Cuckoos, Cowbirds and Other Cheats

N. B. DAVIES

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For Jan, Hannah and Alice

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I dedicate this book to my wife Jan, and to my daughters, Hannah and Alice.

Nicholas Davies
Cambridge, June 1999

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CHAPTER 1

A monstrous outrage on maternal affection

We begin on Wicken Fen, just north of Cambridge in the east of England. It is early June, and the city throngs with students celebrating the end of the University year and with the first crowds of summer tourists. But out in the fens, there is a different world – a vast, flat landscape where the horizon is bounded by waving reeds and where nature provides other summer visitors, with dramas more extraordinary than any dreamt by human kind.

It is late afternoon, and we sit quietly on the bank of a dyke to witness a miracle of evolution. Hidden deep in the reeds and woven around three newly sprouting stems, just one metre above the water surface, is the nest of a Reed Warbler. It is a deep cup, built entirely from the old, pale yellow stems and seed heads of last year's reeds. The female laid her final egg this morning, an hour after dawn, and now she sits on a clutch of four. The eggs are pale green in colour, speckled with olive, grey and darker green, and they fit snugly into the nest as the reeds sway in the wind. The incubating bird seems nervous. Though she may briefly close her eyes and settle deep into the nest cup, the slightest sound alerts her. She peers over the edge when a Pike splashes in the water below or as a Moorhen swims past, and every few minutes she stands to poke into the nest or to turn the eggs with her bill. The male begins to sing his jaunty, scratchy song on the other side of the dyke and the female slips quietly away to join him, flitting between the reeds and catching a damselfly from the water surface as she leaves.

All seems quiet, until a faint rustle of a branch in the hawthorn tree behind leads us to turn and catch a glimpse of a large grey bird gliding straight towards the nest. She lands on the rim and bows into the cup. A few seconds later she lifts her head and, carefully holding one of the warbler's eggs in her bill, she moves forward to sit on the nest. We can see her yellow eye and pale underparts, barred with grey like a hawk (**Plate 1a**). Her abdomen moves down slightly as she lays her own egg. Then, without even a single glance into the nest, she flies off, still carrying the warbler's egg in her bill. She lands in the bushes some 30 m away, swallows the egg whole, and then utters a strange, liquid bubbling cry as if in triumph. She is immediately answered in the distance by the more familiar two-note call of a male, a loud ringing 'cuck-oo', and then she flies off, low between the bushes, with rapid shallow beats of her pointed wings.

The Cuckoo's visit to the Reed Warbler's nest lasted no more than 10 seconds. It is hard to believe she could have laid in such a short time. But we wade out to the nest and, sure enough, she has succeeded. There is still a clutch of four, but now one egg is a little larger, more rounded and glossy than the others, though it is an impressive match of the warbler's eggs both in ground colour and spotting (**Plate 1b**).

We retreat to our sitting place on the bank. A minute later the female Reed Warbler returns. She peers briefly into the nest. All appears to be well. She shuffles down to resume incubation. We watch a Marsh Harrier sail overhead, and the Reed Warbler also tilts her head to watch it pass. Fifteen minutes later her mate arrives with a large yellow and black hoverfly in his bill. He passes it gently to her and she then leaves. The male looks at the clutch, pecks briefly at the bottom of the nest, and then he settles down on the eggs to keep them warm while the female feeds nearby.

Eleven days pass. The reeds have grown and the nest is now well concealed among the new green leaves. In the early morning we wade out into the dyke once more. There are still three warbler eggs, but the cuckoo egg has just hatched. There, among the fragments of its empty egg shell, lies the cuckoo chick, naked, pink and blind. We retreat to continue our vigil. The female warbler arrives, picks up the broken shells and flies off. A few seconds later she is back on the nest.

Later that day we return to observe one of the most extraordinary events in the natural world. The cuckoo chick is just a few hours old but it has become more active and wriggles about in the bottom of the nest. It has an unusually broad back, with a shallow depression, and when, by chance, one of the warbler's eggs touches this spot, it springs into action. Balancing the egg in the hollow of its back, it braces its legs against the sides of the nest. With its head held down, it slowly works the egg up to the nest rim, its wings outspread to help keep the egg in place (**Plate 1c**). The cuckoo weighs 3 g and the warbler's egg is just under 1 g, so the task is not easy. Short bouts of effort alternate with spells of rest, where the cuckoo holds its position, braced against the side. Eventually the cuckoo backs the egg up to the edge of the nest. Clasping the rim with its wing tips, it gives a final push and jerks its load over the top. The egg plops into the water below and the cuckoo collapses back into the bottom of the nest, panting from exhaustion. The whole exercise took four minutes. And there are still two eggs to go.

The Reed Warblers return to their reduced clutch and continue to take turns on the nest. An hour later, the second ejection begins while one of the parents is brooding. It shuffles and tries to keep its position while beneath it the cuckoo chick climbs up the nest. Eventually the warbler is pushed right off. It stands aside to watch and does nothing to interfere as its egg is heaved overboard. The last egg meets the same fate, but this time the cuckoo needs three attempts to accomplish its task because the egg keeps rolling back into the nest cup. But by dusk, the work is done and the cuckoo has become the sole occupant of the nest.

