The Natural History of Endemic Families and Sub-families of Birds of Madagascar

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~Translated from French by Teresa Pegan~

Figure legends are not translated and citations and figure references are not included; see text for figures, pictures, and references.

Note: This is a first-draft translation and my French skills are limited. I used Google translate for the many words I didn't know, and in those cases I can't be sure that I chose the most accurate English words to represent what the French was trying to say. For the most part, I translated everything as literally as possible in such a way that things still make sense in English - so I moved words around in sentences to make them make sense, but I left much of the phrasing and punctuation as it is originally. This is partly because it was faster and easier that way, but it was also partly because now someone can look at the original book and have a good idea of which French words correspond to which English words, which should prove useful to anyone who wants to practice reading French before going to Madagascar. It also means that many of the sentences sound clunky and awkward in English. There are one or two sentences in here that I couldn't make any sense of, even with the help of internet translation. If you would like to see the original book it will be available in Wink's office at some point and if you would like to ask me about the way I translated particular phrases or sections feel free to email me.

Part 1: Introduction to Birds

What Is a Bird?

Birds are animals that lay eggs, have feathers, and can practically all fly, except for some of the largest species. Although these three aspects together define birds, there exist mammals that lay eggs (the platypus, *Ornithorhynchus anatinus,* of Australia and Tasmania), and that can fly (the bats, order Chiroptera), and the fact of having feathers is in effect unique to birds. Feathers are actually modified scales of reptiles, but that aspect is addressed in more detail in the section titled "The history of the first fossils of birds as feathered dinosaurs."

Birds vary in size, ranging from very small animals, the size of a large bee, to the ostrich, massive and incapable of flying. The latter is the largest bird in the world, attaining a height of more than 2.7 meters and weighing more than 150 kilograms. The eggs laid by the ostrich can weigh up to 1.4 kilograms, and they are equivalent in volume to about 24 chicken eggs, and are sufficiently thick to be used like "jerrycans" to transport liquid by African populations. Among the some 10,000 species of birds in the world, there exist considerable differences in size and natural history: their way of living, feeding themselves, etc.

For most of us, when someone asks, "what is a bird?" it is easy to respond by talking about domestic chickens, ducks, geese, and turkeys, which make up part of our diet, and which are sometimes delicious meals on special occasions. In any case, these domestic birds are not

naturally present in Madagascar, but have been introduced by man from regions of the world over the course of the past 1200 years. For example, turkeys originate in the New World, specifically in central American and the south of North America, and chickens for their part original, or "native," in southeast Asia. Therefore, they form part of the exotic or allogeneic birds of Madagascar.

Other people living in Madagascar could respond to that question by mentioning the *fody mena*, a little bird common in urban and rural areas of Madagascar. This bird, whose scientific name is *Foudia madagascariensis,* is in effect an endemic species to Madagascar, but the genus *Foudia* is also found across the different islands of the western Indian Ocean, so it is therefore not endemic to Madagascar at the level of genus. Interestingly, perhaps due to the bright red plumage of the male adult *fody mena* or to their pretty song, this species has been introduced to different islands in the Indian Ocean, like Maurice, Réunion, and the Seychelles. It is therefore a species endemic to Madagascar that has been introduced to other regions of the world.

The forested areas of Madagascar hold marvelous secrets of nature and the birds are no exception. Whether in the dry (deciduous) forests of the west or the humid (evergreen) forests of the east, or the spiny forests of the southwest, there exist many endemic species that only live in forested habitat and cannot be found in habitats modified by man, such as open areas, agricultural areas, and rice fields. It is important to keep in mind that vast areas of savannah, including the areas around Antananarivo, were covered by forests until several decades ago, and were occupied by numerous types of organisms which can't be found there today. These habitat modifications have had a considerable impact on the endemic avifauna. Among the particular and unique groups of birds that are dependent on forests, one can find notably the mesites (family Mesitornithidae, endemic), the Couas, (sub-family Couinae, endemic), the ground-rollers (family Brachypteraciidae, endemic), the cuckoo-roller (family Leptosomidae, endemic to Madagascar and the Comores,) the asities (sub-family Philepittinae, endemic), the Malagasy warblers (family Bernieridae, endemic), and the vangas (family Vangidae, endemic). These different groups are well-known by people who study birds from a scientific perspective (ornithologists) or who spend time watching birds in their natural habitat (birdwatchers). All the same, for the public, the remarkable jewels of the forests of Madagascar remain largely unknown, which is the purpose of this book, especially Part 2. These different types of birds should be considered as part of the island and Malgache population (natural heritage); and given their unique character, it proves important to protect them for future generations and make them known to the world.

All the unique birds of Madagascar fly, although the weakest, like the mesites, walk on their two legs in a vertical position (bipedal). The large majority of these birds are active during the day (diurnal), although some species like the ground-rollers are active at dawn and dusk (crepuscular), when their calls can be heard in the forest. Not one is uniquely active during the night (nocturnal). Some groups among the birds, in particular the couas and the ground-rollers, are large in size and generally move on the ground (terrestrial), although some may be found in the vegetation far from the ground (arboreal). Others, in particular the Malagasy warblers, and the vangas, which are generally small in size, are largely arboreal and can be found in different levels of forest, the undergrowth, and in the canopy.

In a general way, the different species that compose the seven groups have a tendency to be found either in spiny forests, evergreen forests, or deciduous forests. For example, among the ground-rollers, there is one species limited to the dry deciduous forests of the extreme southwest (*Uratelornis chimaera)* and four in the eastern part of the island (*Atelornis pittoides, A. crossleyi, Geobiastes squaminger* and *Brachypteracias leptosomus*). In other cases, particularly among the vangas, some species can be found in different types of forests and are not limited to evergreen or deciduous forests. A good example is the predator *Vanga curvirostris*, which eats a large variety of invertebrates and vertebrates and which is present in all types of native forest in Madagascar. This species, together with the others, clearly has adaptations to a large variety of conditions of life.

These groups of birds have different feeding habits. For the most part, couas and ground-rollers feed on invertebrates (insectivorous), although they are also known to consume vertebrates (carnivorous) and fruits (frugivorous). The asities in the genus *Philepitta* live mostly in the undergrowth and are frugivorous, while the members of the genus *Neodrepanis* can be found between the medium and higher sections of the forest and consume the nectar of flowers (nectarivorous), and the two genera are also occasionally insectivorous. There are many species of Malagasy warblers and vangas, and most are largely insectivorous, but these species have considerably different beak shapes and ways of searching for food. Some vangas, like *Euryceros prevostii* with its large hooked beak, are known to attack large sized insects and and other invertebrates. These habits have been shaped by evolution and that important aspect associated with the seven groups of endemic Malgache birds is called an "adaptive radiation" (see page 35).

Particularly during the breeding season, groups of birds composed of numerous different species can be seen moving and searching for food together in the spiny, deciduous, and evergreen forests. When these animals pass, the agitation is considerable because they teem with activity; some birds feeding actively on the ground, overturning leaves in the litter, others collecting insects on leaves and branches, others probing cracks in ferns, orchids and other plants which grow on trees at medium and tall heights (epiphytes), and some species which probe the bark of trees. On occasion, even diurnal lemurs join these gatherings, which can last less than a minute in front of an immobile observer. These mixed-species flocks clearly bring an advantage to the birds which participate. Many hypotheses have been put forward to explain the reason for which the birds form these groups. The first is that the efficiency of capture is increased, which is to say that the birds which make the troops, compared to solitary birds, have a superior rate of capture. The idea is that the movements of all of the birds stirs the terrain and dislodges potential prey, notably the hiding invertebrates, and make them easier to see and capture. Another idea which has been proposed to explain the collective effort is that the more the number of birds increases, the more chance they have of detecting predators that hunt birds (raptors, Carnivora, snakes) and once detected, sound the alarm bell. The birds evolve in these groups are also less likely to be eaten by predators, compared to solitary individuals.

The groups of high-taxonomic-level endemic birds play numerous important roles in the maintenance of ecosystems and of different ecological functions. A good example from the asities can illustrate the case. The members of the sub-family Philepittinae, particularly the genus *Philepitta*, feed profusely on fruits of small trees in the undergrowth. The seeds contained

in the fruits pass through their digestive systems and are then rejected in their stools far from the mother tree: they act therefore as agents of dispersal, which contributes to the maintenance of the structure of the undergrowth. Another member of the subfamily Philepittinae, the tiny nectarivorous *Neodrepanis*, passes by flower after flower on the search for nectar, with the pollen of different flowers collected on its beak and head feathers. Consequently, it transfers pollen between the different plants, increasing the fertilization of flowers and therefore the fruits and seeds that they produce. This is a considerable benefit for the vitality of the forest and helps the plants reproduce.

The other species of the unique Malgache bird groups, like certain members of the Vangidae or Bernieridae families, feed on a variety of vertebrates and invertebrates, and help balance the delicate relationship between predators and prey in the forest ecosystem. Thanks to that balance, certain groups of animals don't become dominant, which is an aspect of the function of the forest ecosystem. Although the concept can seem abstract, this ecosystem can furnish numerous services for human beings, and supplies continuous water to agricultural areas and brings oxygen to the atmosphere, both primarily important for the survival of man. To be more precise, when an forest ecosystem doesn't function anymore, for example because of deforestation, the capacity of the soil to retain water and lose it slowly is considerably reduced. Moreover, in plains environments, where people cultivate rice, the rivers become more seasonal with floods after strong rains and a weak flow of water during the dry season. Furthermore, deforestation also favors the erosion of soil and sedimentation in the rivers and rice fields. In all evidence, the phenomenon has a major impact on the production of rice fields and consequently on the quantity of food they produce, and on the quantity and quality of water.

The Geological History of Madagascar

One principal reason why the biota of Madagascar is so unique, with respect to any other tropical island in the world, is its geological history. Its elevated level of endemism, that is to say the unique organisms of the island which can be found nowhere else on our planet, is related to the isolation of Madagascar from other continents since deep back in time. This section is consequently furnished to explain the geological history of Madagascar, relative to other continents, across a period of considerable geological time.

Some rock formations in Madagascar are among the most ancient in the world, dating to more than 3200 million years, making it one of the most ancient continental masses in existence. However, the island was not always isolated by the Mozambique Canal. Perhaps the best place to begin is with the Supercontinent Gondwana, which included South America, Africa, Madagascar, Antarctica, India, and Australia. Gondwana stayed a stable, unique continent until around 150 million years ago, when the movements of the earth (tectonics) began.

To put this into perspective, 150 million years lies in the middle part of the Mesozoic, more precisely during the Jurassic period, which was the era of the dinosaurs. An essential point is that that period took place before many modern groups of plants and animals that live in Madagascar or the rest of the world today had evolved. Consequently, they cannot have "floated" along with the separation of Madagascar from the rest of Gondwana, but they found their way toward the island later in geological time. Among the birds, capable of long flights, it

is easier to imagine how the colonization could have occurred, compared to the lemurs, tenrecs, and other non-flying Malgache animals which had to traverse large distances in the water by swimming or otherwise.

When the Island of Madagascar detached from Gondwana, India was still attached and that mass is often designated as Indo-Madagascar. The latter obtained its approximate current about 130-120 million years ago, and 80 million years ago, India separated from Madagascar and began moving toward the north until it collided with the mass that is now modern Aisa.

As cited in the following section, the first proof of the existence of dinosaurs with birdlike features is from around 150 million years ago, roughly in the period of the breakup of Gondwana. The first fossils known of the lineage of existing modern birds are from the end of the Cretaceous, at around 70 million years ago. What is crucial about this date is that Madagascar was already completely isolated from Gondwana and all other land masses when modern birds appeared in the fossil record. The sole medium for birds to attain successful colonization of Madagascar is therefore flying over the vast expanses of water that separated at that time what we now call Africa and Asia. We must suppose that this event was rare and could not have taken place except in ideal circumstances (see page 78).

The History of the First Fossils of Birds as Feathered Dinosaurs

Over the course of the past 20 years, the people who study fossils (paleontologists) have shown that the birds living in our time are in fact remaining members of the lineage of dinosaurs, which represent the first group of reptiles. The studies are strongly based on the anatomic structure of fossils. Feathers, which are modified reptilian scales, are known from the dinosaurs, and this before the evolution of birds we know today. Therefore, these first remains of fossilized animals with the structure and form of feathers play an important role in the understanding of the way that these structures evolved and the transition from dinosaurs to birds.

Until recently, the oldest and most famous fossil of a wing and feathers is that of *Archaeopteryx*, discovered in Germany in 1861, of an animal which lived during the era of the Mesozoic and more specifically during the period at the end of the Jurassic, around 150 million years ago. *Archaeopteryx* is more considered an animal of transition, with characteristics intermediate between those of reptiles and those of modern birds. As we might imagine, given their delicate nature of feathers and the processes of fossilization, the preservation of these structures necessitates special conditions and very fine sediments. [The study of] Some fossils recently discovered in China[,] date[ing] to around the same age as *Archaeopteryx*. It must equally highlight the period of evolutionary transition between dinosaurs and birds, and the anatomical limits between the two groups that are not well defined. The most important is that the first animals with feathers were not birds, but dinosaurs. These dinosaurs were not capable of flying and the initial reason for the evolution of feathers was probably had to do with isolation, rather than locomotion. During the following periods, the modification of feathers took place, like their elongation and their adaptation for gliding, and thereafter, they evolved toward the complex structures permitting flight and utilization for different ornamentation.

The Ancient Fossils of Birds in Madagascar

Numerous researchers have worked on different types of fossils present in Madagascar, in particular in the deposits near Berivotra, about two hours by road to the east of Mahajanga, and the formations of Isalo in the neighborhood of Ranohira in the central-south zone. These deposits have revealed numerous extraordinary creatures like the predator dinosaur *Majungasaurus* (which is translated as "lizard of Mahajunga"), which lived 60-75.5 million years ago, at the end of the Cretaceous, as well as many bizarre crocodiles, one of which was vegetarian. Also, in the deposits situated near the village of Berivotra, which had been enormously prospected by Dr. David Krause and his colleagues during the conjoined expedition of the University of Antananarivo and the "State University of New York at Stonybrook," many fossils of birds dating to the end of the Cretaceous were found, and were studied by Dr. Cathy Forster and her associates. Although the first known fossils of birds are not extensive, given that the lightweight, hollow bones of birds rarely survive in fossil form, these extraordinary recent finds in Madagascar have given a glimpse of the evolution of the first birds.

