

REVIEWS

THE BIOGEOGRAPHY OF AFRICAN NON-PASSERINE BIRDS: SOME COMPARISONS WITH AUSTRALIA

An Atlas of speciation in African Non-Passerine Birds.

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The publication of this volume, the successor to the 1970 study of passerine birds, is a milestone in the analysis of the biogeography and evolution of continental avifaunas. Like the previous work, this is built on distribution maps based on individual records, superimposed upon a vegetation map of the African continent. The species are combined into superspecies, and groups. The Atlas thus focusses on distribution patterns and evolution at the level of the species and just above. Where superspecies and groups of species extend beyond Africa this is shown on inset maps. The work can thus also be used for assessing relationships beyond the continent.

The distributional data are based on museum specimens alone in some cases (as with swifts and honeyguides), but with most species on specimens plus sight records, where the latter are reliable. Breeding and non-breeding ranges are distinguished. Without this, migratory species would show a more or less meaningless scatter of dots over the whole continent. Precise discrimination between breeding and non-breeding ranges is also critical in Australia, and there will long be the need for work in this area.

The African Non-passerine Atlas invites comparisons with other continents, and especially Australia, which lies in the same general latitudes and has equivalent avian habitats. How similar are the two avifaunas; how does the level of endemism compare on the two continents; and finally, how do distribution patterns compare?

The African Non-Passeriform Avifauna and its Relationships

The Atlas distribution maps reveal that Africa has forty-eight non-passeriform families (Table I), of which eight are endemic: Struthionidae (ostriches), Balaenicipitidae (Whale-headed Stork), Scopidae (Hammerkop), Sagittariidae (Secretarybird), Numididae (Guinea-fowl), Musophagidae (turacos), Coliidae (colies), and Phoeniculidae (wood-hoopoes). Ostriches occurred in historic times in Arabia and beyond, and hence are not truly endemic. Only two of eighteen species of honeyguides (Indicatoridae) occur outside Africa, and this group is presumably African in origin.

There are 375 groups of species and superspecies. Of these 270, or 70% are endemic. Relationships of the remainder are as follows: shared with Eurasia alone, 8.9%; Palaearctic alone, 2.4%; Oriental region, 3.8%; Eurasia and the Americas, 3.1%; South America only, 1.0%; Eurasia and Australia, 5.8%; Eurasia, Australia, and the Americas, 5.0%. Thirty per cent of superspecies and groups of species extend to the north. Whether most of the groups originated on the Eurasian landmass and spread southwards to Africa, or the reverse, cannot be stated on present evidence. The extent of interchange of species in late geological time, despite the presence of the Saharan arid barrier, has been great.

In which groups has this interchange with the north been greatest? It has been pronounced in water-birds. All three African grebes belong to widespread superspecies, as does the anhinga, one of the two cormorants, two-thirds of the herons, half the ibises, and one-third of the anatids and rails. Amongst the land-birds, by contrast, twenty-six of the fifty-seven hawks and falcons belong to widespread superspecies; but only one-third of the pigeons, swifts, and kingfishers, a quarter of the cuckoos and

phasianids, and one-fifth of the bee-eaters do so. Only one of the fourteen groups of caprimulgids occurs beyond Africa.

There is hence obviously a general correlation between taxonomic identity, way of life, and level of endemism. Water-birds frequently move widely in response to fluctuating water-supplies, and hawks, being predators and scavengers, tend to be wide-ranging. There has been much interchange between Africa and the north in these groups, and endemism is low. A high level of endemism is shown by groups that tend to be localized, those that are restricted to the sub-Saharan African woodlands and forests, and those to whom the Sahara is a barrier.

African-Australian relationships and some comparisons

Forty-two species groups are shared between Africa and Australia. Since any direct southern connexion between these two continents ceased in the Early Cretaceous (ahead of the evolution of modern birds) it can be assumed that interchange has been by way of Asia, rather than directly across the Indian Ocean. Since the northward drifting Australia achieved its present proximity to Asia only in the Miocene, twenty-five million years ago, interchange must have occurred since that time. Groups shared between Africa and Australia include grebes, anhingas, cormorants, herons, storks, ibises, ducks, rails, accipiters and falcons, phasianids, bustards, dotterels, stilts and avocets, owls, kingfishers and bee-eaters.