Apparently oblivious to the destruction of their own chances of reproduction, the pair of warblers then slave away to feed the imposter. By 10 days of age it completely fills the nest but the warblers continue to bring food from dawn to dusk, even as the chick grows to eight times their own body weight (**Plate 2a**). By the time the cuckoo fledges, at 20 days of age, the nest has disappeared beneath it and has become flattened into a precarious platform. The cuckoo then leaves the reeds and flies to

the bushes nearby, where it is fed for a further two weeks until it becomes independent. During the final stages, the warblers sometimes have to perch on the cuckoo's back in order to feed it and they seem to risk being devoured themselves as they bow deep into the enormous gape with food (**Plate 2b**).

A BLIGHT ON CREATION

Naturalists have marvelled at these interactions between the Common Cuckoo *Cuculus canorus* and its hosts at least since the time of Aristotle (384–322 BC), writing some 2,300 years ago:

> it lays its eggs in the nest of smaller birds after devouring these birds' eggs.[1]
>
> they ... do not sit, nor hatch, nor bring up their young, but when the young bird is born it casts out of the nest those with whom it has so far lived.[2]

A few years earlier, the playwright Aristophanes (414 BC) used the name 'Nephelococcygia', which means cloud cuckoo land, for his imaginary city with a community free from all cares and duties, which suggests that he also knew about the cuckoo's parasitic habits.

In England, too, the cuckoo makes frequent appearances in the oldest writings. This bird riddle, translated from Old English, appears in *The Exeter Book*, a manuscript dating from AD 950–1000, and surely refers to the cuckoo being raised by foster parents:[3]

> In these days my father and mother gave me up as dead; nor was there a spirit for me as yet, a life within. Then a certain very faithful kinswoman began to cover me with garments, kept me and protected me, wrapped me in a sheltering robe as honourably as her own children, until I, under the garment, as my fate was, grew up, an unrelated stranger. The gracious kinswoman fed me afterwards until I became adult, could set out further on my travels.

The young Cuckoo is often quoted as a symbol of greed. In Chaucer's poem, *The Parlement of Foules* (*c.* 1382), the Merlin chastises the Cuckoo (line 612):

> Thow rewtheless glotoun!

In another fourteenth-century poem, *The Boke of Cupide* by Sir John Clanvowe (heavily reliant on Chaucer), the Cuckoo's lack of parental care comes to represent a life with no love at all. An opposition is set up between the Cuckoo and the Nightingale. The Cuckoo says love is nonsense and only brings unhappiness. The Nightingale argues that love is mainspring of 'al goodnesse, al honour and al gentilnesse ... perfyt joy'. The birds decide to have a 'parlement', with an eagle in charge, so that a judgement will be given on the debate. The event will be on Valentine's Day, 'Before the chambre wyndow of the quene'. The reader is left to imagine the result, but there is little doubt that the Cuckoo will become an outcast.

The adult Cuckoo's habit of abandoning all care of its eggs and young to other, host, species has also inspired country superstitions. In the southwest of England, in the county of Somerset, young children were told to run their fastest if they ever heard a Cuckoo, so as to ward off any infections of laziness.

The Cuckoo's cheating of its hosts might be supposed to have given rise to the word cuckold, a husband cheated in love by an unfaithful wife. However, 'cuckold' may have a separate derivation and no original association with the bird. Nevertheless, frequent links are made between the two in English literature. Shakespeare often plays on the word cuckoo when alluding to adultery. In *Love's Labours Lost*, for example, there is the song:

> When daisies pied and violets blue
> And lady-smocks, all silver white,
> And cuckoo-buds of yellow hue
> Do paint the meadows with delight,
> The cuckoo then on every tree
> Mocks married men, for thus sings he
> Cuckoo!

One of the most crazy of all cuckoo theories was inspired by a direct link between the two words. Acworth (1946) suggested that the host male really is a cuckold because the Cuckoo chick is in fact a hybrid offspring of the male Cuckoo and the female host species! Equally strange were the ideas of the Russian biologist Lysenko who, in the late 1940s, formulated a new theory of species formation. He suggested that many species of plants and animals could transform spontaneously into other, quite different species. As an example, he asserted that warblers could give birth to cuckoos.[4] These are mad ideas, of course, and easily refuted by our visit to the fens where we observed the female Cuckoo lay in the host nest. Nevertheless, perhaps we should reserve some sympathy for even the wildest of theories because the behaviour of the Cuckoo is indeed both abhorrent to the layperson and a puzzle to the professional biologist.