One of the first fossils of a Malagasy bird was named *Vorona berivotrensis* (which means "bird" of "Berivotra"). This animal is supposed to have lived 84-70 million years ago and although the remaining fossils are fragmented, they show a mix of characteristics of primitive and modern birds. Another of these ancient creatures coming from the deposits of Berivotra which seem to be a line between dinosaurs and birds, is *Rahonavis ostromi*. The origin of the name of this bird comes from the Malgache meanings of *rahona* "cloudy" or "obscure" and the Latin *avis* or "bird", referencing its uncertain ancestral affinities (phylogenetics). The species name is in honor of the late Dr. John Ostrom, who did a lot of work on ancient birds. Based on the remaining fossils of *R. ostromi*, it was probably capable of flight, but it would have been more clumsy in the air than most modern birds. Another extraordinary aspect of the remains of *R. ostromi* is that some traces of structural protein (keratin) has been found in the fossils and this makes it possible to one day reconstruct the color of its feathers.

Even though a certain number of fossil deposits that have been found in Madagascar contain the bones of ancient birds, a gap of nearly 80 million years exists in the known fossils between the recent Cretaceous period and the recent Pleistocene, a gap all the more deplorable as it is a fundamental epoch in the evolution of modern bird groups. In the following section, we turn to the recently extinct birds that lived on Madagascar.

Subfossils of Birds of Madagascar

Madagascar possesses relatively rich deposits of subfossils from the recent Pleistocene and the Holocene, particularly in the driest parts of the island, where preservation is the best. All the same, these do not replace the rock (fossils), like the ones described in the previous section, but nothing remains except bones, without any sort of mineralization. The oldest bird subfossil in Madagascar is probably not more than 20,000 years old and is therefore very recent geologically, literally a few seconds old compared to the scale of the geological time of the breakup of Gondwana, for example, or the appearance of the first true birds in the fossil record. Although the specimens available don't really allow a clear reconstruction of the moment when the groups of modern birds first colonized the island, they offer some interesting glimpses on the

geologically recent extinctions, the role of changing natural climates, and the modern avian communities of the island.

More than 70 species of birds have been identified among the subfossilized remains. Practically all of the specimens are probably from the Holocene but after being radiocarbon dated, some lived at the end of the Pleistocene. Rather than pass through the numerous details of all the groups recovered in the archaeological and paleontological sites, we present a brief summary of single groups and species of extinct birds.

Aepyornithidae

In 1851, the scientific community was shocked by the communication of Geoffroy Saint Hillaire announcing to the Paris Academy of Science the discovery of an extinct giant bird, called *Aepyornis maximus*. This discovery had its start with Mr. Abadie, captain of the marine market, who had obtained three giant eggs along the coast of southwest Madagascar. It is estimated that *A. maximus* could reach a height of 3-4 meters and a weight of about 400 kilograms. Its eggs had dimensions on the order of 32 cm x 24cm for a volume corresponding to 150-170 chicken eggs!

Since the discovery presented by Geoffroy Saint Hilaire, many species names have been proposed for the rest of the eggs and skeletons of *Aepyornis*, including a second genus, *Mullerornis*. The *Aepyornis* was largely distributed all along the island from the extreme north to the extreme south. The majority of the rest of the skeletons come from sites in the west and the southwest together with the central highlands, and the rest were equally to be found in the cave of Andrahomana near Ranopiso in the southwest.

Etienne de Flacourt (1607-1660), named commander of Madagascar by the king of France in 1648, was based near Fort Dauphin (= Tolagnaro) and wrote important columns on the culture and environment of that region. In his work *History of the Large Island Madagascar*, published in 1658, it made reference, employing the present, to a "*vouron patra*" as a forest species and which was very certainly an *Aepyornis*. In the Antandroy of the regions of Ambovombe and Marovatio together with the populations of other regions on the island, there still exist numerous oral histories about giant birds which are without a doubt the Aepyornithidae. It has been proposed that the eggs of Aepyornithidae found at archaeological excavations correspond with the remains of human meals and that they came from elsewhere. It has also been reported that a bone of an Aepyornithid had been fashioned into a hand tool. From radiocarbon dating the rest of the egg shells of Aepyornithidae, the most recent date we know we can say that these birds still lived in Madagascar is about 1000 years ago. Finally, based on the remarkable densities of *Aepyornis* shell fragments found near Cape Sainte Marie, *A. maximus* probably nested in a sort of colony, with numerous breeding birds crammed in a relatively restricted area.

Phalacrocoracidae

The bones of a large cormorant in the genus *Phalacrocorax* were found in the subfossil sites of Lamboharana and Antsirabe and is a significantly larger match with the sole species actually encountered on the island (*P. africanus*). These bones came from an endemic species which is not yet described but is extinct.

Anseriformes

Two forms of extinct water birds are known from the subfossil deposits. One was a large species, *Centrornis majori*, and another was medium sized, *Alopochen sirabensis*. The first of those species was described from the subfossils and was a hunter with very long legs, long wings and a well developed metacarpal bone spur. One of the most commonly found in the subfossil deposits of Madagascar, an in particular on the central highlands, is *A. sirabensis* which is known from a large variety of sites.

Accipitridae

Three species of raptor subfossils known from Madagascar have disappeared in recent geological times. There are two distinct forms of *Aquila* and a large eagle *Stephanoaetus mahery*. The latter species has very large talons and would have been a formidable predator, certainly including a variety of species of large lemurs now extinct. To the extent the genus *Aquila* is represented by many species, it is not yet clear if the subfossil remains found in Madagascar belong to extinct endemic forms or to forms actually distributed all over the world. The three species of raptors have distributions spread all throughout Madagascar.

Various authors have imagined that *Aepyornis* inspired the historical legend of the bird *roc* or *rokh* in the narrative of *One Thousand and One Nights* and which was referenced by Marco Polo. In the manuscripts of Marco Polo, the Roc was not represented as a large bird without wings, but more as a powerful bird of prey capable of carrying an elephant in its enormous claws. If the inspiration of the Roc is not pure fantasy but based on the observations of the Arab merchants that lived on Madagascar, *S. mahery* could then have played a role in the origin of that legend.

Mesitornithidae

The recent excavations in the cave of Anjohibe have allowed the finding of subfossils of the endemic Malgache family Mesitornithidae, including an undescribed species in the genus *Monias*.

Rallidae

In 1897, *Tribonyx roberti* was described from some subfossils unearthed near Antsirabe and subsequently transferred to the endemic and monotypic genus *Hovacrex*. It was a large species of rail, known from many sites in the central highlands and part of the south of the island.

Charadriidae

Some bones of a lapwing were identified in the deposits of Lamboharana and Ampoza and used in the description of *Vanellus madagascariensis*. The lapwing subfamily, Vanellinae, is no longer represented in the current avifauna of Madagascar, but it was very widespread in different parts of Africa, always in strongly modified environments.

Cuculidae

The remains of two large, extinct couas, *Coua primavea* and *C. berthae* were recovered in the subfossil sites in the west and southwest of Madagascar. The first species was described on the basis of a tarso-metatarsus found near Belo on the Sea and subsequently extracted from the deposits of Tsiandroina, Manombo (Toliara), and Anjohibe. The second subfossil species is known from Ampasambazimba and Anjohibe. The two species are larger than their current congeners.

Brachypteraciidae

One subfossil specimen of this endemic Malgache family was unearthed in Ampoza and described as the extinct species *Brachypteracias lagrandi*.

What is an Adaptive Radiation?

As explained in the preceding section, the birds like those we know today evolved notably after the breakup of Gondwana. Therefore, in this time scale, the only reasonable explanation for their presence in Madagascar is that since the separation of the island from other terrestrial masses, they were capable of flying across the canal of Mozambique and the Indian Ocean and successfully colonizing Madagascar. But a successful colonization does not simply consist of one individual or of several arriving tired on the banks of Madagascar where they could succumb to the long voyage, but rather finding regular food and adapting to the local ecological and climatological conditions, and overall being capable of mating successfully, protecting eggs, and raising. One can imagine that all throughout geological time, a large number of vertebrates arrived on the coast of the island, but were unable to reach the critical steps leading to a successful colonization.

Once an organism was capable of successfully colonizing a continental mass and enlarging their distribution over the course of centuries and millennia, in would come into contact different ecological conditions, types of food, and other species that could eat similar resources (competition). Individuals with certain morphological and behavioral characteristics that allow them to exploit different resources, such as longer beaks, shorter tarsi, a different activity period, etc, have a greater chance at success, leaving a greater number of offspring in the next generations (natural selection).

Today, on an island like Madagascar with many types of forests and climate regimes, many changes can take place allowing species to fill different ecological niches. These differences are further amplified by the effects of natural selection and modified characters transmitted and inherited generation to generation (genetics). The land is a very dynamic mass over long periods of geological time, with the formation and erosion of mountains, climate change, the formation of rivers and changes in their direction, and other modifications of its surface. These factors have a spectacular impact on natural selection. This way, over time, one species can diversify into other taxa, each adapted in a different way to their environment. This is known as an adaptive radiation and has been studied by biologists since Charles Darwin (1809-1882), who can be considered the father of the subject.

Over the past decades, molecular genetics has brought us new glimpses into the history of evolution and speciation. This technique, which concerns aspects of the variation in DNA, offers

an extraordinary tool permitting evolutionary biologists to separate animals which share a common ancestor (monophyletic), as in the case of adaptive radiations, and represent only a single lineage, compared to those which come from other ancestors (paraphyletic); and in this case a similarity, for example in morphology, is convergent evolution. At the base of such studies on Malgache birds with endemism on higher levels of taxonomy, which are examined in detail in the following section, it has been possible to discern if birds with different habits and ways of life, but similar beaks, for example, are from a common ancestor. Even more interesting yet are the many cases of birds that are physically very different from one another, but based on genetic research, appear to be closely related.

This way, adaptive radiations are defined as being a rapid diversification of species from a common ancestor which is accompanied by phenotypic divergence and specialization for exploiting new available resources. Madagascar is well known for exceptional adaptive radiations in many groups in its biodiversity. For birds, there are at least seven endemic monophyletic groups which have diversified since they reached Madagascar. These groups include the Mesitornithidae, Couinae, Brachypteraciidae, Leptosomidae, Philepittinae, Bernieridae, and Vangidae. The dynamically evolving changes may affect morphology, ecology, and behavior by way of ecological niche. Such changes can take place rapidly according to the intensity of selection, but the the most endemic non-passerine groups of Madagascar apparently show a long history of evolution on the island, except certain passerines which could probably have been recent colonizers.

To illustrate an adaptive radiation, one of the most beautiful examples among the birds of the whole world is the Vangidae of Madagascar. A certain number of ornithologists have written on these animals and to better present the functional differences of beak shapes in vangas, they have made comparisons with the diverse tools used by man. Often associated with the aforementioned mixed-species groups that a patient observer can encounter in the forest, many species of vangas can be found feeding in different manners and use their beaks like tools. This allows each species to exploit varied food resources and reduces competition. There are other examples among among the families and subfamilies of Madagascar, like the Malagasy warblers (family Bernieridae), which possess an extraordinary variety of beak shapes and which are discussed in more detail in the second part of this book.

The Avifauna of Madagascar

The modern avifauna of Madagascar comprises a total of 282 species, two of which are recently extinct. Of the 280 living species, 208 are locally breeding (74%), and the other 72 don't breed on the island (26%), including a large number of migratory[1] species. Among those migratory species, there are four which do breed on the island (*Ardeola idae, Glareola ocularis, Cuculus rochii,* and *Eurystomus glaucurus*). Next, at least four species present in nature have been introduced to Madagascar by human beings (*Columba livia, Acridotheres tristis, Passer domesticus,* and *Estrilda astrild*) and another (*Numida meleagris*) was possibly introduced.

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[1] I think that migratory is used interchangeably with vagrant here.

Acridotheres tristis is currently found throughout Madagascar and with the rapid increase in its population, it will be a significant ecological catastrophe if appropriate measures are not taken.

The extraordinary thing about the avifauna of the island is the level of endemism, at higher taxonomic levels and at the level of species. Within the first category, seven groups can be cited as endemic above the level of genus: the family Mesitornithidae or the mesites, the subfamily Couinae or the couas, the family Brachypteraciidae or the ground-rollers, the family Leptosomidae or the cuckoo-roller, the subfamily Philepittinae or the asities, the family Bernieridae or the Malagasy warblers, and the family Vangidae or the vangas. The island also possesses a number of endemic genera also living in African and Eurasia, but these are not of primary interest for this book. The second surprising characteristic of the Malagasy avian community is its paucity of species compared to other tropical countries despite the remarkable heterogeneity of habitats in Madagascar.

Among the 282 species of birds (208 nonpasserine and 75 passerine) known on the island, 104 are endemic (37%). Fifty-two species of passerine are endemic (69%) and 52 nonpasserine (25%). This seems to indicate a higher degree of endemism among the passerines, which for the most part originated in Africa, arriving by flying over the Mozambique canal and remaining isolated from continental populations, and this leading to the speciation of endemic species. Madagascar has one of the highest levels on endemism in the world, which is another reason for the Malagasy people to be proud of their unique natural heritage and devote themselves to its protection.

The number of species of birds known in Madagascar has increased over time. This is associated with the discovery of migratory species or those that have lost their way and show up on the island, and those endemic taxa which were previously unknown to science due to, among other things, insufficient exploration of the land and the expansion of molecular genetics. A recent example of the addition of a migratory species to the list of Malagasy birds is *Larus hemprichii*, which has been observed and photographed in South Toliara. This species breeds in the region of the Red Sea but it is known for wandering occasionally to the Indian Sea.

Over the course of recent decades, a certain number of endemic species new to science have been described by ornithologists, including those belonging to the seven groups mentioned earlier, notably the description of a new genus and species, *Cryptosylvicola randrianasoloi* (family Bernieridae), and many species in formerly known genera, including *Xanthomixis apperti* (family Bernieridae) and *Calicalicus rufocarpalis* (family Vangidae). Also, in recent years, new species have been described in endemic genera, like *Mentocrex beankaensis* (family Rallidae). It is certain that in coming years, other migratory species will be recorded for the first time on the island and new species will be discovered, based on land surveys or the results of studies in molecular genetics. Therefore, contrary to what you might expect, the discovery of new birds in Madagascar has not finished.

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Part 2: The Endemic Groups
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Generalities of the Different Groups of Endemic Birds

In this part, we present precise details on different aspects of the natural history of the seven groups of bird endemic to Madagascar at a high taxonomic level. These different groups comprise the family Mesitornithidae, or mesites, the subfamily Couinae, or couas, the family Brachypteraciidae, or ground-rollers, the family Leptosomidae, or cuckoo-roller, the subfamily Philepittinae or asities, the family Bernieridae, or Malagasy warblers, and the family Vangidae, or vangas. Some aspects of these extraordinary birds are presented in more detail in this part of the book to provide extra information and emphasize their uniqueness in the natural heritage of Madagascar and the world in general.

Species richness

Mesitornithidae - This family is represented by two genera, *Mesitornis* with two species and *Monias* possessing a single living taxon and another undescribed and extinct subfossil species. In total, four species of mesites are known from the island in recent geological history.

