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1

Introduction to the cuckoos

The parasitic breeding behavior of cuckoos has fascinated people for centuries. The brood-parasitic cuckoos lay their eggs in the nests of other kinds of birds, and never rear their own young (Johnsgard 1997, Rothstein and Robinson 1998, Davies 2000). The natural history of the Common Cuckoo *Cuculus canorus* and the Great Spotted Cuckoo *Clamator glandarius*, the two species that live in Europe where they have been observed for many years, is well known. In Classic times, Aristotle studied the brood-parasitic behavior of Common Cuckoos (Friedmann 1964*b*, Aristotle 1991), and in Britain Shakespeare referred to cuckoos in his plays. The term “cuckoldry” was often used in the sense of an adulterous affair, and the implications of immorality in a later period led to a censored version of Shakespeare that eliminated the term “cuckold” (Bowdler 1861, Hamilton 1996). Many other species of brood-parasitic cuckoos live in Africa, Asia and Australia and in Central and South America where they have been watched by resident naturalists. Brood-parasitic cuckoos are diverse with 56 species in the Old World and three in the New World. Nevertheless, brood parasitism is only one of several breeding behaviors in this family of birds. A few cuckoos, the anis and the Guira Cuckoo of the New World, are sociable, with several pairs sharing a nest where they lay their eggs and care for the young; these are the cooperative breeders. Their cooperation is balanced by competition, as a female may remove the eggs of other females when she lays her own. In contrast to these birds which have gone to extremes of parental care and social behavior, most species of cuckoos live in solitary pairs and regularly build a nest and raise their own young.

Even these cuckoos occasionally lay their eggs in the nests of others, either a nest one of their own species or a nest of another kind of cuckoo. One cuckoo species is extinct, and eight cuckoo species are threatened or endangered at the global level. The distribution of cuckoos is cosmopolitan, and most species live in the Old World tropics. The variation in social behavior and parental care of cuckoos may be unmatched among the bird families of the world.

The cuckoos are the most successful brood-parasitic birds. They have the largest number of species, the largest number of host species that rear their young, and worldwide distribution. The cuckoos are one of the five families of birds in which brood parasitism is the only life style for one or more species—the others are two families of songbirds (the Old World finches and the New World cowbirds), the honeyguides, and the ducks. One duck is a dedicated brood parasite; indeed other waterfowl sometimes lay their eggs in the nests of other ducks of the same species or a different species. In each of these other families, an obligatory breeding style of brood parasitism has evolved only once (Sorenson and Payne 2001, 2002). Brood parasitism has originated more than once in cuckoos. Results of molecular analysis in this study indicate that the parasitic lineages of cuckoos are not all each others’ closest relatives. Because brood parasitism has evolved more than once, the cuckoos provide a replicate test of the behavioral context of the course of evolutionary changes when parental care was transformed into brood parasitism.

Young cuckoos are altricial. They remain in the nest where they depend on their parents or foster

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parents to provide food, and they grow rapidly. The young of nesting cuckoos leave the nest days before they are able to fly, while the young of brood-parasitic cuckoos take longer to fledge and are well-developed when they leave the nest. Nesting cuckoos in the New World have the shortest incubation periods and the shortest nestling periods of any birds. Even the Old World coucals have a short nestling life, unusual for such large birds. The variable period in which the cuckoos depend upon parental care is closely associated with the life style of nesting and brood parasitism.

The mating systems and social organization of cuckoos range from monogamous pairs that stay together in a social bond, to the cooperatively breeding anis and Guira Cuckoo where incubation and nestling care are shared by group members that use a single communal nest to rear their young. Among these birds there is genetic evidence of polygyny and polyandry as well as social monogamy.

Cuckoos have a long evolutionary history. Studies in molecular genetics have estimated that cuckoos occurred as a distinct lineage more than 60 million years ago, a lineage as ancient as that of any modern bird (Sibley and Ahlquist 1990). Fossil cuckoos have been known for only a part of this time. These fossil birds are as varied as modern cuckoos, and some appear to have been flightless. Cuckoos occur throughout the world on all habitable continents and on the island areas of southern Asia, and they are an important part of the biological diversity of tropical birds.