Why does the Cuckoo readily abandon its eggs and offspring to the care of others? We are so familiar with our own strong parental urges and with our observations of birds defending their nests and feeding their young that we may suppose that these instincts should be part of the normal behaviour of all species whose offspring require nurture and protection. The Cuckoo's behaviour seems both cruel and unnatural. It is not surprising, therefore, that early writers sought for explanations based on abnormalities in cuckoo design. A common view was that the Cuckoo had defective parental instincts and so its parasitic habits were bestowed by a benevolent Creator. In *The Fowles of Heauen* (1614), Edward Topsell admired 'that naturall discretion with which the Grand Creator hath bestowed upon this siely fowle for the propagation of her oune kinde ... it understandeth her oune frigiditie, or coldnes of nature, utterly disablinge it to hatche her oune kinde. Nature beinge defective in one part is wont to supply by another ... want of streingth is recompenced with witt ... the worke of God is wonderfull, and his mercy to his Creature magnificent.'

Others thought that the Cuckoo's defect laid not so much in its parental

behaviour but rather in its anatomy. In 1752 the French anatomist Herissant proposed that the Cuckoo's strange gut prevented it from incubation. He noted that its stomach was large and protruded low into the belly, and suggested that were the Cuckoo to sit on her eggs she would surely smash them.[5] In his *Natural History of Selborne* (1789), the British naturalist Gilbert White also regarded the Cuckoo's parasitic habits as unnatural and 'a monstrous outrage on maternal affection, one of the first great dictates of nature'. He dissected a Cuckoo and concurred with Herissant that 'the crop placed just upon the bowels must, especially when full, be in a very uneasy situation during the business of incubation'. However, he went on to show that other species, including the Nightjar, Swift and Hen Harrier, which do care for their own eggs and young, also had similar internal anatomy and concluded that 'Monsieur Herissant's conjecture, that cuckoos are incapable of incubation from the disposition of their intestines, seems to fall to the ground: and we are still at a loss for the cause of that strange and singular peculiarity in the instance of the cuculus canorus'.[5]

Edward Jenner (1788) agreed that 'the principal matter that has agitated the mind of the naturalist respecting the Cuckoo [is] why it should not build a nest, incubate its eggs and rear its own young'. He tested Herissant's idea directly by experiment. He placed two partly incubated eggs of the Pied Wagtail under a two-week-old Cuckoo nestling that was being raised in the nest of a Hedge Sparrow (= Dunnock). After a week, the wagtail eggs hatched so Jenner concluded that if the young Cuckoo was capable of incubating a clutch then surely the adult could do so too. Instead, he suggested that the reason the Cuckoo does not raise its own young is the fact that it spends such a short time on the breeding grounds. In the Cambridgeshire fens, for example, most Cuckoos lay their first eggs in early June and they depart for African winter quarters in the second week of July. This six-week breeding period would, Jenner argued, hardly be sufficient to enable the Cuckoo to look after its own eggs. The Cuckoo lays at two-day intervals, so even a modest clutch of three, for example, would take five days to complete. To this we need to add, say, a week to build a nest, 11 days' incubation, 20 days to feed the nestlings and another two weeks' care after fledging, a total of at least eight weeks for a single brood. Jenner's idea was that the Cuckoo's habit of laying at two-day intervals, coupled with its early migration, compelled it to be a parasite.

This is a fascinating argument, but it seems odd to today's naturalists who are familiar with the idea of evolution. Jenner's assumption that the Cuckoo is stuck with an immutable habit of early migration seems unlikely, given the variable migratory patterns within many species. Instead, it seems obvious that Jenner has got his argument back to front – the Cuckoo chooses to depart early precisely because it is a parasite and has no need to stay longer. In fact the adult Cuckoos' departure in the second week of July coincides with the time that the Reed Warblers cease to start new clutches and so marks the end of the season's opportunities for parasitism.

In 1824, John Blackwall was one of the first to appreciate that the various instincts of the Cuckoo, including the early migration of the adults and the ejection behaviour of the newly hatched nestling, made good sense in relation to its parasitic lifestyle and concluded that 'the history of the Cuckoo, by the evident marks of design which it displays in the admirable adoption of means to ends, affords a most

convincing proof of the existence of a Great First Cause, the mysterious source of all that is good and beautiful in nature'. But it was Charles Darwin who showed how such beautiful design could come about; far from being unnatural, the Cuckoo's parasitic habits could have evolved from a non-parasitic ancestor as adaptations to increase its own selfish reproductive output.

NATURAL SELECTION

Darwin's revolutionary idea in *The Origin of Species* (1859) was the theory of natural selection. The idea is so simple that, on first hearing it, Darwin's friend T.H. Huxley remarked 'How extremely stupid of me not to have thought of that myself!' But its far-reaching implications for how we expect animals to be designed are still keeping biologists busy today. There are five steps to the argument and we can illustrate them by considering the Reed Warbler, which we saw playing host to the Cuckoo on Wicken Fen.