Couinae - This subfamily is represented in Madagascar by a single genus, *Coua*, and nine living species. Besides two extinct subfossil species, *C. delalandei,* which was documented on the island of St. Marie, disappeared 160 years ago. Therefore, a total of 12 species of *Coua* are known from the recent geological history of the island.

Brachypteraciidae - This family is represented by four genera, *Atelornis* with two species, and *Brachypteracias, Geobiastes*, and *Uratelornis,* which are monospecific. Including an extinct subfossil species belonging to the genus *Brachypteracias*, six species of ground-rollers are known from the island in recent geological history.

Leptosomidae - This family is found only in Madagascar and the Comores, and is therefore considered as a family endemic to the Malagasy region. One study based on the difference between the plumages of the populations of *Leptosomus discolor gracilis* on Madagascar and Grande Comore finally resulted in the elevation of the population of Grande Comore to the rank of species.

Philepittinae - This family has two genera, *Philepitta* and *Neodrepanis*. Each is represented by two species.

Bernieridae - This family is currently represented on Madagascar by eight genera (*Bernieria, Crossleyia, Cryptosylvicola, Hartertula, Oxylabes, Randia, Thamnornis,* and *Xanthomixis*) and 11 species.

Vangidae - This family is represented on Madagascar by 15 genera (*Artamella, Calicalicus, Cyanolanius, Euryceros, Falculea, Hypositta, Leptopterus, Mystacornis, Newtonia, Oriola, Pseudobias, Schetba, Tylas, Vanga,* and *Xenopirostris*) and 21 species. *Cyanolanius*

madagascarinus also lives on the Comores, and therefore constitutes a species endemic to the Malagasy region. With the exception of *Calicalicus, Newtonia,* and *Xenopirostris*, all of the genera are monotypic, or each represented by a single species. A recent study based on a very old specimen found near Andohahela National Park has revealed a new species of *Hypositta*, designated as *H. perdita*. We aren't considering this here for various reasons discussed in other works.

Systematics

Mesitornithidae - Traditionally, the mesites of Madagascar have been placed in the endemic family Mesitornithidae in the order Gruiformes. However, the results of recent molecular genetics studies on this group showed certain contradictions such that the phylogenetic relations of mesites are no longer resolved. Former phylogenetic studies based on samples coming only from *Mesitornis unicolor* revealed that the mesites form a group genetically divergent from Gruiformes. Their clade appears to be closer to the seriemas (family Cariamidae) of South America and perhaps the bustards (family Otididae). The information coming from this work appears to suggest that this group is a very old lineage. However, other morphological studies concluded that the Mesitornithidae are a sister group to buttonquails (family Turnicidae). A previous analysis of molecular genetics indicated that they would be sister taxa to the owlet-nightjars (family Aegothelidae) of Australia, New Guinea, and New Caledonia. The most recent phylogenetic analysis carried out on a large scale has resulted in the conclusion that mesites are actually close relatives of pigeons (family Columbidae) and sandgrouse (family Pteroclidae). Although this relationship seems more plausible than the preceding conclusions, it still seems weak and the mesites still merit particular attention to the definition of their true phylogenetic placement.

Couinae - Different authors have divided the current species of *Coua* into two distinct groups, arboreal or climbing species including *C. caerulea, C.cristata,* and *C. verreauxi*, and terrestrial or running species represented by *C. coquereli, C. cursor, C. gigas, C. reynaudii, C. ruficeps,* and *C. serriana*. Recent molecular genetic studies on the subfamily show a clade which distinguishes arboreal forms and another group composed of terrestrial species, supporting that decision. Further, the current couas can be categorized into four different classes based on their size: large sized (*C. gigas*), medium sized (*C. caerulea*), medium-small sized (*C. coquereli, C. cristata, C. reynaudii, C. ruficeps,* and *C. serriana*) and small sized (*C. cursor* and *C. verreauxi*). Therefore, in a general way, it is rare that two species of the same size and the same mode of locomotion are sympatric.

The taxonomy within the genus *Coua* has remained largely stable in recent years. The principal exception concerns the two subspecies *C. r. ruficeps* and *C. r. olivaceiceps*, which has been elevated to the rank of species, this conclusion based on the fact that the two forms live in sympatry (in the same habitat) but don't show any sign of hybridization and show a clear difference in their vocalizations and coloration. The specific details of this taxonomic change are not yet published.

Different hypotheses on the relationships between couas and the other members of the order Cuculiformes have been advanced. The classic systematics has couas in this order, between the Centropodinae of the Old World and the Neomorphinae of the New World. Together these are placed in the family Cuculidae, which contains many other subfamilies. Thereafter, studies of molecular genetics have allowed the proposal of different ideas. One published study placed couas in a tribe, the Couini, sister group to the tribe Phaenicophaeini (Asian malkohas). Recently, another study indicated that the genus *Centropus* (which is generally placed in the subfamily Centropinae) is the sister taxon to couas, rather than the Asian malkoha genus *Phaenicophaeus*. Therefore, these two studies present contradictory points of view, as on the close relationship within the Couinae, than on the order Cuculiformes.[2]

Brachypteraciidae - A molecular genetic study permitted the conclusion that ground-rollers were monophyletic and constitute a lineage within the Coraciiformes. These results are reinforced after a more recent study which placed the family Brachypteraciidae within the order Coraciiformes, sister group to the genus *Coracias*, and further, ground-rollers are remarkably distance from *Leptosomus*. In effect, within the ground-rollers, *Geobiastes squaminger* is found in a different clade of *Brachypteracias leptosomus*, consequently, the authors proposed that *G. squaminger* be placed in the genus the species was classified as in the past.

Leptosomidae - This family is either monospecific, or contains a complex of species, and until recently, the name Leptosomatidae has been used. However, as Leptosomatidae was previously used for nematodes or round worms (order Nematoda), the name of the bird family had to be changed to Leptosomidae.

The mysterious genus *Leptosomus* was initially considered close to the cuckoos (order Cuculiformes). All the same thereafter, different anatomical characteristics placed it in its own family (order Coraciiformes) which is considered as closely related with the other families in that order, particularly with the rollers (family Coraciidae) and the ground-rollers (family Brachypteraciidae). A recent study based on molecular genetic data still questions this conclusion and indicates that the sister groups of *Leptosomus* are the woodpeckers (order Piciformes), the Coraciiformes, and the trogons (order Trogoniformes). This conclusion must be studied thoroughly and the phylogenetic relations of Leptosomidae remain unclear.

Philepittinae - The four species currently placed within this subfamily were previously placed in their own family, Philepittidae, considered a family endemic to Madagascar. This family was considered separate and isolated from the suboscines, a group in the order Passeriformes having a relatively simple syrinx structure. At the beginning of the 1990s, the ornithologist Richard Prum, studied the anatomy of suboscines and a phylogenetic analysis revealed that the family Eurylaimidae of the Old World was not monophyletic and contained members of the genera *Philepitta* and *Neodrepanis*. To resolve this inconsistency, the Philepittidae family had to be abandoned and the members of those two genera were placed in Eurylaimidae, inside of a separate subfamily, Philepittinae. In a subsequent study of molecular genetics, this relationship

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[2] I'm not sure what they're trying to say with the latter half of this sentence.

was supported. In this present work, we adopt the classification of asities in the subfamily Philepittinae and the family Eurylaimidae.

The asities represent an adaptive radiation whose evolutionary change, among other things, is in relation to their feeding habits, ecology, morphology, and reproductive behavior. Prum indicated that the diversification of the beak morphology could have occurred after colonization, in response to selective pressures on feeding habits.

Bernieridae - Recently, before molecular genetics studies concerning the endemic passerines of Madagascar, the family Bernieridae was not recognized. This family, generally designated here under the name Malagasy warblers, currently includes different genera and species which, based on external morphological characters, were previously placed in the families Timaliidae (*Oxylabes madagascariensis* and *Crossleyia xanthophrys*), Sylviidae (*Thamnornis chloropetoides, Randia pseudozosterops,* and *Hartertula flavoviridis*) and Pycnonotidae (*Bernieria madagascariensis* and *Xanthomixis* spp.) This recent work constitutes an extraordinary example of adaptive radiation and the importance of molecular studies in the understanding of evolutionary models. Even more, this research highlights the fact that classical morphological studies of museum specimens cannot always, in some cases, differentiate well between convergent characters with different origins and those that come from a common ancestor (monophyletic).

The recognition of this group of birds in Madagascar was extraordinary news for the ornithologists of the world. Lastly, the members of the genera *Bernieria* and *Xanthomixis* were previously placed in with common bulbuls, of the genus *Phyllastrephus* of South Africa (family Pycnonotidae). This is proven equally incorrect because these birds constitute, in reality, another remarkable case of convergence in plumage and other characters of external morphology. The genus and species *Cryptosylvicola randrianasoloi* was named a species new to science in 1996, on the basis of a specimen collected in the Maromiza forest which is found near the Special Reserve of Analamazaotra.

Vangidae - Parallel to the case of Bernieridae discussed above, following recent molecular genetic studies on Malagasy passerines, new and surprising information has allowed knowledge of the composition of species in the family Vangidae. Vangas are monophyletic and appear to be descended from a common ancestor which would colonize the island. The diverse species which from now on compose this family represent therefore one of the most extraordinary adaptive radiations of birds in the world. Different studies have demonstrated a great local diversification of this family in Madagascar, and this elevated diversity was not the result of multiple colonizations from elsewhere. The great morphological diversity of the family appears to have been reinforced thanks to the use and ultimately occupation of vacant ecological niches on the Main island.

The new configuration of Vangidae henceforth includes birds which were previously placed in other families based on their external morphology, like Timaliidae (*Mystacornis crossleyi*), Sylviidae (*Newtonia* spp.), Oriolidae (*Tylas eduardi*), and Monarchidae (*Pseudobias wardi*). Without the use of molecular tools, a large number of these phylogenetic relationships would be blurred, and our knowledge of the evolutionary history of birds would be therefore

very limited. Even more, this research highlights that classical studies of morphology on museum specimens do not always, at a certain point, correctly distinguish the difference between convergent characters and those coming from a common ancestor. Moreover, a recent cladistic analysis of morphological characters showed a phylogeny in conflict with that obtained from information coming from molecular genetics.

The species *Calicalus rufocarpalis*, of the limestone zone, on the old road linking Toliara to Saint Augustin, was named as new for science in 1997.

Distribution and Habitat

Mesitornithidae - All members of this family are terrestrial. They are clearly forest species and their distribution is not yet well known. The species *Mesitornis unicolor* appears to be largely distributed within evergreen areas, *M. variegata* in deciduous forest of the central west and certain evergreen forest sites, and *Monias benschi* is found in spiny forests. The latter has a more restricted distribution than the other two.

Couinae - Some members of the genus *Coua* are terrestrial, others arboreal. Some species have a large distribution within different vegetation types, while others have a tendency to have limited distribution and are found in a single type of forest. An example of the first group is represented by *C. caerulea*, which lives in all forms of evergreen and in the deciduous forests of the northwest. *Coua gigas* is also a species largely distributed in deciduous and spiny forests of the west and south of the island, and extends its distribution to the evergreens in the extreme southeast and on the western fringe of the central highlands. *Coua verreauxi* is by comparison a good example of a limited species: it is confined to the spiny forest along the Mahafaly Plateau in the southwest.

Some species present geographical variations in their plumage coloration, and each population is considered a distinct subspecies. The case of *C. cristata* constitutes the best example of these variations. This species is divided into four subspecies: *C. c. cristata*, found in the north in deciduous forests near Ambanja until the region of Antsiranana, then south, in the evergreen forests along the low altitude eastern forests near Farafangana; *C. c. dumonti* is found in the deciduous forests south of the Sofia River until south of the Tsiribihina River; *C. c. pyropyga* lives in the deciduous forests south of the Mangoky River, in the spiny forest in the extreme south of the island and the foothills of the western side of the Anosyenne Mountains; and *C. c. maxima* is known by a specimen from the coastal forest of Tolagnaro, and is now extinct.

Brachypteraciidae - Among the five species of ground-rollers, four have a large distribution within the intact evergreen forests. They are particularly secretive, and are generally diurnal but often active at dawn, and their presence is often revealed by their repetitive morning songs, "whoop." *Brachypteracias leptosomus* frequents the intact evergreen forests with undergrowth dark and humid enough that the herbaceous vegetation forms a discontinuous carpet, and with thick litter; *Geobiastes squaminger* is encountered mainly in the same type of forest but with enough lush undergrowth and less humidity, a less important herbaceous carpet and an important

litter of dead leaves; the species *Atelornis crossleyi* is widespread in mountainous evergreen forests; the species *A. pittoides* can also be found in disturbed forests and blocks of forest fragments, and it is clearly less sensitive to perturbations of habitat than the three preceding species. Some sites show a remarkably elevated abundance of the latter species, such as the mid-altitude forest between Andringitra and Ranomafana.

All species are for a large part terrestrial, even if they can be observed singing on perches situated several meters from the ground, or even indeed in certain cases, notably with *B. leptosomus*, searching for food in the canopy. *Uratelornis chimaera* cannot be encountered anywhere but in the spiny forests of Mikea, north of Toliara, where the species is also terrestrial and can be seen running between tufts of vegetation. It can be active during the night (nocturnal). Even though all members are largely terrestrial, the ground-rollers are capable of flying with vigorous wingbeats to escape predators and return to their nest.

Leptosomidae - *Leptosomus discolor* of Madagascar generally frequents forested zones where the species is largely distributed in all forms of evergreen, deciduous, and spiny forests on the island. It can also be found in strongly disturbed environments, adjacent to intact forest. This species has been observed in the vast non-forested, outside of the breeding season, such as the periphery of Antananarivo. These observations are probably related to the dispersal of these birds.

Leptosomus discolor is a masterful flier, and its aerial acrobatics associated with its piercing calls are immediately perceptible to people visiting the forest, or passing along the edge where its undulating flights and sharp descents are visible. The bird can remain remarkably immobile when it perches very high in the fine branches of trees, often at rest or looking for prey.

Philepittinae - Among the four members of this family, three are found in evergreen forest. This is overall true of the species *Philepitta castanea*, which has a large distribution and can be common in some sites; and of the two members of the genus *Neodrepanis*, including *N. coruscans* which is a bird with a large range, but apparently less frequent than *P. castanea*; *N hypoxantha* is found at higher altitudes and can be abundant in some sites. The fourth member of the subfamily, *P. schlegeli*, lives in deciduous forests. According to available information, its density appears to be relatively weak, even though it seems not to be rare in localities like the forests of Beanka, east of Maintirano. Only the species *P. castanea* can live in disturbed forest, the others confined principally in relatively intact forest.