Much of what is known about cuckoos came from birds collected in the 1800s when they were first discovered by western Europeans. A few cuckoos were described by their collector and discoverer, Stamford Raffles (1781–1826), natural historian, ethnologist, Governor of Java and founder of the trading station that became Singapore (Raffles 1817, 1830). He began his work as a clerk in London and read widely, mastered languages, cultivated friends and gained a position in Penang. Based on his interests and his rewarding discussions with the Viceroy of India, he was able to study the area's history, culture and wildlife (Raffles 1830, Mearns and Mearns 1998). Raffles was unusual among early collectors for his access to the publishing world. Later collec-

tors visited the same areas and prepared specimens that made their way back to natural history museums, and in some regions resident naturalists were able to observe the details of their behavior and breeding biology. These collectors were employed by governments and private collectors, and most of their specimens were sent to natural history museums in Europe where the species were described and named (e.g. Blyth 1842, Gould 1845*b*, Cabanis and Heine 1863, Salvadori 1881, Shelley 1891). Linnaeus described more kinds of cuckoos than any other taxonomist, and half of the 22 species that he described are currently recognized as distinct kinds of birds (some others included a second sex), although the specimens from which they were described are no longer in existence. Tommaso Salvadori appears to hold the record for the number of new cuckoos described by a post-Linnaean ornithologist. Museum patrons employed bird collectors who visited Borneo, the Moluccas and New Guinea, and from specimens that made it safely back to Europe, Salvadori described 11 kinds of cuckoos which are now recognized as species and subspecies (Salvadori 1874, 1875, 1876, 1878*a,b*, 1879, 1881, 1889). He was based at the museum in Turin (Elter 1986, Violani *et al.* 1997), and his many type specimens in Turin, Genoa, Leiden and other museums rank him highest among his ornithological generation (Payne 1997*b*). He usually did not designate a single specimen as the holotype of a species, but rather syntypes of a type series, many of which went to other museums as "duplicates", with some still being discovered in these collections. Salvadori worked with other families of birds as well. He worked for two years at the National Museum in London where he wrote monographs on parrots and pigeons, and he lived in Leiden where many of his type series are located (van den Hoek Ostende *et al.* 1997). In other museums in Germany, Cabanis and Heine (1863) described nine cuckoos which are now recognized as species and subspecies, and they described several cuckoo genera as well.

A few species of cuckoos are known only from museum collections. The nests of several cuckoos have never been found, and the life histories of these and many other cuckoos are unknown. Many cuckoos live in the Old World tropics where few

observations of their life histories have been made in the forests, where these birds are hard to see as the nests are well hidden. Once a nest is found a predator is also likely to find it. Little collecting of anatomical and genetic materials for scientific research has been done in recent years, and the careful field studies that were the fieldmark of resident ornithologists have waned with changes in land ownership. Current research efforts have been limited by nationalistic zeal, and by the difficulty of productive research by unacclimated field biologists in the malarial tropics. The museum specimens that have been collected over the past two centuries are a valuable and unreplaceable resource and are our primary record of biological diversity. We continue to learn new details from these museum specimens, such as geographic variation and the plumages and molts of birds, and we can now retrieve genetic information from feathers or skins of these specimens. Field studies on behavior and recordings of the songs of cuckoos are much needed to understand these birds in natural conditions, and great opportunities remain to discover the life styles and the changing distribution of birds such as the cuckoos.

What are the cuckoos?

Cuckoos are zygodactyl birds with the inner and outer toes directed backward and the other two toes directed forward. The bill is usually slender and slightly arched. The plumage of most cuckoos is soft and lax. The body form varies among species with their systematic relationships, body size and life style. Most arboreal cuckoos have a slender body and long tail, whereas terrestrial cuckoos are heavy-bodied and have long tarsi for their size (weight). The nostrils are round in many cuckoos, but slit-like in the coucals, in the crested cuckoos *Clamator* and Thick-billed Cuckoo *Pachycoccyx audeberti*, and to a lesser extent in Long-tailed Cuckoo *Urodynamis taitensis*, Common Koel *Eudynamis scolopacea* and Dwarf Koel *Microdynamis parva*, and slit-like in some malkohas also. Many cuckoos have long eye-lashes. The bill has no cere; the tarsi are scutellate and often unfeathered. The base of the tail has a naked and bilobed oil gland.