- Individuals within a species differ in their morphology, physiology and behaviour (**variation**). For example, some Reed Warblers are slightly larger than others, or have more pointed wings, or darker plumage, or their eggs differ in ground colour or spotting patterns. There is also variation in their behaviour; for example, some are bold and exploratory when confronted with new situations or a predator near the nest while others are more nervous.
- Some of this variation is **heritable** so offspring will tend to be like their parents. As shown for other bird species, it is likely that many aspects of Reed Warbler morphology and behaviour are influenced by genes, including body size, egg colour, boldness, and so on.
- Organisms have a huge capacity for increase in numbers. A pair of Reed Warblers has time for two broods per year, each of four chicks. In captivity, small birds may live for 10 years or more. If, in the wild, the parents and all their offspring survived, then in the following year the population would have increased five-fold and after 10 years it would be several million times as large! Clearly this does not happen. Numbers do vary between years but in the long term, provided the habitat available does not change, many populations remain more or less steady in numbers. This means that in nature there must be heavy mortality. In the Reed Warbler, only half of the nests produce fledged young. The rest fail through predation, parasitism by Cuckoos and occasional destruction in heavy wind and rain. Thus each pair raises, on average, four young to the fledging stage. About half the adults die between breeding seasons, so if the population remains constant then three out of four young fledged per year must die before they have the chance to breed. Darwin concluded that there must be a struggle for existence with strong **competition** for scarce resources, such as food and places to live.
- Some of the mortality may occur simply through bad luck. A particularly ferocious storm may destroy all the Reed Warbler nests, for example. But sometimes mortality will vary depending on the characteristics of the individual and some variants will leave more surviving offspring than others. The offspring

will inherit the characteristics of their successful parents and so, by the inevitable process of **natural selection**, organisms will become **adapted** to their environment. The individuals that are selected by nature will be those with characteristics which best enable them to survive and reproduce.

- If the environment changes, then new variants may win the competitive struggle. So natural selection can give rise to **evolutionary change** between generations. Populations may gradually evolve different characteristics (behaviour or structure) over time. Darwin's argument was a verbal one but has now been modelled mathematically. For example, if there are two variants in a large population which differ by just 1% in their chance of surviving to breed, then this small difference will be sufficient to cause the more successful variant to increase from 1% of the population to 99% in under two thousand generations, a mere blink of an eye in the aeons of evolutionary time.[6]

Darwin assumed that evolution by natural selection would proceed so slowly that we would not be able to observe the changes ourselves. Indeed, *The Origin* does not document a single case of natural selection in action, and in a famous passage Darwin wrote, 'natural selection is daily and hourly scrutinising, throughout the world, the slightest variations; rejecting those that are bad, preserving and adding up all that are good . . . [but] we see nothing of these slow changes in progress, until the hand of time has marked the lapse of ages'.

However, there are now several examples of variants having such a strong selective advantage in nature that evolutionary change takes place even within a few years. Two recent studies of wild bird populations provide wonderful cases of evolution in action. The first comes from a study of the Medium Ground Finch on the island of Daphne Major in the Galapagos. Darwin spent just three weeks in the Galapagos, but Peter and Rosemary Grant and their co-workers from Princeton University have been there for the past 25 years, carefully measuring the beaks of the finches and the sizes of the seeds available. Some individuals in the Medium Ground Finch population have small beaks and they prefer small seeds, while others have larger beaks and prefer larger seeds. In 1977 there was a terrible drought, the plants withered and 85% of the finch population starved to death. Peter Boag and Peter Grant found that it was the small-beaked birds which suffered the greatest mortality because the small seeds became especially scarce. The larger-beaked individuals survived better because they were more efficient at dealing with the larger seeds. This differential mortality was a dramatic demonstration of Darwin's principle of natural selection. The result was a greater proportion of large-billed birds in the breeding population. Their offspring inherited their parents' large bills and so the average beak size of the population increased over the following generation. The magnitude of this evolutionary change, observable over just a few years, was exactly that predicted from detailed measurements of the feeding efficiency of different beak sizes and their heritability from parent to offspring.[7]

A second example comes from the remarkable studies of bird migration by Peter Berthold, from the Max-Planck Institute at Radolfzell, Germany. The Blackcap is a small warbler which breeds in Europe and migrates to Africa for the winter. Over the last 30 years or so, with warmer winters, there have been more and more records of Blackcaps spending the winter in Britain. At first it was assumed that these were

British breeders which had stayed on, instead of migrating. But ringing recoveries showed that the winter birds came from central Europe, and had adopted the new migration route of going northwest to Britain in the autumn instead of south to Africa. Berthold was able to study the migration direction of the Blackcaps in the laboratory, by keeping birds in cages where they could see the star patterns of the night sky, which they use as a means of navigation. During the migration period the birds fluttered against one side of the cage, indicating the direction they wanted to fly. He showed that migration direction is genetically controlled, with offspring from parents which migrate northwest inheriting the preference for the new migration direction.[8] This is a fascinating example of a recent evolutionary change in behaviour likely to have been favoured as a result of global warming.