Bernieridae - The spatial range of Malagasy warblers in the diverse types of habitat or microhabitat testifies to their diversification following various ecological conditions of places. The different members of the family are often observed moving and searching for food at the undergrowth level, but some, like *Cryptosylvica randrianasoloi* and *Randia pseudozosterops*, can also perch very high, to sing in the trees, often in exposed places. The majority of these species, with few exceptions, have a large distribution. The species *Xanthomixis apperti* is known from some localities situated at the transitional zones between evergreen and deciduous (Analavelona, Zombitse-Vohibasia National Park) and in the deciduous forests of Mikea in the extreme southwest; *Thamnornis chloropetoides* is encountered in the spiny forests of the

southwest and *X. tenebrosus* within dispersed evergreen sites. Also, each of these species is found in a particular forest type, and rare is the case where they cross into different types. One of the exceptions is *Bernieria madagascariensis*, which can be in evergreen and deciduous forests.

Within the humid forests, some species are largely distributed all along these massive forests, like, for example, *B. madagascariensis, X. zosterops,* and *Oxylabes madagascariensis*. Others are found in a given altitudinal band: *X. tenebrosus* is contained in the forests at base altitude, generally below 800 m, and *X. cinereiceps* and *Crossleyia xanthophrys* frequently in mountain forests above 1400 m.

Vangidae - Among the 21 species in this family, a single one is found both on the main island and the Comores (*Cyanolanius madagascarinus*). The vangas can be found in all different natural forest types of Madagascar, including evergreen, deciduous, and spiny. Numerous species can be sympatric at the level of a single site. The specific diversity is principally concentrated in the humid forest, with 16 of the 21 species. In the evergreen forest, 13 species are known, for example in Andringrita National Park, versus nine species in the deciduous forest of Kirindy CNFEREF (Centre National de Formation, d'Etudes et de Recherche en Environnement et Forestrie) and of Ankarafantsika National Park.

Although most of the vangas are typically dependent on the forest, some taxa can be found in strongly disturbed habitat. *Vanga curvirostris* and *Leptopterus chabert* can be encountered in plantations of introduced trees and in open wooded areas in village regions.

Unlike the other groups of endemic birds already mentioned in this work, numerous species of vangas are not contained to a sole forest type and have a large distribution within the evergreen forests of the east, deciduous of the west, and spiny of the south. For example, the species *Newtonia brunneicauda, L. chabert, Artamella viridis*, or *V. curvirostris* can be encountered in all three types of forest. However, some species are limited to one specific type of forest and in some cases, in restricted geographic areas. *Xenopirostris damii* does not appear anywhere except in some deciduous localities where *Calicalicus rufocarpalis* has not been identified outside of the spiny forest, along the Mahafaly Plateau. *Euryceros prevostii* is often encountered in the northern half of the island while *N. favonanae* is found rather in the southwest of the island.

Feeding Habits

Mesitornithidae - Few details are available on the feeding habits of mesites. In general, *Monias benschi* digs in the sand to find ground invertebrates and the two species of *Mesitornis* tend to search the litter and overturn leaves to search for prey. The stomach contents of *M. unicolor* from a forest in the north of Tolagnaro included the remains of cockroaches (Blattodea), beetles (Curculionidae, Scarabidae), flies (Diptera), ants (Formicidae), and mollusks. Even more, this species is known to eat seeds.

Studies on the feeding habits of *M. variegata* in some areas of dry western forests have shown that the species consumes, in order of importance, crickets (Orthoptera), beetles, cockroachs, caterpillars and butterflies (Lepidoptera), larvae or millipedes (Diplodpoda), spiders

(Araneae), mantises (Mantodea), and flies. Seeds are also reported in the diet of *M. variegata*. In the case of *Monias benschi*, the species consumes termites (Isoptera), small beetles, millipedes, cockroaches, and invertebrate larvae, and less often, small fruits and seeds.

Couinae - In general, most species of *Coua* are insectivores, even though the type of food consumed differs considerably by species, region, and season. Some species are also known to eat vertebrates (*C. caerulea, C. coquereli, C. cristata,* and *C. gigas*), mollusks (*C. cristata*), eggs (*C. cristata* and *C. gigas*), and some regularly eat plants, particularly fruit (*C. caerulea, C. coquereli, C. cristata, C. cursor, C. reynaudii, C. ruficeps, C. serriana,* and *C. verreauxi*). *Coua caerulea* seems to show preference for reptiles, particularly chameleons, and the absence of these birds and other members of the genus on Nosy Mangabe has been advanced as an explanation for the abundance of geckos from the genus *Uroplatus* on that island.

Studies on terrain have shown that the feeding habits of some species vary as a function of season. For example, with *C. ruficeps* of Ampijoroa, 98.3% of prey captured during the humid season are arthropods (essentially the larvae of butterflies and grasshoppers), and by comparison, during the dry season, invertebrates are less important but the species eats a large proportion of vegetable material like seeds, resin, and flowers. Some species appear to be generalists in the food they eat. For example, in the stomach contents of two individuals of *C. serrriana*, the following were identified: spiders (Araneae), cockroaches (Blattodea), beetles (Scarabeidae, Curculionidae, Tenebrionidae), ants (Formicidae), mantises (Mantodea), crickets (Gryllacridae, Gryllidae), and the remains of small vertebrates.

The ingestion of fruits is not necessarily accidental. For example, the species *C. reynaudii* has been observed in the coastal forest actively feeding on *Macaranga* fruits. *Coua caerulea* and *C. cristata* are known to eat the resin and flower buds of trees. The stomach and small intestines of the species *C. caerulea*, captured in an evergreen forest near Tolagnaro, contained a viscous and sticky liquid which was not soluble in water. Resins are an important energy source composed principally of water, a complex of polysaccharides, calcium, and trace minerals.

Brachypteraciidae - Few quantitative details on the feeding habits of ground-rollers are available, given their secretiveness, which makes observation difficult. In general, these animals look for their prey on the surface of the ground and feed abundantly on a great variety of ground and litter invertebrates. Among the species from evergreen forests, the following types of prey were identified: millipedes (Diplopoda), snails and slugs (Gastropoda), beetles (Coleoptera, Carabidae, including Curculionidae and Tenebrionidae), flies (Diptera), ants (Formicidae), and even some vegetable material. The ground-rollers are also known to eat small vertebrates like frogs, reptiles, and mammals. *Uratelornis chimaera* consumes beetles, cockroaches, and katydids.

Leptosomidae - The available data on the diet of *Leptosomus* indicates that the genus is in a large part insectivorous and carnivorous, feeding on beetles (Coleoptera), mantises (Mantodea), katydids and cicadas (Orthoptera), different invertebrate larvae, and chameleons and geckos like

Uroplatus. The stomach of this bird has been often observed as lined with "fur of hairy caterpillars."

Philepittinae - The members of this subfamily are divided in two based on their diet: the frugivores, composed of the two species of *Philepitta,* and the nectarivores, the two *Neodrepanis*. The members of the genus *Philepitta* live in the underbrush of the forest and possess a particularly large beak which undoubtedly corresponds with an adaptation for eating fruit. At the same time, the two representatives of this genus also have a brush-tipped tongue, characteristic of nectarivorous birds. These animals are thereby adapted for eating both fruit, and nectar and pollen, following the availability of these products and the season. Practically no information is available on the diet of *P. schlegeli*.

A certain number of studies on the diet of *P. castanea* have been conducted at Ranomafana National Park, where the species generally eats the orange and red fruits of small trees in the families Rubiaceae and Myrsinaceae, which grow in the undergrowth. The experiments on the seeds consumed by this species indicate that those which pass through the digestive system and are defecated have a higher rate of germination relative to those which simply fall on the ground. *Philepitta castanea* therefore plays a measurable role in the regeneration of the undergrowth vegetation. Also, by the structure of its tongue, this species also feeds occasionally on the nectar of flowers, together with arthropods.

Some details concerning the plants on which the *Neodrepanis* spp. find their food are available. These birds are principally nectar specialists thanks to their long recurved beak and long tongue tipped with a brush. Contrary to the two species of *Philepitta*, which are often encountered in the undergrowth, the *Neodrepanis* tend to exploit the higher strata of the forest and often visit flowers in the canopy of the trees, and are consequently obviously harder to observe.

Some plants have an preferred link with their pollinators, developing a reciprocal attraction which favors their fertilization. The case of the genus *Bakerella* (Loranthaceae) and *Neodrepanis* well illustrates this situation. This genus of plant is composed of parasitic species living dependently on woody trees, and because of this most are found in the evergreen forest of the east. These birds forage on the very colorful bell-shaped flowers of *Bakerella* and the resemblance between the shape of the beak and that of the spur of the flower demonstrate remarkable coevolution between the plant and the animal.

The *Neodrepanis* species are also known to feed from flowers of balsams (*Impatiens humbletonia*, Balsaminaceae), which have a similar shape. Also, they eat arthropods like spiders (Araneae). Some individuals in *Neodrepanis* caught in nets during wildlife surveys wore pollen on their front and in their nasal holes and therefore probably play a role in the pollination and fertilization of flowers.

The original diet of these two genera was, it appears, frugivory, and from that developed the nectarivory observed in the genus *Neodrepanis*. The latter probably evolved thereafter toward a specialization for nectar and lost its frugivory thanks to a varied diet, rather than the adoption of a new source of food.

Bernieridae - For the species of small birds which live in the often shadowy undergrowth of the forest, few details are known on their diets. All are largely or exclusively insectivores, feeding principally on invertebrates captured in full flight or gleaned from the vegetation with their beak. These birds often make up a part of mixed-species flocks. With some species, especially *Bernieria madagascariensis*, the form and length of the beak of males is significantly different than that of the female (sexual dimorphism). Within this species, for which information on stomach contents is available, different types of invertebrates have been identified: spiders (Araneae), beetles (Coleoptera) of the families Chrysomelidae, Cleridae, Curculionidae, Elateridae, and Tenebrionidae, cicadas and leafhoppers (Homoptera) of the families Cicadidae and Cicadellidae, cockroaches (Blattodea), ants (Hymenoptera) of the family Formicidae, and unidentified Orthopterans. Other debris found in their stomachs includes seeds from plants and remains of vertebrates like geckos.

Within one type of habitat, while searching for food, members of the family Bernieridae exploit different parts of the habitat. Even if some species have similar size and diet, the diverse microhabitats offered by the forest ecosystem reduce competition between species (interspecific) and permit them to exist together. *Bernieria madagascariensis* specializes on dense clusters of leaves and on insects hidden in shallow holes; *Xanthomixis zosterops* perches on thin branches or in the bushes of the undergrowth and catches insects on the overhanging leaves; *X. tenebrosus* and *X. apperti* are principally terrestrial while *X. cinereiceps* clings with long toenails to the mosses that cover branches to find invertebrates.

Vangidae - The vangas occupy all of the main ecological niches available in the forest ecosystem all along their distribution range because of the absence of certain families in Madagascar like the woodpeckers (Picidae), nuthatches (Sittidae), tits (Paridae), and shrikes (Laniidae), which seem to have left their diverse niches vacant and available. The diversification of species in this family is manifested externally by, among other things, their diet, beak shape, coloration, song, and morphology.

The exceptionally distinctive traits of vangas are particularly tied to trophic functions. The beaks present a large range of shapes, from the smallest to the strangest that some species feature and which translate to a specificity in their mode of eating and diet.

As written in part 1, the shape of beaks and the way they function among the different species of vangas constitute a way for species living in the same forest (sympatric) to divide between them the different types of food available and therefore to reduce competition. The species with similar methods of feeding also have other ways to further reduce competitive interactions. Some, for example, forage on or near the ground or higher in the canopy in the search for prey; others hunt on the small branches or on the trunks of trees. The vangas can be divided into many groups based on their type of beak:

* Most species with short beaks with pointy ends, like *Calicalicus madagascariensis, C. rufocarpalis, Cyanolanius madagascarinus, Leptopterus chabert, Pseudobias wardi,* and the members of the genus *Newtonia,* inspect the leaves, branches, and trunks in their quest for food;

* *Mystacornis crossleyi*, with its beak long and pointy, explores the ground to find food among the litter of dead leaves, leaves, and mosses;
* *Falculea palliata* often climbs along the large trunks of trees, and hops from branch to branch in the search for insects and larvae that the bird will pick from deep fissures and cracks with its long sickle-like beak from rotted wood and bark flaps;
* *Hypositta corallirostris* and *Randia pseudozosterops*, which posses small and triangular pointed beaks, climb along the bark of trunks and branches of trees, going around in a spiral, entering all the cracks and exploring to find their prey;
* The members of the genus *Xenopirostris*, with a strong and thick beak, search for their food on the dead branches and trunks, digging to dislodge their eventual prey, or in the clusters of detritus on epiphytes and arboreal ferns;
* *Oriola bernieri* prospects the vegetation debris that accumulates at the base of the leaves of *Pandanus* and *Ravenala* and palms, and hops on trunks to find its prey;
* *Vanga curvirostris* can localize its prey by scrutinizing its surroundings from its perch, and shredding large insects and often small vertebrates with its strong and pointed beak;
* *Tylas eduardi* and *Artamella viridis* look for their prey in small cracks and shallow fissures, undoing clusters of detritus and cocoons to hunt mostly for caterpillars;
* *Euryceros prevostii* is mostly a passive hunter and usually captures its prey on branches and trunks, but the role of its enormous and brilliant blue aquiline beak is not yet known.

Given that many vangas live in the dry deciduous forest, following them and observing their diet is relatively easy. A certain number of quantitative data obtained from direct observations and the analysis of stomach contents is available. The Vangidae consume a large range of food types, dominated by invertebrates, but small sized vertebrates and fruits (frugivores) are also swallowed. Observations in the nest of *Xenopirostris polleni*, for example, indicate that this species feeds abundantly on crickets (Orthoptera), as well as larvae and chrysalises of butterflies (Lepidoptera).

Recent work conducted by "The Peregrine Fund" on the Masoala Peninsula has provided information on the diet of two poorly known species belonging to this family. The diet of *Oriola bernieri* contains 91% invertebrates, 9% vertebrates, and the rest is unidentified. Spiders (Araneae) and crickets are the most commonly consumed invertebrates, as well as *Phelsuma* and their eggs. In the case of *Euryceros prevostii*, the prey brought to the nest was composed of 88% invertebrates, 9% vertebrates, 3% earthworms (Annelida), and 1% millipedes (Diplopoda). The observations made in the Masoala Forest revealed much of the prey hunted by *E. prevostii*: geckos such as *Phelsuma* spp. and *Uroplatus* spp. (Reptilia), milipedes (Diplopodae), locusts (Orthoptera), crabs (Decapoda), cockroaches (*Blattidae*), stick bugs (Phasmitodae), beetles (Coleoptera), wasps (Hymenoptera), spiders, larvae and adult butterflies, cicadas (Homoptera), mollusks, and other unidentified prey.

