated, strangely uninhabited appearance of a large part of the quite obviously altered and eroded landscape. Instead of relatively recently, did the main episode of forest destruction occur early and rapidly, just after the initial invasion of people (from southeast Asia, not from Africa) around 1,000 years ago? To date the only known extinct birds in Madagascar are nonpasserines including the giant ratites *Aepyornis* and *Mullerornis* which indeed disappeared only after man arrived.

But I must confess I can't really believe that the deficient passerines will be found, even, or especially, in Madagascar where subfossil hunting is so rewarding. While various evolutionists predict excessively high natural extinction rates, especially on small oceanic islands close to the continents, the rub is that no late Pleistocene extinction not timed to the arrival of prehistoric or modern man has been documented. Having now succumbed to the pitfall preached against I will withdraw behind the thought that Africa and its islands may yet prove

saturated, at least in those groups of organisms not decimated by ancient or modern man.

Meanwhile the naturalist traveling south of the Sahara, whether particularly interested in birds or not, will (if he cares about the search for explanations) include Moreau's book in his 22 kilo baggage allowance. Hopefully Moreau's readers will also include growing numbers of upper division biology students in the very promising new African universities. To emulate Moreau will be far more difficult, requiring the development of a great deal of ornithological experience and ecological insight, both to be gained only through many years spent in the field in Africa.