DARWIN ON CUCKOOS

Darwin's theory of natural selection showed, for the first time, how adaptation and complex design could come about without a Creator. In chapter 8 of *The Origin of Species* he used his theory to explain the parasitic behaviour of the Common Cuckoo. His argument involved comparing its habits with those of the 'American cuckoo', which makes its own nest and rears its own young. It is not clear exactly to which species Darwin is referring here, but it was probably the two North American cuckoos in the genus *Coccyzus*, the Yellow-billed Cuckoo and the Black-billed Cuckoo, which are similar in size and appearance and have the same nesting habits. Although they are classified in a different genus to the parasitic Common Cuckoo, they are placed in the same family, the Cuculidae, and so are close relatives. Darwin learnt from his correspondents that the American cuckoos occasionally laid eggs in the nests of other species, which later studies have confirmed. He then suggested the following evolutionary sequence:

> Now let us suppose that the ancient progenitor of our European cuckoo had the habits of the American cuckoo, and that she occasionally laid an egg in another bird's nest. If the old bird profited by this occasional habit through being enabled to migrate earlier or through any other cause; or if the young were made more vigorous by advantage being taken of the mistaken instinct of another species than when reared by their own mother, encumbered as she could hardly fail to be by having eggs and young of different ages at the same time; then the old birds or the fostered young would gain an advantage. And analogy would lead us to believe, that the young thus reared would be apt to follow by inheritance the occasional and aberrant habit of their mother, and in their turn would be apt to lay their eggs in other birds' nests, and thus be more successful in rearing their young. By a continued process of this nature, I believe that the strange instinct of our cuckoo has been generated.

Darwin packs more good ideas into these four sentences than all previous commentators on the Cuckoo since Aristotle, so it is worth going over his argument more slowly. He raises three questions, and these form the basis for much of this book. First, he points out the positive advantages of parasitism. Not only is the adult

relieved of all parental duties, so it can migrate earlier and, we might add, has the potential to lay more eggs, the young may also gain a benefit. They are raised alone in the host nest and escape competition for food, so may gain better nurture than they would if reared in a brood by their own parents. Put this way, the worries of Jenner and his contemporaries 70 years earlier can be turned on their heads – why are there not lots of species of cuckoo in Britain, instead of just one, to take advantage of the work force offered by all the honest parental species?

Second, Darwin suggests that the host's acceptance of the cuckoo egg and chick is the working of a 'mistaken instinct'. The Reed Warblers are designed by selection to be efficient at raising their own offspring. They sometimes raise a Cuckoo simply because they are tricked into doing so. This interpretation seems so obvious now that it is difficult to appreciate the revolution brought about by Darwin's ideas. But consider the following explanation of the host's response to a cuckoo, offered by Bechstein in pre-Darwinian days.[9]

> It is wonderful to observe what great apparent delight the birds show when they see a female Cuckoo approach their abode. Instead of leaving their eggs, as they do when disturbed by the approach of other animals, they seem quite beside themselves for joy. The little Wren, for example, when brooding over its own eggs, immediately quits its nest on the approach of the Cuckoo, as though to make room to enable her to lay her egg more commodiously. Meanwhile she hops round her with such expressions of delight that her husband at length joins her, and both seem lavish in their thanks for the honour which the great bird confers upon them by selecting their nest for its own use.

Here, the hosts are assumed to behave for the good of all Creation and their alarm calls are mistaken for glee. But there is no room for such generosity in Darwin's world. Any hosts which preferred to raise cuckoos rather than their own young would, of course, fail to pass on their generous instincts to future generations. Their habits would soon be weeded out by natural selection. As Darwin himself wrote,[10] 'If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.'

However, all the evidence, from both theory and observations, points to a world full of organisms pursuing their own selfish interests. We don't have to look far to realize that hosts are not designed for the good of cuckoos. For example, the neat, domed nest of the Wren is a perfect fit for a brood of their own young, but the young Cuckoo becomes so enormous that it has to burst through the roof. Reed Warbler nests have a deep cup to keep their brood safe and snug as the reeds sway in the wind, but the young Cuckoo soon outgrows this home and the nest sometimes disintegrates beneath its bulk, with the result that it falls into the water below and drowns. Clearly, the Cuckoo has had to adapt its life as best it can given host adaptations that have evolved for the good of the hosts themselves. As we shall discover, this includes beating defences that hosts evolve to thwart the Cuckoo. The result is 'an evolutionary arms race' in which each party is selected to outwit the other.[11] One of the main aims of this book is to explore the consequences of this

battle. Why, for example, don't Reed Warblers evolve instincts that are not susceptible to the mistake of accepting a cuckoo chick?

The third suggestion made by Darwin is that the parasitic habits of the Common Cuckoo evolved gradually from a parental ancestor. In fact, we now know that only 40% of the world's cuckoo species are parasitic (57 out of the 140 species in the family Cuculidae), so the majority of cuckoos raise their own young. Darwin went on to discuss possible examples of the gradual perfection of parasitic instincts in birds, but field studies of bird behaviour were still in their infancy during Darwin's time and he had little information to support his conjectures. However, during the last 30 years, field workers have produced a wealth of new observations on the extent of brood parasitism in birds. Furthermore, new methods for studying the evolutionary relationships of bird species now offer the possibility of testing ideas for how parasitism may have evolved.