After remains in stomach contents of several different vanga species were identified, it was found that *Calicalicus madagascariensis* feeds on spiders, beetles, crickets, butterflies (including larvae), and grasshoppers; *Falculea palliata* eats spiders, cockroaches, beetles, ants (Formicidae), crickets, butterflies (including larvae), leafhoppers (Tettigoniidae), and grasshoppers (Orthoptera); *Leptopterus chabert* consumes different invertebrates, as well as

fruits and seeds; and *Vanga curvirostris* eats spiders, cockroaches, millipedes (Geophilomorpha), cicadas (Cicadidae), beetles, ants, beetles (Homoptera), mantises (Mantodea), grasshoppers, and centipedes (Scolopendromorpha), and with some frequency, geckos, small birds, and other unidentified vertebrates.

Conservation

Mesitornithidae - All of the mesites have a "Vulnerable" conservation status. However, little information is available. Considerable pressure exists on the remaining populations due to the reduction of the area of evergreen (*Mesitornis unicolor* and *M. variegata*), deciduous (*M. variegata*) and spiny forest (*Monias benschi*), along with occasional hunting (for bushmeat) and predation by indigenous and introduced predators. Using various information coming from the forest of Mikea, based on territory size and the results of "playback" experiments, the remaining population of *M. benschi* is estimated at between 98,000 and 152,000 individuals. The remaining population of *Mesitornis variegata* is evaluated at between 3,000 and 19,000 individuals in the Menabe region and between 6,000 and 26,000 individuals at Ankarafantsika, as of twenty years ago. Since these evaluations, the destruction of habitat has not stopped and other human pressures have not ceased to increase. Not one estimation coming from reliable data on the current population size of *M. unicolor* is available.

Couinae - All members of *Coua* are prey to a large number of natural predators, including various Carnivora (indigenous and introduced), raptors, and snakes. Among the predators of eggs and chicks of *C. coquereli* there are snakes and other reptiles. Further, given their often large size and the ease with which they can be captured, couas are frequently considered game or bushmeat for populations near rivers or forested areas. All of the current species face pressure to different degrees, and the largest species are the most hunted.

Among the living species of *Coua*, only *C. verreauxi* has a conservation status of "Near Threatened" and the others are classified as "Least Concern." In general, the various species seem to be sensitive to forest degradation, in particular that of their natural habitat. They have been proposed as an excellent group to be used as bio-indicators for following the state of the environment. However, some exceptions such as *C. coquereli, C. cristata, C. cursor, C. reynaudii, C. serriana* and *C. ruficeps* can be found in secondary forest which are, in certain cases, close to or contiguous with relatively intact forest areas.

Coua ruficeps displays tolerance to significant degradation of natural forest. In effect, in certain regions of the west, the species is often the only terrestrial coua that resists significant anthropogenic change. *Coua caerulea* seems to show mixed resilience to degradation of habitat; the species is absent or present in weak densities in forests where the vegetation structure is degraded, and it is also found in blocks of fragmented forest that are relatively intact.
The case of *Coua cristata maxima* in the Tolagnaro constitutes a concrete example of the speed with which some populations of coua can disappear. In Feburary 1948, Philippe Milon found some individuals of *C. c. maxima* in the area of Tolagnaro and captured an individual designated as the holotype for the subspecies. A large coua, potentially this form, was seen at Lake Lanirano, just north of Tolagnaro in August 1988, but a year after, in 1989, the population had

disappeared from this location. The forests in the immediate proximity of Tolagnaro and farther north, near Manafiafy, were intensively explored by numerous ornithologists, but this very distinctive coua apparently didn't exist anymore. Given that forested habitat which seems to be appropriate for this subspecies still exists in this region, we presume that the local disappearance is associated with hunting.

Brachypteraciidae - All four species of ground-rollers that live in evergreen forest, with the exception of *Atelornis pittoides*, appear to be quite sensitive to habitat degradation. *Brachypteracias leptosomus, A. crossleyi*, and *Geobiastes squaminger* can only be found in largely intact forests. These taxa represent therefore an excellent group which can also be used as bio-indicators for following the state of the environment. *Uratelornis chimaera*, which mostly lives in the spiny forest, has a rather reduced range, as its natural habitat has suffered a lot of degradation induced by man. Three species have a "Vulnerable" conservation status (*B. leptosomus, G. squaminger,* and *U. chimaera*), a single species is considered "Near-Threatened" (*A. crossleyi*), and one other is classified as "Least Concern" (*A. pittoides*). The remaining ground-rollers are encountered along trails in the forest and following forest edges, where they are hunted by river people for bushmeat. This combined situation of natural predation only accentuates the pressure which weighs on the remaining populations of these birds. Among the species, *U. chimaera*, in addition to its already very limited distribution, lives in a sensitive habitat where ecological conditions are adverse and an eventual disappearance of the forest area would be nearly irreversible.

Leptosomidae - The conservation status of *Leptosomus discolor* is "Least Concern." The species can be found un small forest fragments, forests that have been exploited, and burned forests. However, even if it is apparently tolerant to degradation of a forest ecosystem, the species at least depends on relatively intact areas for different parts of its annual cycle, in particular for nesting. Therefore, the conservation of remaining forests is important for the long-term survival of these birds. Many predators like the Carnivora and raptors feed on *Leptosomus*. Further, the species is the object of a certain amount of hunting, both for bushmeat and for the preparation of magic potions.

Philepittinae - As all members of this family are dependent on the forest, the continuing destruction of remaining forested habitats puts their future in peril. As mentioned elsewhere, the asities, in particular *Philepitta*, play an important role in the regeneration of plants in the undergrowth and therefore are essential elements for the functioning of the forest ecosystem. Two species have the conservation status "Least Concern" (*Neodrepanis coruscans* and *P. castanea*), one is classed as "Vulnerable" (*N. hypoxantha*), and one other is "Near-threatened" (*P. schlegeli*).

Bernieridae - As mentioned earlier, all members of this family live in the forest and human pressures on their remaining habitats clearly have negative impacts on the future of these birds. The conservation status of Malagasy warblers include two species considered

"Vulnerable" (*Xanthomixis apperti* and *X. tenebrosus*), three "Near-threatened" (*Crossleyia xanthophrys, Hartertula flavoviridis* and *X. cinereiceps*) and six "Least Concern" (*Bernieria madagascariencis, Cryptosylvicola randrianasoloi, Oxylabes madagascariensis, Randia pseudozosterops, Thamnornis chloropetoides,* and *X. zosterops*).

Vangidae - The large majority of vangas are dependent on the forest and partially uninterrupted human pressures on remaining forest habitats have predictable negative impacts on the future of these birds. The members of Vangidae have the following conservation statuses: one species is classified as "Endangered" (*Xenopirostris damii*), four species "Vulnerable" (*Calicalicus rufocarpalis, Euryceros prevostii, Newtonia fanovanae,* and *Oriolia bernieri*), one "Near-threatened" (*X. polleni*), and 15 "Least Concern" (*C. madagascariensis, Cyanolanius madagascarinus, Falculea palliata, Hypositta corallirostris, Leptopterus chabert, Artamella viridis, Mystacornis crossleyi, N. amphichroa, N, archiboldi, N. brunneicauda, Pseudobias wardi, Schetba rufa, Tylas eduardi, Vanga curvirostris,* and *X. xenopirostris*.)

Evolution

Since the separation of Madagascar from Gondwana, at the beginning of the Cretaceous 150 million years ago, the majority of birds of Madagascar, particularly the forest species, no longer had contact with those from continental environments, and therefore evolved separately. Particularly among sedentary species, this lead to the installation of an original avifauna where the majority of taxa are not found anywhere else. In effect, more than 50% are endemic and certain species are endemic at higher levels. This endemism is more remarkable for forest species, because they make up more than 90% of this group.

The endemic birds of Madagascar descend from colonizing species, which for the most part come from African lineages. The displacements were apparently possible thanks to the proximity of the African continent, whose coast is 400 km from Madagascar. The dispersal of African ancestors was facilitated during periods ranging from the mid-Eocene until the beginning of the Miocene, when the sea level was very low, and exposed mountains which are today submerged in the Mozambique Canal, and which appear to have served as bridges or "stepping stones." However, the idea that the island was actually exposed and acted as a springboard has been criticized by specialists who study the Earth (geologists). Others have also suggested that some groups endemic at higher taxonomic levels appear to have diversified from Asian lineages, like the members of the genus *Coua*. But the medium adopted by their common ancestors for getting to Madagascar remains an enigma, especially for species which are not good fliers like couas.

To conquer different available spaces, evolution takes place at variable speeds following the response of each group to natural selection from the environment. Therefore, the endemic groups represent ancient lineages as some families, such as the Mesitornithidae, the Couinae, and the Brachypteraciidae. Some groups have had a rapid evolution and are currently diversified into numerous endemic genera and species, but descend from a single colonization followed by adaptive radiation. Observation of the current population of birds, which are very remarkable in

terms of their ecological and morphological designs, reflects the different processes of their evolution.

Beyond being tied to speciation based on trophic functions, diversification seems also to be tied to territory sharing between some species, permitting them to adapt and survive in the ecological conditions of diverse forest or forest level types. Among the Vangidae in humid evergreen forests, the abundance of biomass and the existence of varied microhabitats allows the cohabitation of some species within the same habitat. But a specification of their ecological niche seems to have been produced. *Cyanolanius madagascarinus, Artamella viridis, Calicalicus madagascariensis* and *Hypositta corallirostris* are canopy species whose activities usually take place at the upper half of the vertical stratus; *Schetba rufa, Xenopirtostris polleni,* and *Tylas eduardi* often exploit the undergrowth and *Mystacornis crossleyi* is terrestrial.
In dry forests, leaves are often deciduous or very small in areas where droughts are most prominent, precipitation does not fall except during a few months and is poorly distributed through the course of the year, and aridity progressively increases the farther south you go. Within this biome, *Xenopirostris damii* frequents the deciduous forest of the northwest; *Calicalicus rufocarpalis* and *X. xenopirostris* are found in the spiny forest of the southwest; and *Newtonia archiboldi* particularly uses the areas of the southwest, the south, and the southeast.

Speciation

Speciation is the evolutionary process by which new living species appear, which generally necessitates tens of thousands of years to produce. Following diverse factors, like natural selection and genetic drift, which are two drivers of evolution, geographic isolation and the speed at which the process takes place, the world that surrounds us is filled with an immense diversity of animals and plants. The succession of numerous climatic events and the existence of refugia, where some species have been able to remain during unfavorable periods, have therefore played a major role in the diversification of species. Birds represent one of these extraordinary examples which illustrate the different steps in the process of speciation, with their many shapes and colors and behaviors as proof. This differentiation of species generally corresponds with the contrasting requirements of different habitats and the diverse ways of life that are possible.

The recent use of molecular genetics in the study of the systematics of birds of Madagascar is a very important medium in the distinction of animals that evolved independently but which seem to have similar morphologies (convergent) from those descended from the same ancestor (monophyletic) but with different morphological characters (divergent). Following the process, two types of speciation can be observed in nature, allopatric speciation and sympatric speciation. Of the latter case, no conclusive proof has been found among the birds of Madagascar, so we will concentrate on allopatric speciation, which is also the most widespread type in each group.

The principle concept of allopatric speciation originates with the presence of apparent obstacles along the distribution of one species, which interfere the movement of individuals and genetic exchange (gene flow). These barriers are often made of geographic features, like rivers

and streams, the development of mountains, or other geological factors. The separation of two areas that were once continuous is called a vicariant event. Another way this can be produced is by dispersal across an area, probably in different habitats, or through barriers, leading to vicariance. In this case, the populations are isolated physically and reproductively.

In Madagascar, after the isolation of the main island, climatic changes which happened over the course of geological time and took place at different periods, have had a major impact on the landscape. These different events are closely associated with the remarkable speciation of the birds of Madagascar. For example, over the course of the Pleistocene, the Earth became significantly cooler and vast areas of fresh water were transformed into impressive glaciers. During these periods of glaciation, mountain vegetation of the summit ericoid vegetation area, dominated by the genus *Erica*, descended lower and replaced many lower altitude vegetation types, often forming continuous vegetation bridges between different mountaintops. The high peaks of Madagascar, in particular Andringitra, had glaciers.

These movements permitted a large dispersal of species which had been apparently limited to the upper part of some mountaintops. At the end of the Pleistocene or during interglacial periods, the sea level increased following the melting of large glaciers and the Earth became warmer and more humid on the whole. Therefore, the older mountain communities, with a large distribution, which existed during different periods of the Pleistocene, shrunk back toward the high mountains of the island along with all the organisms associated with these habitats, creating populations isolated by vicariance on the different peaks. This model, repeated many times, gave rise to different waves of isolation and connection.

Following the incomplete information available, recent geological time shows evidence that a vast portion of southwest Madagascar was once distinctly more humid. Today, the presence of humid forest species of birds in dry regions, like the humid canyons of Isalo, supports the idea of a connection from the east to the west. But these types of forests have considerably changed following the aridification and desiccation of this part of the southwest over the course of the Holocene. Proof of these dramatic events can be found in numerous subfossil formations, like at Ampoza, an area which today is poor in fresh water and where the forested areas are dominated by deciduous forest. Among numerous animal remains recovered from the Ampoza deposits, there are currently extinct species like the hippopotamus and some geese (*Alopochen sirabensis*).

The rare isolated forests in the western region have resisted the challenges caused by Analavelona thanks to their peculiarities: the presence of sources of water in the forest, and its elevated altitude compared to the surrounding area which gives it a different daily climate and maintains the presence of this vestige of humid forest. Following these climatic changes, the species typical of eastern humid forests have been split and currently show discontinuous distributions on either side of the eastern cliffs of the southwest. The separation of these populations and their subsequent differentiation have induced a speciation between the totally vicariant species. For example, *Xanthomixis cinericeps* and *X. apperti* belong to the family Bernieridae and are sister species, genetically and morphologically close and apparently in allopatry.

The genus *Coua* is also a good illustration. *Coua cristata* has four subspecies, which differ in the coloration of their plumage, and in certain cases their size, and few intermediate

forms exist in the overlapping areas of the subspecies. Although molecular genetic studies are necessary to understand the level of differentiation between the subspecies, perhaps the case of *C. cristata* could be treated as an example of speciation, where geographically isolated forms undergo a subsequent process of genetic differentiation.