Cuckoos have a wing with 10 primaries and 9 to 13 secondaries (9 in several malkohas, in the large Caribbean species of *Coccyzus* ("*Hyetornis*" and "*Saurothera*"), and in some squirrel cuckoos *Piaya*; 9 or 10 in *Cuculus* cuckoos; 10 in hawk-cuckoos *Hierococcyx*, Thick-billed Cuckoo *Pachycoccyx*, African Crested Cuckoo *Clamator leuallantii* and in some coucals; 11 in koels *Microdynamis* and *Eudynamis*, in some couas and coucals and in the Great Spotted Cuckoo *Clamator glandarius*); 12 in some other coucals, and 12 or 13 in the Channel-billed Cuckoo *Scythrops novaehollandiae* (Stephan 2001a). The alula is small in most cuckoos but large in the New World ground-cuckoos *Neomorphus* and *Carpococcyx*, and in the brood-parasitic American Striped Cuckoo *Tapera naevia*. In the last two cuckoos the large alulae are extended when the wings are spread in display. The wing is eutaxic. The pattern of wing molt is peculiar to cuckoos, where a wave of molt jumps over the neighboring old feathers. The odd-numbered primaries first drop and grow, followed by the even-numbered primaries. Cuckoos are capable of flight, varying from the swift and direct flight of the long-winged, long-distance migrant Common Cuckoo *Cuculus canorus* and Black-billed Cuckoo *Coccyzus erythrophthalmus* of northern temperate regions, to the gliding flight of short-winged tropical forest-living malkohas and the slow awkward flight of anis, couas and coucals.

The tail usually has 10 rectrices, though only 8 in anis *Crotophaga* and Guira Cuckoo *Guira guira*. The tail of some cuckoos is shorter than the wing, particularly that of the glossy cuckoos *Chrysococcyx*. The tail of other cuckoos is one and a half times the length of the wing, as in the arboreal squirrel cuckoos *Piaya cayana* and *P. melanogaster*, the yellowbills *Ceuthmochares* and several Asian malkohas, and the terrestrial ground-cuckoos *Geococcyx* and *Neomorphus* (Stephan 2001b). In North and Central America where all cuckoos have long tails, the area of the tail is larger in cuckoos than in any other family of bird of comparable body size (Hartman 1961). In many cuckoos the tail is strongly graduated, with the central feathers longest and the outer feathers short, and the steps marked by the conspicuous white tips of the tail feathers. In others the tail is rounded, square, or even forked, with the central

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feathers shorter than the outer feathers, especially in the Fork-tailed Drongo-cuckoo *Surniculus dicruoides* and Moluccan Drongo-cuckoo *S. musschenbroeki*.

Cuckoos span a wide range in body size, with most species 16–70 cm in overall length. They vary in mass from 17 g with the smallest, Little Bronze-cuckoo of Australasia, to 400 g with Giant Coua *Coua gigas* of Madagascar, and 700 g with the largest brood-parasitic bird, Channel-billed Cuckoo *Scythrops novaehollandiae* of Australia (the next largest brood parasite is Black-headed Duck *Heteronetta atricapilla* at 513–565 g, Carboneras 1992). The largest nesting cuckoos are coucals in the New Guinea region, where Greater Black Coucal *Centropus menbeki* and Violaceous Coucal *C. violaceus* are more than 500 g, Goliath Coucal *C. goliath* are over 600 g, and Buff-headed Coucal *C. milo* are as large as 770 g.

The major groups of cuckoos

The major groups of cuckoos include two groups with a common ancestry in the New World, two groups in the Old World, and one group that occurs in both regions. In the past, some of these groups have been called families, and others have only recently been recognized as lineages with a common evolutionary history, especially the Cuculinae, which include both New World and Old World cuckoos, and both nesting species and brood-parasitic species.

1. *Crotophaginae* The crotophagines are group-living cuckoos and all cuckoos with this life style live in the New World. They have robust legs and a long tail, streaked brown plumage in the South American Guira Cuckoo *Guira guira* and black plumage and a deep compressed bill in the three ani species *Crotophaga*. Living in aggressive and noisy social groups, several pairs defend a common territory and share a joint communal nest where two or more females lay their eggs (in anis, some nests may be of single females) and the adults all rear their common young together as cooperative breeders. The nest is flat or a shallow bowl, built in a tree. The nestling mouth is pink with white marks on the palate and tongue. Anis often have a pungent odor, noticed when birds are held in the hand or when they are at their night roost. The social or adaptive