Whilst Australia shares with Asia eight of the twenty-four groups of accipiters and falcons, seven of the thirteen groups of herons, and many genera of herons, ducks and rallids, these cases are the exceptions among the Australian avifauna. Endemism is clearly higher at the generic level than in Africa. All the Australian owls, apart from the Tytonids, most of the genera of kingfishers and pigeons and the the genera of parrots (except for a couple that extend to Indonesia), are endemic. Australia is, in turn, rich in endemic families, although most of these are passerines. Even in groups that are shared with Africa, the Indonesian region has obviously been a filter: thus only one species of bustard, bee-eater, hornbill, lark, pipit (etc.), all groups that are highly diversified in Africa, penetrate through to Australia. Many Asian groups, do not, of course, get east of Wallace's Line.

In summary, in both Australia and Africa the aquatic niches are dominated by cosmopolitan or wide-ranging groups. A higher proportion of African land birds belong to widespread groups of superspecies than is true in Australia. This reflects the greater isolation of Australia, today and in the past.

Distribution Patterns within Africa and Australia

Whereas the distribution of species of passerines in both Africa and Australia is generally closely tied to specific vegetation types, this is often less true with the non-passerines, many of which are generalized in habitat needs and/or are wide-ranging. Species of water-birds, in particular, are widely distributed, commonly occurring throughout sub-Saharan Africa. Most avoid the Congo rainforest block but a couple (e.g. the Tiger-heron, *Tigriornis*; the ibis, *Bostrychia rara*; and the duck, *Pteronetta hartlaubii*) are confined to it. A small minority are confined to the far south (the ducks *Tadorna cana* and *Anas smithii*), and one or two to the far north (the goose *Cyanochen cyanoptera* and the rail *Rougetius rougetii*). The bald ibises (*Geronticus*), exceptionally, are represented by disjunct southern and north species.

Amongst the diurnal birds of prey most vultures range throughout the savannah and woodland areas, although the grif-

fin vultures (*Gyps*) are represented by separate species in the north and south. Most eagles are equally widespread. The serpent Eagle *Dryotriocheis spectabilis* is confined to the Congo rainforests. Only a few of the smaller accipiters have restricted ranges. There are several Congo species but again, most avoid the rainforests. The small Pygmy Falcon *Polihierax semitorquatus* has a discontinuous distribution, with populations in the dry savannahs of the southeast and northeast separated by the extensive central woodland belt. Most owls are very widespread but there is a number of rainforest species (*Otus icterorhynchus*, *Jubula lettii*). One genus has allopatric species in different habitats (*Glaucidium capense* and *G. perlatum* groups).

Contrasting with most non-passerines, the phasianids and bustards are relatively rich in allopatric forms. The genus *Francolinus* is particularly so as the taxonomic studies of Pat Hall have shown. The *F. afer* and *F. bicalcaratus* groups are represented by four and nine species, respectively. In the latter, species are confined to the west, north, central east, southeast, and far south of the continent. Ecological separation on the basis of habitat is marked. Some species are linked to the Sahel and Guinea savannas in the north, others to the *Acacia* of the south and Cape fynbos in the far south. Amongst the bustards the *Neotis denhami* group has four allopatric species.

How do distribution patterns in equivalent taxonomic and ecological groups compare in Africa and Australia? There are twelve groups of pigeons in Africa. Of these seven are very wide-ranging e.g. *Columba guinea*, *Streptopelia reichenowi*, *S. semitorquata*), and about six are represented by pairs, or series, of allopatric species. The general picture is not dissimilar to that in the pigeons of the Australian mainland. Predominantly inland genera like *Phaps* and *Geopelia* are composed of wide-ranging species. There are some good examples of allopatric species, e.g. *Petrophassa scripta* and *P. smithii*. In both continents groups are confined to the rainforests. Australia, however, has monotypic genera (*Leucosarcia*, *Lopholaimus*) here. Thereafter parallels cease. Several Australian pigeons belong to groups with wide ranges in Indonesia (*Macropygia*, *Chalcophaps*). A few Australian rainforest species belong to New Guinea groups (*Ptilinopus superbus* and *P. regina*). The most striking difference in distribution patterns in the Ethiopian and Australian regions, however, is that the former contains, in essence, a single fauna, while the Australian one contains twin sub-faunas, in Australia and New Guinea. The latter, tropical and montane, has an extremely rich and diversified tropical pigeon fauna with no parallel in Africa. Africa, of course has a Palaearctic segment in addition to the sub-Saharan one but this is relatively poor in species.