Among the other groups of Malagsy birds endemic at high taxonomic levels, other examples of pairs of species which appear in non-overlapping (allopatric) areas exist on the island. Of the two species of *Philepitta*, which are especially frugivores, *P. castanea* is distributed in evergreen forest while *P. schlegeli* frequents deciduous forest and the transition forest between humid and dry forest. The only place where these two species are in sympatry is situated at 785 m of altitude, in the humid forest of Manongarivo, in the northwest of the island, a narrow band where in general the birds show biogeographic affinity to central Highlands. Another example marking the existence of vicariant populations is also observed in the family Vangidae in which one species *Cyanolanius madagascarinus*, is found both on the Comores and Madagascar. A critical point is represented by the Comores which are made up of an volcanic archipelago formed over the course of prior geological periods and which has never had a direct connection with Madagascar. Consequently, the only manner of dispersal *Cyanolanius* had to reach the archipelago was to fly the hundreds of kilometers which separate Madagascar and the Comores. Following current classification, the subspecies which exists on the Comores is *C. m. comorensis,* whose plumage differs slightly from that of the Malagasy subspecies, *C. m. madagascarinus*. Therefore, as in the case of *Coua cristata* from before, it is probably a nascent species. For *Cyanolanius madagascarinus*, the Comorian and Malagasy populations are completely isolated, whereas the different subspecies of *Coua cristata* could be partially in contact.

Secondly, in the family Vangidae, the genus *Xenopirostris* is represented by three distinct species which frequent different vegetation types. *Xenopirostris polleni* is found in humid evergreen forests of the east and the central Highlands, *X. damii* is very restricted to deciduous forest and *X. xenopirostris* is located in the deciduous and spiny forests of the southwest and the south.

But the results of molecular genetics on some species cause, in some cases, confusion concerning knowledge we obtained from observations of living forms and of museum specimens. In the following case, models of distribution based on morphologic variation don't coincide with those founded on molecular analysis. Among *Bernieria madagascariensis*, the two subspecies have been long considered as representing eastern and western forms, following plumage color and geographic situation. *Bernieria m. madagascariensis*, darker, is distributed in the humid evergreen forests of central Madagascar and the east, from Souht-Anjanaharibe and Marojejy in the north to Andohahela in the south. While *B. m. inceleber*, lighter, is found in deciduous forests of the north and then south until Toliara. But after recent work by Nick Block at a molecular lab, the models coming from genetic studies have revealed the presence of two populations that don't correspond to the two subspecies previously described, which are genetically very similar. The most astonishing is that in place of having an east-west differentiation based on vegetation, a cryptic diversification is found following latitude. The two clades are otherwise genetically very different, but the birds cannot be distinguished by their morphology or their vocalizations. One of the two populations is confined to the humid

evergreen forest of the southwest of the island, and the other is widespread over the rest of the range of the species, and the two clades therefore appear to be allopatric.

One crucial question concerns the impacts of human (anthropogenic) activities, which have modified the ecological landscapes together with communities of birds. As mentioned before, a large majority of endemic birds of Madagascar are species that are typically dependent on the forest, and cannot locally or regionally survive without appropriate forest habitat. Modifications have taken place following two different manners: 1) the complete destruction of vast areas of forest habitat has only permitted the persistence of some endemic species and 2) the land clearing of some parts of the forest has created a series of forest fragments in which some endemics remain. Ambohitantely is a site which has often been the subject of studies concerning the impact of forest fragmentation on the central Highlands.

In such a site, parallel to the breakup of forest cover, metapopulations have been subdivided and the subpopulations are more or less isolated, and each evolves independently from the others over the course of time. Put another way, the initially interbreeding have been evolving into subpopulations or species following geographic isolation. The impact this could have over the medium and long term remains yet to be determined, but at a certain level, the subdivision of the populations constitute artificial experiments in the processes that prevent gene flow and cause the genetic differentiation of populations.

Ecological Services

Seed and Pollen Dispersal

The natural dispersal of seeds and pollination are among the very important ecosystem services rendered by biodiversity, for the regeneration of the forest and the fruiting of native (indigenous) and non-native (introduced) trees. Numerous are the direct and indirect benefits that man draws from biodiversity and functioning ecosystems. Many modes of seed dispersal are observed in nature following the methods used by plants for spreading their seeds and pollen (wind, water, animals, etc.)

Seed Dispersal

The phenomenon of animals feeding on seeds (granivores) or fruits (frugivores) and contributing to dispersal is known by the term zoochory. This process presents the advantage of allowing seeds to travel large distances from their mother plants, and dispersal by zoochory is overall performed by flying species which have the capacity to move very far, like canopy species. Among these transporters, birds play a fundamental role in the regeneration of the forests, but on Madagascar very few species of birds are exclusively frugivorous. The diet of a large number of species of Malagasy birds is made up essentially of insects, and even the frugivores occasionally eat invertebrates, particularly when fruits are rare.

Among the eight species of Malagasy frugivorous birds, *Philepitta castanea* is confined to humid evergreen forests and principally eats fruits. Studies conducting in Ranomafana National Park on the diet of this species show that it eats the fruits of over 24 species of undergrowth plants belonging to more than 13 families in the humid forests. A large proportion

is made up of the small berries of the families Myrsinaceae and Rubiaceae (44%) and this species overall consumes *Psychotria* sp (family Rubiaceae), *Oncostemum* sp (family Myrsinaceae) and *Piper* sp (family Piperaceae). Because of this, *Philepitta castanea* seems to play an important role in the regeneration of the undergrowth. Following our observations in many humid evergreen forest locations, a positive apparent correlation exists between the abundance of feet of *Psychotria* spp and the abundance of *Philepitta castanea*. In addition to the fruits of Myrsinaceae and Rubiaceae, these birds eat and disperse other fruits belonging to at least 12 families of plants according to their availability, thereby ensuring the regeneration of a variety of vegetation in the undergrowth. *Philepitta castanea* swallows fruits well colored with red or blue black, and undigested seeds are rejected to the outside in excrements. The intestinal transit of seeds of certain species seems to favor their germination, relative to fruits that simply fall on the ground. The stomach acids of the animals apparently soften the external coverings of seeds and therefore permits their development.

Very little information is available on *P. schlegeli*, given that it is a very local species and its population size in nature is significantly smaller than that of *P. castanea*; its role in the regeneration of the forest has not yet been demonstrated, but observations of droppings from birds captured in nets in the deciduous forest of Beanka, in the center-west of the island, have revealed the presence of minuscule intact seeds.

Compared to other tropical forest zones in the Old World, the Malagasy forests contain less species of birds that specialize on fruit and seeds. Among the forest species endemic at high taxonomic levels, only five fit that category and two (*Monia benschi* and *Mesitornis variegata*) apparently regularly consume seeds. The others, like *Mesitornis unicolor*, some members of the genus *Coua*, *Leptopterus chabert,* and *Cyanolanius madagascarinus* don't seem to ingest seeds except occasionally. In most cases, seed digestion has not yet been clearly determined, whether the birds leave entire seeds that have passed through and are viable, or if they actually eat them, and consequently the role of seed specialists in the regeneration of the forest is not yet clear and merits more study.

Pollination

This is the process by which pollen is transported from the stamen (male organ) to the pistils (female organs) of the same species. Pollination is the mode of reproduction favored by plants. More than 70% to 90% of plants with seeds (angiosperms) are pollinated by species of vertebrates and arthropods. In agriculture, pollination is an essential production factor involved in diverse agricultural areas. Recent studies could calculate the pollination activity of insects at 153 billion euros in the world, or 9.5% of the total value of world food production.

The plants and their pollinators are inseparable: a source of food for the animal and an asset for reproduction for the plant. This beneficial mutualism which connects two organisms has led to the diversity of species seen in nature today. The number and variety of pollinators strongly influences the vegetation biodiversity vice versa. By their interaction with plants, birds play an important role in the regeneration of the forest by means of pollination. But on Madagascar, very few birds provide this role; among the endemic families and subfamilies, only two species are specialists for consuming nectar and occasionally insects. They are the members

of the genus *Neodrepanis* which are typically species of the humid evergreen forests. The long tube-like tongue tipped by a tuft of fine bristles forms a sort of brush, along with the long pointed and recurved beak, are perfectly adapted to draw sweet nectar from flowers with often colorful petals. Secondly, *Philepitta castanea* occasionally takes nectar from different species of *Bankerella* (family Loranthacaea). Note that this species also possesses a long tongue which on the end carries a small brush of narrow and stiff fibers. When birds like those in the genera *Philepitta* and *Neodrepanis* visit flowers to suck nectar with the aid of their tongues, at the same time they pick up pollen which collects on their tongue, beak, head and head feathers. Given that birds forage on one flower after the other, they eventually deposit on the female sexual organ of a flower from the same species over the course of their search for nectar, and therefore favor the reproduction of the plants they visit.

Morphological Adaptation

Given the remarkable diversity of the birds endemic to Madagascar at high taxonomic levels and their multiple adaptations, it is not surprising that certain unique morphological features have evolved in these animals. One of the most striking is the caruncles of the members of the Philepittinae, which have been the object of much study. Numerous organisms have the capacity to view the colors. For example, the dark blue color of the caruncle of *Neodrepanis* can be measured with a special apparatus and the structures observed reflect close to the range of the ultraviolet, which is invisible to the human eye but perceptible by some birds.

This was the first discovery of an ultraviolet skin color in a bird. This is probably very important in different types of communication between individuals. So, when we, humans, look at the caruncle of these animals, we don't see the color and the reflection in the same way that an individual of *Neodrepanis* would. When the caruncle of *Philepitta castanea* is examined closely, with the naked eye, a series of cone-shaped buds can be observed. At the microscopic level, these buds are organized in a series of fibers, precisely aligned, like the crystals in certain kinds of rocks, forming a fine microstructure. The differences in the arrangement of the structures give the diverse colors of the caruncle. The astonishing discovery and the description of the microstructures have important implications in the domain of fiber optics and telecommunication. This is an example which shows the importance of natural history and morphological studies for human society.

Ecological Adaptation

This is defined as being an adaptation, in the physiology or behavior of a living species, which allows the support of variation in one or more factors of an environment, while continuing to operate. The Malagasy birds are, on the part of their biological and ecological requirements, restricted to different environments. These environments present varied characteristics which lead to the ecological adaptation of species. This adaptation affects several aspects whose importance depends on the degree of their needs associated with the constraints of the environment in which the species evolved.

Feeding Adaptation

For feeding, the shape of the beak varies among birds as a function of the type of food and the type of microhabitat of their prey. The adaptation of this function resulted in a large range of shapes of beak. Within the members of the nonpasserines like the Mesitornithidae, Brachpteraciidae, and Couinae which have the habit of searching for their food on the surface of tree trunks, leaves, and the ground in the debris, the beak is strong, thick, and rather short with slightly pointed tip. For insectivorous species which essentially eat small prey and pick them off of leaves, tree trunks, and branches like the Bernieridae, their beak is straight, thin, and short; for those that eat large insects, their beak is strong and pointed.

The most extraordinary shapes can be found principally among the family Vangidae. Given that they have already been covered in several sections of this book to explain their exceptional adaptive radiation and the ecological niche, we recall as examples only some particular cases in the group. For the species that prune the barks of trees, destroying the rotten wood and overall dissecting fat insects like *Schetba rufa, Vanga curvirostris, Leptopterus chabert, Artamella viridis* and *Xenopirostris* spp, their beak is very robust and very pointed. For *Falculea palliata* which searches for its prey in the cracks and holes of trunks or under bark, it beak resembles a very long and laterally compressed sickle. Among the nectarivores of the subfamily Philepittinae (genus *Neodrepanis*) which are adapted to suck nectar from the depth of flowers, their beak is very long and recurved and even takes the shape of the spurs of the flowers. The tongue shape of gutters or long tubes have at the end a brush of very fine bristles, which permit the intake of nectar.

Ecological Niche

In a variable environment, like a forest ecosystem, the individuals in each species are in an incessant search for compromise, in a way that will optimize three principal needs: diet, reproduction, and protection from predators. The habitat resulting from the search that satisfies these needs, the habitat, and the functional role played by these individuals in this habitat determines an ecological niche. Generally, each species occupies a particular niche in a given biota, and sometimes over the course of different steps in their biological cycle, they occupy more than one biological niche. The change of niche during a specific period of their biological cycle probably corresponds with a critical phase in their development. Most often, the change coincides either with the depletion of the principal source of food, or with the need for another more secure location.

In nature, at times the niches of several species seem to be similar, such that we have the impression that several species share the same space. But closer observation allows discernment of the very narrow limit between the different ecological spaces of these habitats, but which are well organized in the way that the different species exploit resources differently in time and space. Each species of vanga or asity, for example, in the function of the shape of its beak, is adapted to a well-defined niche, and their corresponding feeding behavior was largely discussed in the section on speciation.

Distribution of species of birds within ecological niches

Following the nature of their feeding behavior, the place in which they search for food, and their breeding place, the species of Malagasy forest birds are distributed within 28 different ecological niches. The 54 members of the endemic families and subfamilies are distributed in 19 different niches. It is overall the species which are strictly insectivorous and arboreal in the medium levels of the forest that make up the dominant group in the Malagasy forest ecosystem. This niche overall encompasses the species which feed on different sorts of invertebrates like flying insects, larvae or caterpillars, and spiders. A large part is composed of Malagasy Warblers and some of them are vangas. The groups of insectivores and arboreal birds is followed by the terrestrial species which generally feed on insects but which occasionally consume seeds. The ecological niche of this latter group is distinguished from that of species having the same diet but with nesting which happens higher, in the trees, contrary to their daily life which passes principally on the ground level. Most of the mesites and couas make up this niche. *Coua cristata* feeds on a large variety of types of food (omnivorous), with its diet composed of insects, mollusks, small vertebrates (lizards and frogs) and even seeds.

Ecological Specificity

Depending on the tolerance of each species for the environment's ecological conditions, some can be adapted to a broad level of ecological factors. These are the species called generalists, such as *Calicalicus madagascariensis* and *Newtonia brunneicauda.* Others are more specialized or possess a preference for their vital needs not only matters of habitat but also for their ecology, making their ecological niche much more restrained. Such is the case between others of *Uratelornis chimaera,* of *Coua verreauxi*, and of *Xenopirostris damii*. These species with more detailed requirements are called specialists, and are therefore more vulnerable vis-à-vis the degradation of natural forest, and merit particular attention in a conservation program.

Specificity in terms of habitat

Each type of habitat contains ecological characteristics which are unique to it and which respond specifically to the needs of the species of animals that it accommodates. The ecological distribution of some species depends principally on the presence of these characteristics and also manifests on the vertical and horizontal planes.

On a mountaintop forest for example, *Geobiastes squaminger, Schetba rufa, Oriolia bernieri,* and *Hypositta corallirostris* are typically forest species of the humid evergreen forest at the base altitude up to 1200 m, and principally prefer habitats with large trees. *Geobiastes squaminger* is a secretive terrestrial species of the rather dense undergrowth, and it hunts at the ground level and rummages through thick litter to search for its prey; *S. rufa* hunts on trunks and branches and the in foliage of large trees; *O. bernieri* and *H. corallirostris* frequent the high level of the forest and inspect the large trunks of trees in the quest for food. On the other hand, *Xanthomixis tenebrosus* is also a specialist of this altitudinal slice but the species prefers the

shadowy and thick undergrowth where the temperature is apparently cooler and the level of humidity elevated.