significance of the smell is unknown. The crotophagines have large and unique anal glands, but whether these produce chemical deterrents to predators or chemical signals to social partners or are accessory reproductive structures is unknown (Quay 1967). The ridge on the bill is shaped by an underlying ridge in the nasomaxillary skeleton, especially in Greater Ani *Crotophaga major*. Awkward in movements with the wings and tail seemingly disconnected from the body, anis are unlike the graceful arboreal cuculine cuckoos. Anis are slow and clumsy as they flutter and clamber through low bushes and weeds, where their flopping wings and waving tails flush out insects in dense vegetation; Guira Cuckoos fly like kites in the wind.

2. *Neomorphinae* Ground-cuckoos of the New World have short wings, long legs and a long tail. They include a dry scrub-forest terrestrial cuckoo of Central America (Lesser Ground-cuckoo *Morococcyx erythropygus*), lizard-catching roadrunners (*Geococcyx*) of the semi-arid regions of North America, and large South American ground-cuckoos *Neomorphus* that follow ant swarms in the tropical forests and eat the insects that escape the marauding ants. Roadrunners run across the ground at speeds of up to 30 km/hr in chase of their lizard and grasshopper prey, the birds holding their heads and tails level with the ground and swinging their tails like rudders. They often course along roads, paths and dry stream beds, and walk and run on their daily rounds for food and to patrol their territories. These ground-cuckoos can fly, though when they survey their area from an elevated perch they stay within a hop and a flap of the ground. The nesting ground-cuckoos build a nest and rear their own young nestlings which have conspicuous colored spots inside their mouths. The ground-cuckoos also include three species that are brood-parasitic (two species of *Dromococcyx*, both shy and secretive, and the American Striped Cuckoo *Tapera naevia*), and are forest dwellers. They parasitize several species of passerine hosts that breed in covered or domed nests, and occasional other hosts that breed in open nests.

3. *Centropodinae* Coucals are large ground-foraging birds with long stout feet, a long straight

claw on the inner hind toe in most species (the claw is the “foot spur” of the genus *Centropus*), short rounded wings and a long broad tail. The plumage is black, rufous brown, or white, or a combination of these colors; the plumage is shaggy and in many species the neck and breast have spiny hackles. Coucals live in the Old World, mainly in the tropics from Africa and Asia to Australia, New Guinea and the Solomon Islands, and on many islands in Wallacea and the Papuan region. Coucals live in forest, swamp and marsh habitat, and spend most of their time on the ground, and in dense marshes they are most often seen in their slow and awkward flight. Most coucals build large globular or domed nests of grass and leaves with a side entrance. Most make deep resonant cooing calls, some species in a “water-bubbling” pattern which recalls the gurgling sound of water as it rushes from a narrow-necked bottle, and some species call in duets. Nestling coucals have an odd set of stiff natal down (trichoptiles) and as the body feathers grow these hair-like structures are attached to the tips of growing feathers, then fall off when the birds fledge; and they have conspicuous raised colored spots on the palate. Adult coucals have a pheasant-like body form with long, robust legs and a long tail, coarse plumage with stiff hackles, and a bronchial syrinx. Males of some coucals have a single testis while others have two testes; the number can vary between one and two within a species and a local population (Mayr 1937, Mayr and Rand 1937, Rand 1942a).

4. *Couinae* These are large colorful ground-cuckoos of Madagascar and southeast Asia and have long tarsi. Ground-cuckoos *Carpococcyx* of tropical forests in Asia have plumages of dove-like greens and blues, bright bare skin around the face and long eye lashes, and they build flat platform nests. Couas *Coua* are large cuckoos in Madagascar. They have soft and lax plumage with dove-like colors of pastel pinks, purples and peach (blue in the Blue Coua *Coua caerulea*), a long tail and large feet, colorful bare areas of skin around the eye, and long eye-lashes. Most are terrestrial. The arboreal Blue Coua has long legs like the terrestrial couas and like them it walks, but in the trees. The Red-capped Coua *Coua ruficeps* is mainly terrestrial and walks on the ground,

and along branches when it is in a tree (Berger 1960). One species of coua, a snail-eating specialist on Ile Sainte Marie northeast of Madagascar, was last seen around 1835. This is the only cuckoo species known to have become extinct in the past two centuries. Nestling couas and Asian ground-cuckoos lack natal down, and the palate and tongue have conspicuous patterns of raised white or blue spots that contrast with the red mouth lining and may be a signal to their parents during parental care.