Our field trip to Wicken Fen to watch the Common Cuckoo and its Reed Warbler hosts has provoked some fascinating questions. Before we tackle them, however, we need to widen our scope and look at other species that are also brood parasites.

CHAPTER 2

One hundred brood parasites and some puzzles

According to the latest taxonomy, there are 9672 species of birds.[1] Of these, one hundred, or about one per cent, are obligate brood parasites. That is to say, they never raise their own young but, like the Common Cuckoo, rely entirely on other host species to do all the work of nest building, incubation and chick rearing. The hundred species and their hosts are listed in the Appendix. The parasites come from six families or subfamilies, which are likely to reflect six different evolutionary origins of the parasitic habit in birds (see chapter 15). The aim of this chapter is to provide a brief introduction to the six groups. We need to know who they are, and what they do before we consider the details of how they make their living from tricking other species. The map below shows how they are distributed around the world.

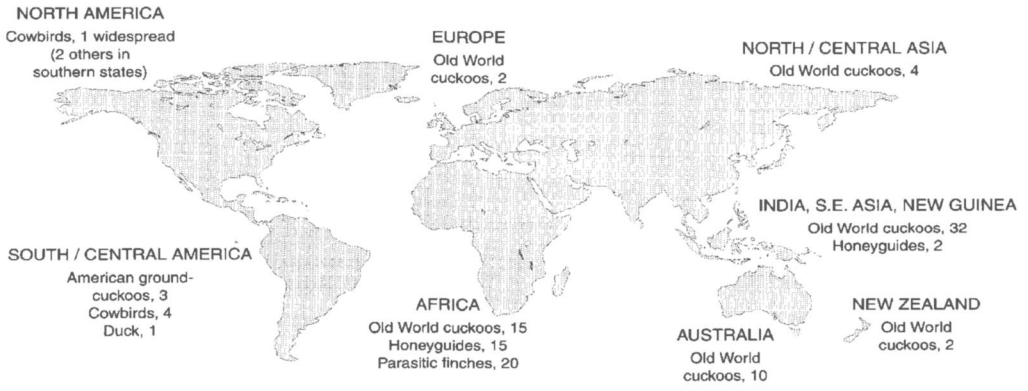


Figure 2.1 Distribution of parasitic birds around the world. The numbers indicate the number of species of each parasitic group in different regions. Some species occur in more than one region.

THE CUCKOOS

Traditional taxonomy, based on anatomy, suggests that the cuckoos are most closely related to the turacos and combines these two families in the order Cuculiformes. However, recent studies of similarities in DNA indicate that the cuckoos have no close living relatives, which suggests that they should, perhaps, be placed in an order of their own. There is also disagreement over classification within the cuckoos because information based on similarities in anatomy and DNA sometimes conflicts. Here, we follow the recent treatment by Robert Payne of the University of Michigan.[2] The cuckoos are placed in one family, Cuculidae, with six subfamilies, three in the Old World and three in the New World. The parasitic cuckoos are in bold.

- OLD WORLD CUCKOOS
  Cuculinae: Old World parasitic cuckoos (54 species)
  Phaenicophaeinae: malkohas (16 species)
  couas (10 species)
  Centropodinae: coucals (28 species)

- NEW WORLD CUCKOOS
  Coccyzinae: American cuckoos (18 species)
  Crotophaginae: anis and Guira Cuckoo (4 species)
  Neomorphinae: non-parasitic American ground-cuckoos (7 species)
  parasitic American ground-cuckoos (3 species)

The parasitic cuckoos occur in just two of the subfamilies. All 54 species of the Old World Cuculinae are parasitic, while three of the 10 species of the New World Neomorphinae are parasitic. All the other cuckoos are non-parasitic – they build nests and rear their own young, just like most other birds. According to this classification, the Old World and New World cuckoos evolved their parasitic habits independently from nesting cuckoo ancestors (chapter 15).

Old World cuckoos

There are just two species in Europe; most live in Africa, Asia and Australasia. They are arboreal birds, with a slim elongated body, long tails and long pointed wings. With their swift and direct flight they often look like birds of prey as they dash past with rapid wing beats. The legs are short and, like all the cuckoos, they have zygodactyl feet, with the middle two toes pointing forwards and the other two (the inner first and outer fourth) pointing backwards. The bills are stout, usually with a hooked tip.

The 54 species are easier to remember if we divide them into groups.