Neodrepanis coruscans is a specialist at the middle altitude between 1200 and 1400 m. The species can be found frequently in the relatively thick undergrowth of valleys and on the slopes populated by plants with bright flowers, and preferably those shaped like bells; *Atelornis crossleyi, N. hypoxantha, X. cinereiceps* and *Crossleyia xanthophrys* are specialists at high altitudes and are generally confined in mountainous forests over 1400 m of altitude. This habitat is characterized by the abundance of mosses and lichens, associated with the relatively elevated humidity due to the orographic phenomenon, smaller trees with relatively weak diameters, and and by a cooler temperature than that of inferior altitudes. *Atelornis crossleyi*, a terrestrial species, can be found in the undergrowth where the vegetation is not dense with a rather thick litter and a discontinuous herbaceous carpet, where it travels the ground in search of its prey; *N. hypoxantha* is specialized for the medium level, in rather thick undergrowth. Being a nectarivorous species, it visits flowers of shrubs, lianas, and epiphytic plants on trees. *Xanthomixis cinereiceps* also exploits the undergrowth with rather dense vegetation. *Crossleyia xanthophrys* is typically terrestrial, although sheltered in the undergrowth with a rather high and dense vegetation carpet. The animal travels over the herbaceous carpet to hunt prey while rummaging with its beak in the dead leaves accumulated on the ground.

Horizontally, one of the preponderant factors which varies both with latitude and longitude is the precipitation characterizing the quality and type of forest habitats. The progressive lowering of pluviosity following the north-south and east-west gradients increases the aridity and thereby modifies the biomass, together with the quality of feeding resources. The extremes of this cline are represented by the Peninsula of Masoala on one hand, with areas that receive about 7 m of rain annually, and areas in the extreme southwest on the other, where the medium rain level is less than 400 mm each year. Numerous species prefer habitats with abundant precipitation well distributed over the course of the year and with very elevated biomass. The forest habitats of these areas in the northerly half of the island are characterized, among other things, by an evergreen forest throughout the year with tall trees with large diameters, a continuous forest ceiling whose percentage of opening is a function of its degree of degradation, and a relatively elevated humidity. So as not to extend the example, only some cases are presented here. *Euryceros prevostii* and *Oriolia bernieri* are species that are overall restricted to this type of habitat in the northeast and central east of Madagascar. These forest species frequent the relatively intact forests with a rather closed canopy.

Concerning the other extreme cline, *Uratelornis chimaera, Monias benschi,* and *Xenopirostris xenopirostris* are uniquely well adapted to the spiny forest of the southwest where the ecological conditions are very seasonal and unfavorable. Their natural habitat receives scant precipitation throughout the year, with increased aridity and vegetation with biological adaptations for drought (dwarf trees, deciduous leaves or leaflessness, with leaves reduced or absent or transformed into spines, succulence, or "bottle trees[3]") such as species of *Didierea, Alluaudia* (family Didiereaceae) and *Euphorbia* (family Euphorbiaceae).

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[3] a French term referring to trees from various families such as *Brachychiton rupestris* which have bottle shaped trunks.

Specificity for breeding location

Several criteria determine the choice of a place to nest: survival, success of reproduction which includes features such as protection against bad weather and predation, and the abundance of food resources in the area. Some groups or species present a particular preference for a type of medium or support. To give this idea, among the available information on our current knowledge of the reproduction habitats of different species of endemic birds of Madagascar, the nests and young of several species have not yet been described or have only recently been described.

The mesites make their nest at the ground level or between branches close to the base of trees, and these birds erect a nest in the shape of a cup, roughly constructed and composed of fragments of bamboo or leaves of *Pandanus*, small intertwined branches, etc.

Geobiastes squaminger digs on a slope or on tilted ground in full forest to construct its nest whose opening is sometimes well camouflaged by vegetation. This type of underground nest is common for all the members of the Brachpteraciidae because they nest at the bottom of a burrow. Natural cases have been observed in which these birds share the nesting tunnel with other vertebrates like endemic rodents.

The nest of *Neodrepanis coruscans*, like those of the other species of asities, which differ in only some characteristics, is in the shape of a large upside down pear with a lateral opening, well protected by large leaves and foliage. This species along with the other members of the subfamily has preference for particular trees, on which they also construct their nests. By way of example, *Philepitta castanea* and *N. coruscans* use trees like *Tamourissa obovata* (family Monimiaceae). With *P. schlegeli*, a nest has been observed sheltered under long leaves of *Coptosperma* sp. (family Rubiaceae) in the forest of Beanka. This is also a nest in the shape of an upside down pear, hanging in the fork of branches situated at a height of 3-4 m above a calcium substrate or *tsingy*.

The members of the genus *Xanthomixis* construct their nest in the shape of a small cup, suspended between two small branches of a shrub, well camouflaged by leaves and mosses used like constitutive material at a height varying between 1.5 and 2.5 m above the ground. With *X. tenebrosus*, the nest is not yet described but the species probably has similar characteristics as those of the other members of the Bernieridae.

In the humid forests, *Bernieria madagascariensis* places its nest on the banks of a stream.

Among the vangas, *Schetba rufa* often constructs its nest at the level of a fork formed by three large branches about a dozen in diameter, situated between about 10 and 15 m above the ground, and the nest is well camouflaged between the branches. The nest is often constructed in a large tree, well sheltered from predators thanks to the resemblance of the color of the nest with that of the trunk on which it is found. From the location of the nest, the adults can survey surroundings. The nests of *Euryceros prevostii* have been found between 100 and 200 m of altitude. They are made with mosses and palm fibers which camouflage them perfectly between the fork of branches at around 8 m above the ground. These nests are often found in the fronds of *Cyathea* (family Cyatheaceae) and *Pandanus* (Pandanaceae).

Predation and protection strategy

Predation holds an important role in ecological function and, given that birds are part of the trophic chain, they constitute prey for diverse predators like raptors, snakes, the Carnivora, and other mammals. All the different stages of development from the egg to the adult stage can be easily attacked by predators and it is overall during the three first stages (egg, chick, and juvenile) that birds are the most vulnerable. Strategies like behavior and camouflage are adapted to avoid being prey for predators.

Behavior

Reactions in the face of danger are variable by species and circumstance. Often the bird flees by flying or taking refuge in a place where the predator can't follow. The fleeing behavior is often accompanied by an alarm call which is generally recognized by the other species found in the areas which either cause them to emit calls to make the predator flee or to take caution. This behavior is observed throughout the small passerines like the Bernieridae and some species of Vangidae. But in a good number of cases, the species are cautious, silently fleeing far from predators and hiding in refuges or places where they feel safe, which is the behavior of the majority of the members of the Mesitornithidae, the Couinae, and terrestrial passerines like *Crossleyia xanthophrys* and *Mystacornis crossleyi*. Unlike the latter species, species that are not very shy seem to be indifferent to the approach of a danger and they don't flee unless the predator is very close.

In most cases, colonies or groups react shyly and give strident cries all together to intimidate the intruder. The piercing calls of *Falculea palliata* are tangible examples. Other species of Vangidae like *Artamella viridis* or *Leptopterus chabert* chase and harass even large raptors like *Buteo brachypterus*.

Camouflage

Like other animals, camouflage, which is means of survival for some animals trying to escape predators in the environment where they live, is found also in a large number of species of birds. It is most frequent in the species which are not equipped with the ability to move instantly, specifically to fly rapidly, like species that live in the dense undergrowth and terrestrial species. Among the birds that live in the low levels, like most of the Bernieridae, the general coloration of plumage is a dull dark green imitating that of the foliage and mosses. For example, *Crossleyia xanthophrys*, a terrestrial species, is a dark olive green resembling the color of the grasses and mosses of the herbaceous carpet. The plumage of the members of the Mesitornithidae and terrestrial Couinae, and that of certain other passerines, taking the color of the branches and dead leaves, allows them to merge with the area that surrounds them. However, the system of camouflage is not clearly evident in certain birds, particularly among males of species which show sexual dimorphism, evolving in the higher levels of the forest and able to fly easily. Their well colored plumage distinguishes them remarkably from their environment. The azure blue of *Cyanolanius madagascarinus* or the bright red of *Schetba rufa* for example clearly

emerges in the foliage of the forest roof. Among other species, like the members of the genus *Philepitta*, the females have a plumage which forms a camouflage, but the males with bright color in their caruncles stand out and are probably visible to various predators, like diurnal birds of prey.

Social Adaptation

Aspects tied to reproduction

Birds show a large variety of social organizations, some are solitary, others live permanently as a pair (monogamous), and still others form colonies or groups with particular social systems. Several reasons determine the grouping of birds: proximity to breeding season, a particular abundance of their food, to conserve heat during winter nights and for better protection against predators. The knowledge in this area concerning Malagasy birds is very insufficient, given the complexity of the subject and the rarity of long-term studies.

Individuals of a generally solitary species tend to gather, between the same species or between different populations, at least temporarily. The couas are generally solitary but during the breeding season the reproducing adults form pairs. After nesting, this association is still maintained to form a familial group. In effect, the two parents together care for their young until the young couas are completely independent. In cases of pairs of *Coua caerulea, C. ruficeps, C. cristata,* and *C. reynaudii* feeding their young, teaching their young to fly, searching and inspecting the litter for prey, and singing have been observed many times. The ground-rollers of the family Brachypteraciidae are also often solitary, but the birds form a pair at the approach of the breeding season. For this taxon no information about their familial group or parental care is available.

Several species maintain social groups outside of the breeding season, at the level of which exist complex systems for which information at our disposal is still insufficient. One of the most extraordinary social systems in Madagascar is found in the Philepittinae, in particular *Philepitta castanea*. The males of this species possess a parade ground (lek) of about 20 to 30 m in diameter which is occupied by a lone male or by a group of five males or more, placed side by side. Unlike the territories defended by males of other species of birds which contain resources, like fruiting trees, the areas surrounding leks occupied by *P. castanea* don't contain an elevated concentration of resources. These leks are simply intended to attract females for mating. The males jealously defend these leks from intruders and put on elaborate parades expressed with visual methods and songs there. The same group of males occupies the same territory over the course of several breeding seasons, probably keeping the same position in the lek.

A hierarchy seems to be ingrained in the social organization of this species. A male with nuptial plumage of brilliant black and texture like soft velvet is beautiful, and with narrow elongated caruncles over the eyes, of a very bright beautiful blue-green, seems to be the dominant male. He is often surrounded by a certain number of females, up to four individuals, or males with female plumage. These latter are difficult to distinguish from females without careful observations. According to the available information, these males with female plumage are capable of producing sperm. Their plumage tricks the black males, which confuse them with

females, and they are therefore allowed to enter the lek, where they can mate on the sly with true females.

This species has an interesting and complex nuptial dance. The male perches over the lek, on horizontal tree branches or lianas about 1 to 5 m above the ground. The display is composed of six different phases which are carried out in this series: (1) erect posture, (2) flaring of wings, (3) horizontal position, (4) beak open, (5) acrobatics with beak open, and (6) perching with perilous hops. During the erect position, the male stands tall and slightly elongates his body, which is leaned forward, and erects the brilliantly colored caruncle to expose the light blue part over the eye. At the moment the body is in a vertical position, the male hops briefly upwards and forward, and does some maneuvers, then all of a sudden opens and closes the wings and spreads the remiges. This part of the display corresponds with the phase of wing flaring. When the wings are now open, the bright yellow feathers on the wing coverts show remarkable color. The next step corresponds with an elegant horizontal posture, with the neck slightly elongated, a gesture often associated with his reaction to the call of another male in his vicinity. The bird then beats the wings one or two times before leaving the perch. In the next step, during the phase of the open beak, the male perches with his beak open, neck shortened and tight to his body and gives a series of songs. In some cases, the male flies from one perch to another, several times, and calls incessantly. The following sequence is the acrobatics with beak open - which is optional if the male stays on the perch - he throws his body downward, with the tail in a vertical position, the wings tight against the body and the beak open. The last step is perching accompanied by perilous hops executed by two males, and which is similar to the acrobatics with beak open, but the males continue to make full turns 360 degrees around the perch, rather than simply holding the head low, and when they come back to a vertical position, they recommence the phase with beak open.

In this species, the male doesn't form a permanent pair with a female during the breeding season, except during the moment of mating. The nest construction, incubation, and parental care are entirely assumed by the female. But outside of the complex intraspecific social system, the individuals of this species also integrate in multispecies groups. Among the other members of the Philepittinae, like *P. schlegeli* and *Neodrepanis coruscans*, no information concerning lek system is known, but these birds are in pairs at least during the breeding season; the two partners participate actively in nest construction. The species *P. schlegeli* has been observed in a multispecies group in the dry deciduous forest.

The species of Mesitornithidae live each in a family group in which the members are from at least two successive generations. Little information is available on the social organization of the *Mesitornis* spp. *Mesitornis variegata* lives in almost exclusively familial territorial groups outside of the breeding season. The two species each live in small groups and are apparently monogamous.

Monias benschi is the best studied species because it has been followed for several seasons by Nathalie Seddon and her colleagues in the region of Ifaty. This species constitutes a detailed example that shows the importance of studies on the ground and in the laboratory for revealing remarkable information on the natural histories of some endemic birds of Madagascar. *Monias benschi* lives in a group, which can have up to 10 individuals, and is rarely solitary or in pairs, and the group shows evidence of much cohesion. The group is dominated by a female and

has more males in it than females, but the composition of the group can change from one year to another. In the case of danger, the birds flee rapidly, all the while keeping the cohesion of the group. During the night, they perch and sleep together on a low horizontal branch.

The group sings in a choir and the contribution of a given individual seems to be tied to its status within the group and its eventual sexual interest in certain members of neighboring groups. They have a very complex manner of vocalizing, which depends on the context of communication, such as for maintaining contact within thick vegetation or for defending territories. Actually, with the mesites, the male and female of the pair sing a sort of duet, and the question is the role of the song. Several ideas have been proposed by biologists studying evolution and behavior, such as: 1) the duet is a way to defend the territory, in this case, the strong signal emitted by the two members of the pair is sent as a strong message for signaling that the territory is occupied, or 2) the duet is a way of defending its partner, which supposes that the bird singing in response to its partner wants to prevent it desertion of the territory, and wants to fend off the tentative rivals that could potentially take control of a female or a territory. The research done on *M. benschi* indicates that it is the second hypothesis which best explains their behavior.

A cooperative polyandry makes up part of the social organization the group where a female is paired with several males over the course of the breeding season. Unlike most of the other endemic birds of Madagascar, the time of breeding does not follow a strict season like the rainy season. More than one female can lay in the same nest. The females and males take part in incubation over the course of the nesting period assume nocturnal brooding duties. The males in the group also participate in the feeding of young.