A situation comparable to that for the pigeons occurs in the kingfishers and cuckoos. Of the thirteen groups of kingfishers occurring in Africa, six are represented by wide-ranging single species, four have pairs of allopatric species, and the remainder are single species with restricted ranges. Australia has nine groups of kingfishers, which fall into two distributional categories: widely ranging woodland and dry-country species (in *Dacelo*, *Halcyon*); and peripherally distributed water-kingfishers. Two *Halcyon* species (*H. sancta* and *H. chloris*) are peripheral members of Indonesian-Pacific groups, and the other (*H. pyrrhopygia*) is inland-dwelling and endemic. New Guinea species (e.g. *H. torotoro*) enter marginally in the north. But New Guinea has a rich and diversified kingfisher fauna, with various endemic

genera, lacking from Australia.

Of the nineteen groups of cuckoos in Africa, thirteen are represented by widespread single species. Allopatric pairs of species occur in two. The Australian cuckoo fauna is made up of members of Asian-Pacific groups, others that are of New Guinea origin, and some endemic species. Again New Guinea has distinctive tropical fauna duplicated, to a minor degree only, by a Congo rainforest one.

Ten groups of bee-eaters (Meropidae) occur in Africa. Three are represented by a single species (two of them with restricted ranges), the remainder by allopatric pairs of species (in the north and south, or west and east) and in a couple of cases by pairs of species that co-occur over wide ranges. Australia, by contrast, has a single bee-eater and it belongs to an African super-species.

Nightjars (Caprimulgidae) comprise thirteen groups in Africa. Of these five are species with restricted ranges, three are widespread single species, and the remainder are made up of pairs of species, some of which overlap. Australia has four groups of nightjars, all with extensive ranges. A couple of species are limited to New Guinea.

A major difference in the avifaunas of the two continents is in the parrots. The Australian parrot fauna is rich and diversified, to a unique extent, as is the New Guinea one. Some twenty-four genera, fifty-six species (forty superspecies and groups) occur in Australia, and genera and species show high levels of attachment to habitat or specialization. Allopatry is marked in many genera. Africa, by contrast, has only about half a dozen groups of parrots, most inhabiting woodland and savannah. The great diversity of structural types, monotypic genera, and distributional patterns shown by Australian parrots is largely lacking. The African hornbills and barbets that, to a degree, occupy parrot niches do, however, show specializations in habitat similar to those of the Australian parrots.

In summary, there are some broad parallels between the non-passerine birds of Africa and Australia, both in terms of the avifaunas as a whole, individual groups, and distribution patterns. There are, however, basic differences. Some of these are directly attributable to differences in the two continents as living areas. The larger African avifauna goes with a continent having four times the land surface area of Australia and greater contact with Eurasia. In both continents the climatic and vegetation belts are zonally distributed from the coast inland, and the belts are the basis of major faunal divisions. Africa straddles the equator so there is some duplication of zones in the north and south. This is notable in the case of desert habitat. In effect, Africa has three deserts, the huge Sahara and smaller Somali arid zone in the north, and the Kalahari-Namib in the south. The central core of Africa is rainforest (Congo rainforest), that of Australia desert. Since Australia thus has only one desert there has been limited opportunity for geographic isolation and speciation. Australia has few species of ground-dwelling arid zone birds. Compare this with the remarkable diversity of savanna and desert birds in Africa: sand-grouse, coursers, francolins, larks, pipits, and others. This has been built up both internally and by interchange with the adjacent deserts of Eurasia.

J.A. Keast

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