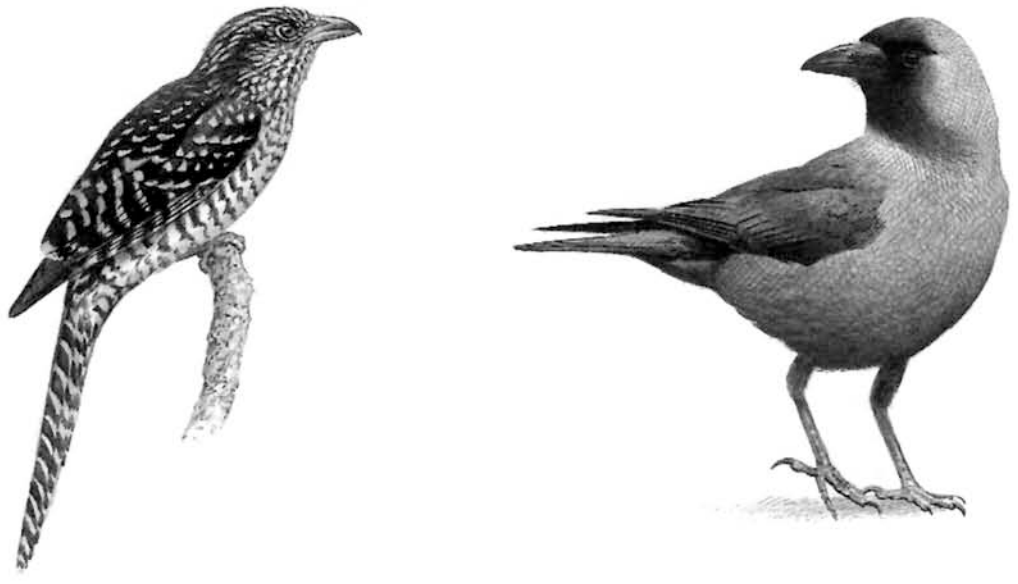
- The genus *Cuculus* contains 14 species; eight breed in Asia, three in Africa, one in Madagascar, one in Australia and one, the Common Cuckoo, breeds throughout the Palaearctic. Most of them are similar in appearance, with greyish or brownish

upperparts and paler, heavily barred underparts. They vary in size from the Lesser Cuckoo (25 cm length from bill to tail tip; 52 g) to the Large Hawk-Cuckoo (40 cm; 150 g).

- The genus *Cacomantis*, which includes eight species, has smaller birds (18–26 cm; 22–44 g) again with greyish upperparts but mostly plain brown or rufous underparts. Five occur in southern Asia and three in New Guinea and Australia.
- The genus *Chrysococcyx*, with 15 species, has the smallest cuckoos of all (15–20 cm; 17–35 g). They are known as the glossy or bronze-cuckoos and are often iridescent metallic green or bronze above and plain or barred below. Most of them (11 species) occur in southeast Asia and Australasia with the other four species in Africa.
- The koels, *Eudynamys*, (two species in Asia and two in Australasia) are large cuckoos (38–46 cm; 120–320 g), some glossy black in plumage and others brown and barred.
- The three species of long-tailed cuckoos, *Cercococcyx*, all live in Africa. They are medium-sized (31–34 cm; 55–65 g) and look like long-tailed versions of the *Cuculus* cuckoos.
- The four *Clamator* species are large cuckoos (34–46 cm; 70–125 g) and their scientific name refers to their loud chattering calls. The Levaillant's Cuckoo is restricted to Africa while the Jacobin, or Pied, Cuckoo has a disjunct range, including Africa and the Indian sub-continent. Both these species occur in two morphs; a black and white morph (glossy black above and mainly white below) and an all-black morph (with a white wing patch). The two other *Clamator* cuckoos have longer and more pointed wings, and they lack the black morph. The Chestnut-winged Cuckoo lives in Asia while the Great Spotted Cuckoo ranges from southern Europe to Iran and throughout much of Africa.
- The six other cuckoo species are thought to be sufficiently distinct that they each command their own separate genus. One lives in Africa, the Thick-billed Cuckoo (36 cm; 115 g). One lives in southeast Asia, the Drongo Cuckoo (25 cm; 35 g). Three are from New Guinea: the Long-billed Cuckoo (18 cm; 31 g), the White-crowned Koel (33 cm; 117 g) and the Dwarf Koel (20 cm; 43 g). Last, and by far the largest of all the parasitic cuckoos, is the Channel-billed Cuckoo of Australia (60 cm; 620 g), a huge grey bird with an enormous bill.

The koels and the Channel-billed Cuckoo eat a lot of fruit but most species favour invertebrates, especially the larvae of moths and butterflies, including hairy caterpillars, which other birds find noxious and avoid. Many caterpillars have guts filled with toxins from the leaves they have eaten. Cuckoos extract these contents by the neat trick of snipping off one end and then passing the caterpillar back and forth through the bill to squeeze out the insides before they swallow it. Alternatively, they may remove the gut contents by bashing the caterpillar repeatedly against a branch. The hairs of hairy caterpillars form a mat in the stomach of the cuckoo and are then regurgitated as a pellet.

Cuckoos are solitary and shy, more often heard than seen. Their vernacular names are often derived from the monotonous calls of the males, such as 'cuck-oo', 'ko-el' and 'dee dee dee diederik'. In his poem, addressed to the Common Cuckoo, the English poet William Wordsworth gently complained:



Asian Koel (left) with one of its main hosts, the House Crow.

Oh Cuckoo! Shall I call thee Bird
Or but a wandering Voice?