In different sections of this book, we have discussed the importance of molecular genetics for helping resolve the phylogenetic relations of different groups of birds, vis-à-vis their origin and their mode of speciation, since they colonized Madagascar. This type of study is equally very instructive for understanding the social behavior of birds. A lovely example is found with *M. benschi*. For this species, the males living within groups and having a large genetic diversity (more heterogenous) than the other members have also had a larger range of songs for defending their respective territory, and a larger territory. This implies that females don't make a random decision when choosing males, but they make specific choices, accepting those males with a more diverse repertoire. One study used molecular data to understand the mode of pairing in this species, whose reproduction is carried out by cooperative reproduction; the link between the young animals has also been examined. The results have shown that some groups contain monogamous pairs, that is to say a sole male for one female, while others have shown polygynandry, that is to say a male and female each having several sexual partners.

Some members of the Bernieridae are similarly gregarious. The individuals of each species live in a pair during the breeding season and in a social group formed by at least two successive generations during the periods after reproduction. These individuals remain together even during the night when they sleep side by side. The size of the group varies by species. Several examples can illustrate this case: three to 10 individuals in *Bernieria madagascariensis*, 4 to 20 individuals in *Xanthomixis zosterops*, 4 to 10 individuals in *X. apperti*, and three to 10 individuals in *Oxylabes madagascariensis*. These birds are encountered more frequently in mixed species groups.

The ornithologists have proposed different hypotheses to explain why the subadults of these birds which are "nest assistants" participate in the raising of their brothers and sisters, which is known as cooperative breeding:

1) Advantages exist for the assistants, for whom remaining at the nest perhaps is protection from predators, or also to acquire the know-how which they will need later when they get their turn to reproduce.

2) The clutches and young of the same parents are entirely the same family as the assistants, and they are genetically as close as their own young. Helping their parents becomes as productive as if the young were their own, and this is even more true with skilled parents. This notion is called "kin selection" in English.

3) Future advantages are seen by the assistants, they inherit the territory of their parents, this last explanation is particularly convincing if suitable territories are easy to miss.

The research in the field on the different species of generally gregarious vangas living in a well established social organization has been used for testing some of these hypotheses. Among *Schetba rufa*, the birds form a monogamous pair, even though a quarter to roughly half of pairs have helpers, which are generally young males born of the same parents which guard the territory and remain on the territory where they were born. The contribution of these males is very weak during the construction of the nest and incubation. After hatching, it is the parents who take care of their young, but the role of the assistants becomes more important during the second stage of development, over the course of which it is the older males who participate a lot in the feeding of young. All the same, nests with assistants have approximately the same success in production of young as those which don't have any. This research therefore supports hypotheses 1 and 3 above.

Falculea palliata are very gregarious and often live in troops of 10-15 individuals and sometimes up to 30 individuals composed of at least two generations. The parents feed their three or four young, long after they have left the nest. These birds together emit loud and plaintive calls repeated several times, which resemble the crying of a newborn. They reunite for the night, sleeping with up to 40 individuals or more. When *Falculea* sense danger, they gather in an aggressive manner and give strident calls to intimidate the predator. During mist netting, used in the dry forest of Tsimanampetsotsa National Park on the southwest of the island, an individual of this species was taken in a net and during the whole operation to free it, about thirty individuals were grouped all around with repetitive strident voices and dangerously menacing behavior.

Leptopterus chabert lives in the degraded forests of the east and west. The individuals live in a large group of about twenty individuals and sometimes up to 30. They prefer to perch high in large trees where they fly easily from branch to branch, in search of the insects on which they feed. During the night, they gather in large numbers to sleep in an isolated tree in a clearing. The recent research in the field on this species has shown that these birds follow a system of cooperative breeding, with three or four individuals which feed the chicks in the nest and even after they have left the nest, these assistants also protect them from predators. With other species of vangas studied in detail, like *Tylas* or *Calicalicus madagascariensis*, no evidence of cooperative breeding has been revealed.

Mixed-species flocks

As briefly mentioned in Part 1, some species of birds group together in flocks with several species (mixed-species). These birds search for their food and move in the same direction. They are normally insectivorous but they can hunt together without having apparent competition thanks to their specialization in diet and the behavior they use to search for prey. Each individual finds advantages there. Some rummage the mosses and humus on trunks and branches, others explore the foliage or barks and cracks, and still others wait for prey which are disturbed by the movements of the other members of the group from their perch. Moreover, this method of association is advantageous for each member of the flock and facilitates the search for food. In forested habitats for example, the insects which shelter in the foliage or on branches and trunks take flight rapidly when they are disturbed by the movements of birds therefore making available to the species capable of hunting in the air a non-negligible quantity of food. This type of association appears equally beneficial for everyone and offers better protection against predators, which are easily spotted by many individuals. Once an alarm call is given by any member of the group in a case of danger, all members of the group emit aggressive calls to make the predator flee.

During some seasons the birds are territorial but they temporarily leave their domain for the time of the flock. One band is generally directed by the vigilant group leaders, possessing loud calls and seeming to be composed of a permanent core and occasional or temporary members. The members of the core appear to gather in a given place, principally in the trees in a sunny clearing for mixed-species flocks of the canopy, where they warm up in the sun and are very active and loud before departing. The brouhaha of birds which is not interrupted during movements and hunts facilitates the cohesion of the group. The temporary progressively join the group over the course of movement through the forest. Moreover, there is a sort of separation within the group in regards to the position of each species, overall for birds which feed on the same type of food like insectivores.

Two types of flocks are observed in the Malagasy forest birds: the mixed-species flock of the canopy, which frequently searches for their prey in the crowns of trees, and that of the undergrowth, generally frequenting the lowest half of the vertical stratus. Most of the time each group is not exclusive to the canopy or undergrowth. The loud activities and calls produced by the birds during their movement incites certain individuals along the way to follow the flock even for a short way. Depending on the forest level occupied, and overall for species which frequent the medium level of the forest, they can at the same time make a part of one or the other flock type. It is not therefore surprising to see individuals of *Bernieria madagascariensis*, for example, either in the mixed-species flock of the undergrowth or in that of the canopy.

Mixed-species flocks of the canopy

The core of this group is generally formed by members of the family Vangidae and the "leader" seems to be often *Dicrurus forficatus*, *Calicalicus madagascariensis*, or *Artamella viridis*. In the first case, between the director and the members, there is probably a certain

mutualism. Once the small passerines find prey, *D. forficatus,* which watches everything that happens all around from its perch, rapidly flies and steals the prey of the small birds or it captures prey disturbed by the movements of the members of the group. This sort of competition seems to be tolerated by the others because for their part, the latter seem to benefit from the protection from predators potentially brought with this species. It is the vigilant leader who dares to confront and chase raptors despite its small size.

Moreover the elements of the core of the troop, there are also often other species within the flock like *Coracina cinerea, Terpsiphone mutata, Bernieria madagascariensis, Philepitta castanea*, and some are with a large number of individuals like *Neomixis* spp or *Zosterops maderaspatana.* Numerous cases have been observed which can be cited but we content ourselves with one found in the humid forest of the north to illustrate: pairs of *D. forficatus, P. castanea, C. cinerea, Oriolia bernieri,* and *Calicalicus madagascariensis*, four individuals of *A. viridis*, three individuals of *T. mutata*, *Cyanolanius madagascarinus* and *Pseudobias wardi*, a dozen *Z. maderaspatana* and at least thirty *Neomixis* spp. In total, more than 60 bird made up that group! Mixed-species flocks can also be found in dry deciduous forests.

Mixed-species flocks of the undergrowth

This is formed in a large part by species exploiting the lowest half of the vertical stratus of the forest and the core is overall made up by members of the family Bernieridae represented by *Bernieria madagascariensis, Xanthomixis zosterops, Oxylabes madagascariensis* and other species like *Dicrurus forficatus* which plays the role of "leader." But others also make a part of the temporary species like *Terpsiphone mutata*, *Philepitta castanea, Nesillas typica, Copsychus albospecularis, Hartertula flavoviridis,* and *Ploceus nelicourvi*. As with the mixed-species flocks of the canopy, the prominence of its size varies as a function of the number of individuals, the number of species, and the type of forest in which they evolved.

Sun-bathing

A certain number of species of birds directly expose their bodies to the rays of the sun, with feathers ruffled, and wings and tail spread. Under the bristling dorsal plumes, the black down absorbs solar energy. The duration of the sun bath varies from a few moments to about thirty minutes, depending on the intensity of the solar rays and whether the plumage is wet. It is generally followed by an intense phase of preening the feathers. It is presumed that this behavior gives birds a way to warm up their body, in particular in the coolness of the morning or after the rain. Other explanations have also been proposed, such as the elimination of ectoparasites, the maintenance of feather condition, and the soothing of discomfort caused by molt.

A number of Malagasy birds show this behavior. For example, various *Coua* spp take a sun bath on the trunks of fallen trees lying on the ground, on their perch or in trees. They back is turned to the sun, the feathers and wings and tail are well spread and slightly lowered and the dorsal black feathers are exposed to absorb the sun. These dark patches on the back likely play the role of a thermal receptor capable of capturing the heat provided by the sunlight.

Threats and the future of the endemic birds

Deforestation and impacts

In other times, Madagascar was described as a promised land by naturalists, but today it is considered among the countries most threatened in the world because of its pace of deforestation. Nevertheless this island holds an extreme richness and an exceptional diversity of largely endemic flora and fauna. The runaway developmental growth associated with socio-economic problems and politics of Madagascar does nothing but further worsen the current already precarious situation of natural heritage of the island. Its biodiversity, including endemic birds, has never in recent geological times known as large a change as today. Several factors are at the origin of the change, but only some major causes have engendered destruction of natural habitats on a grand scale and therefore have shaped the current avian community.

Given that the majority of Malagasy people are peasants whose survival depends essentially on agriculture and livestock (subsistence), each year, vast forested areas disappear because of the practice of slash-and-burn farming (*tavy*) mostly for rice and corn; not only in the eastern evergreen forests but also in the dry deciduous forests of the west. The lowlands are the most affected in the central and eastern parts of the island and currently, it is rare to encounter a forest at the base altitudes even in the system of protected areas. In the dry biome, the spiny forest of the southwest is also exploited. By this practice, only the most inaccessible areas are spared. In certain cases, even protected areas have been the object of destruction. Moreover, the repetitive brushfires for pastures or slash-and-burn farming or simply caused by voluntarily fires which each year ravage thousands of hectares of savannah and forest only further worsen the forest destruction.

The selective exploitation has also largely contributed to the deforestation and the loss of natural habitats for forest species. The woods are used for industry, construction, and overall for the need for charcoal and firewood for heating. On the 7,856,000 m^3 of timber exploited each year in all the forests of Madagascar, only 807,000 is destined for industrial use while the largest part serves for the production of charcoal. Although *Eucalyptus*, a tree which comes from Australia and is introduced to Madagascar, are used for wood needs, a large part of these products are directly extracted from the natural forest given that people have a particular preference for the forest wood as much for construction as for charcoal. From the beginning of the political crisis in Madagascar in 2009 to today, the massive exploitation of large-sized trees, principally those with precious wood like rosewoods, the pace, and the loss of biological diversity is without precedent in past decades. In 2009 precious wood from Madagascar represents at minimum 52,000 tons of precious wood felled, from 100,000 trees of rosewood and ebony of which more than 60,000 were situated in protected areas, which represents at minimum 4000 hectares of park and 10,000 hectares of non-classifying intact forest, made the object of selective cutting. More than 500,000 other trees and dozens of thousands of lianas have been cut to facilitate the transport of precious wood. Among the zones most exploited for precious wood are the National Parks of Masoala and Marojejy though these forests serve as preferred natural habitats for a number of typically forest species like *Euryceros prevostii* and *Oriola bernieri*.

Coming from diverse factors, a reduction of 33% in all types of primary vegetation has been arising since 1970. Between 1990 and 2000, the reduction in cover of humid evergreen forests increased to more than 6% and that of dry forests by more than 7% on average. In the western region, the reduction of the cover of spiny forests is estimated at more than 8.5%. Therefore, these different practices currently provoke an inestimable biological loss of natural habitats as much as biodiversity. For birds, six dependent forest forms are known as totally extinct (*Monias* sp, *Coua berthae*, *C. delalandei*, *C. primavea, C. cristata maxima* and *Brachypteracias langrandi*) and all the forest species have had a reduction in their area of distribution and a modification of the quality of their natural habitat.

Forest fragmentation also constitutes a threat for Malagasy avifauna and for biodiversity in general. This phenomenon combined with deforestation has brought about modified landscapes. The case of the central highlands where remnants of small forest fragments and *lavaka* are observed among the vast savannah regions demonstrates the impacts of this fragmentation. Information on the effects of this phenomenon on birds have shown that the number of species diminishes progressively and as a measure of the reduction of the fragmentation area and can cause local extirpation. It is the endemic dependent forest species which are the most vulnerable and it is the generalist species or those of open habitats like *Hypsipetes madagascariensis* and *Foudia madagascariensis* which invade the small forest islands.

In the case of the Special Reserve of Ambohitantely which is a very fragmented protected area, several species endemic at a high taxonomic level should normally be found in the forest but they are no longer represented in the reserve, including *Mesitornis unicolor*, *Atelornis crossleyi, Brachypteracias leptosomus* and *Neodrepanis hypoxantha*. Although these species are found in the forest of Anjozorobe, a relatively large block of forest on the central highlands to the east of Ambohitantely, which was still recently connected to the large eastern forest.

In summary, the current state of Malagasy avifauna and biodiversity in general is the result of various successive phenomena and anthropogenic threats have truly played a critical role.

The future

A large number of species from the endemic families and subfamilies are classified as "Near-threatened" and "Threatened". They represent more than 45% of the species given classification by IUCN and *Coua delalandi* is considered extinct. Also, numerous other species are already extinct like all the members of the family Aepyornithidae (estimated to be eight species) and other species.

Recently, initiatives to increase the amount of protected areas in Madagascar has increased the representativeness of species within the system of protected areas. For example, since 2006 with the creation of Mikea National Park where two endemic "Threatened" species, *Monias benschi* and *Uratelornis chimaera,* are found, these two species which are restricted in the area are found in the park.

Initiatives associated with efforts of different projects of conservation directed by non-governmental organizations, governmental institutions, and associations play in favor of the

conservation of Malagasy birds and biological diversity. But the non-enforcement of laws over the use of natural resources, the failure of the judicial system, the increasing deforestation, the annual brushfires and repetitive twists and socio-economic and political crises in Madagascar do not assure conservation in the long term for most species, especially those with restricted distributions. Faced by the dangers that surround the Malagasy biodiversity which makes up part of world natural heritage, we must make this the object of a major preoccupation because with their reduction, the entire world will lose one of the most unique biotas on the planet.