5. *Cuculinae* These include the long-tailed arboreal nesting cuckoos of the Old World and New World. The Old World nesting birds in this group are known as the malkohas and are now grouped into six genera in Asia: *Rhinorhina*, *Taccocua*, *Zanclostomus*, *Phaenicophaeus*, *Dasylophus* and *Rhamphococcyx*, and a seventh, *Ceuthmochares*, is found in Africa. “Malkoha” is a Sinhalese name in Sri Lanka (Ceylon) for the Red-faced Malkoha *Phaenicophaeus pyrrhocephalus*. It has been widely used for other species in the Oriental Region (Levaillant 1806, Raffles 1822, Jerdon 1862) and as a generic name *Malkoha* Schinz 1821. Malkohas have strong, unfeathered tarsi, short rounded wings, and long graduated tails tipped with bold spots and bars. Malkohas are skulking arboreal cuckoos of forests and thickets. Many have brightly colored bare skin around the eye and face, and the bill is large, often arched and brightly colored. The German term for the birds, “Buntschnabelkuckucken,” translates as the descriptive “colorful-billed cuckoos.” The wing feathers often have wide vanes and the body feathers have stiff, shiny shafts in a color that contrasts with the rest of the feather. Malkohas build shallow nests, lay chalky white eggs and rear their own young. The malkohas are brightly-colored in plumage, with swollen and brightly colored bills, short wings and long tails. All are arboreal except for Sirkeer Malkoha *Taccocua leschenaultii* which is terrestrial. A cultural awareness of cuckoos as brood parasites in Europe caused some ornithologists to guess that the other cuckoos were also brood parasites, and Newton (1896) suggested that malkohas were brood-parasitic, but field ornithologists in India and the Malay Peninsula, Borneo and Sulawesi had by that time observed adult malkohas at their own nests. Little is known

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about the details of nesting such as the incubation period, nestling period and parental behavior in these birds. The brood-parasitic Old World crested cuckoos *Clamator* appear to be closely related to the malkohas.

Several cuckoos of the New World are the ecological counterparts of malkohas and are closely related to them. Most are arboreal insect-eaters and have long tails. The coccyzine cuckoos including *Coccyzus* have long wings, and several species are long-distance migrants between continental North and South America, or between temperate South America where they breed and tropical South America where they winter. Others are large-bodied cuckoos that live on islands in the Caribbean and feed on lizards. The New World cuckoos build saucer-shaped nests, lay white or blue eggs, and rear their own young. The young have raised papillae inside the mouth; the color of the papillae contrasts with the palate.

Cuculines also include the brood-parasitic cuckoos of the Old World, the tribe Cuculini. Many are migratory with long, narrow, pointed wings, long tails, and short legs with the tarsus feathered at the base. The tail is often graduated with the central feathers longer than the others. As noted by Aristotle, Common Cuckoos *Cuculus canorus* look like hawks (notably Merlin *Falco*

columbarius) in plumage, shape and flight; and now we know the hawk-cuckoos *Hierococcyx* have rounded wings like bird-hawks (*Accipiter*). Most brood-parasitic cuckoos are dull in plumage, and their cryptic appearance may help them to avoid detection by their hosts (Payne 1967). The parasitic glossy cuckoos *Chrysococcyx* of Africa and Australasia, however, are conspicuous in their colorful plumage. They are small and at first glance could pass for insect-eating songbirds, and sometimes they even feed in mixed-species flocks with songbirds. Old World brood-parasitic cuckoos lay their eggs in the nests of many passerine host species. Their eggs vary from blue and green to chocolate brown to white, spotted or unspotted, and some species of Old World brood-parasitic cuckoos have more than one kind of egg marked by different colors and patterns. The nestlings are naked when they hatch (young Shining Bronze-cuckoos *Chrysococcyx lucidus* and Little Bronze-cuckoos have sparse natal down). Inside the mouth the young lacks visual effects except for a healthy color of red, orange or yellow. The young of one brood-parasite, African Thick-billed Cuckoo, however, have a bright orange palate with contrasting pale spots, and nestling Rufous Hawk-cuckoo *Heirococcyx hyperythrus* have a palate of yellow and pink.