Others have taken more drastic action. The persistent calls of several species have led to them being known as 'brain-fever' birds; this includes the Pallid Cuckoo of Australia, the Common Hawk-Cuckoo, Plaintive Cuckoo and Brush Cuckoo of Asia and the Black Cuckoo of Africa. The mournful notes of the Black Cuckoo, 'whoo-whoo-wee', rendered as 'I'm so sad' or 'No more rain', may go on for hours, often through the night, and some people have found the persistent calling so unendurable that they have called the offender over, by mimicking its whistle, and have then promptly shot it!

David Lack was succinct with his explanation for these loud, simple and distinctive calls:[3] 'The song is loud presumably because the birds are rather scarce, so it has to carry far, it is simple presumably because the young cannot learn it from their parents, so it is entirely inherited, and it is distinctive presumably to assist specific recognition, especially where several species of cuckoos breed in the same area.'

Thus, throughout its range, the Common Cuckoo gives the same familiar call, with the emphasis on the first note, and its common name hardly changes as we move from its western limits (Cuckoo in Britain, Coucou in France, Koekoek in Holland), east through Germany (Kuckuck) to Japan (Kak-ko). In Japan, the call is used to alert humans at pedestrian crossings in big cities, a tribute to natural

selection's ability to pick out those sounds which are most distinctive against the background noise. In support of Lack's suggestion, playback experiments show that each cuckoo responds only to its own species' call. For example, the African Cuckoo, which looks very similar to the Common Cuckoo but differs in bill colour and details of its plumage, gives the same two-note call but with emphasis on the second note, cuck-oó, and with the second note rising, rather than falling, in pitch. This subtle change makes all the difference; the African Cuckoo responds, by counter-calling and approach, only to its own species' song.[2]

The earliest known records of brood parasitism have been collated by Herbert Friedmann.[4] The oldest reference is to the Asian Koel, in ancient Vedic writings from India around 2000 BC, some four thousand years ago. The bird was given the name 'anya-vapa', which means 'reared by another', so its parasitic habits were known, though no further details are given. The first reference to its hosts are in Sanskrit literature (*c.* AD 375) where koels are described being raised by crows, now known to be the major hosts of this cuckoo. The earliest definite reference to the Common Cuckoo as a parasite is in Aristotle (384–322 BC), quoted in the last chapter. We then wait nearly two thousand years before another brood parasite is mentioned by Jehangir (1605–1627), a Moghul emperor of India, who referred to the Pied Cuckoo using babblers as hosts. In 1806, Levaillant recorded the parasitic habits of some African cuckoos (the Black, African and Diederik). In 1853, Brehm presented the first evidence that the Great Spotted Cuckoo was a parasite in North Africa and in 1879 Meyer reported that Channel-billed Cuckoos in Sulawesi parasitized crows.

The genus *Pachycoccyx* (the Thick-billed Cuckoo) was not known to be parasitic until Townley observed it in 1936. In 1939 Moreau and Moreau suggested for the first time that the long-tailed cuckoos *Cercococcyx* were also likely to be parasitic.[5] They saw a Barred Long-tailed Cuckoo sitting briefly on the nest of an akelat but the cuckoo then returned and apparently destroyed the clutch. Later, the Moreaus caged an injured cuckoo of this species and it laid an egg which closely resembled that of the akelat. Another egg of this type was also observed in the nest of a broadbill, which later contained only a young cuckoo, of unknown species. Bit by bit, therefore, the jigsaw of observations was put together to glimpse a picture of another parasite. But even today, for none of the long-tailed cuckoos are the hosts well known. Indeed a question mark appears in the host column of the Appendix for no fewer than 15 of the 54 Old World cuckoos. There is plenty of bird watching still to be done.

Nevertheless, we now know enough to make some general conclusions. Most hosts are song birds smaller than the cuckoo itself, usually insectivorous species of moderate size (e.g. babblers and shrikes) or of small size (e.g. warblers, chats, sunbirds). In most of the species, just like the Common Cuckoo, the female lays one egg per host nest and then the newly hatched cuckoo chick ejects the host eggs or young and so it is raised alone. This applies to all the *Cuculus*, *Cacomantis* and *Chrysococcyx* cuckoos that have been studied, as well as to *Pachycoccyx*, *Cercococcyx*, *Surniculus* and two of the koels (the Australian Koel and the Long-tailed Koel). However, the Asian Koel does not eject, nor does the Channel-billed Cuckoo. Both these cuckoos parasitize crows of a similar size to themselves. It would be interesting to know whether in these cases the young cuckoo attempts to eject, but soon gives

up because the host eggs and chicks are too large, or whether it simply does not try in the first place. Nestlings of the *Clamator* cuckoos likewise do not eject, and apparently never try to do so. They also parasitize largish hosts, including crows and large babblers. Even so, although these non-ejecting cuckoos are sometimes raised alongside the host young, they often outcompete them for food with the result that the host chicks are crushed or starve to death. In species where the cuckoo is raised with the host chicks, the female cuckoo may sometimes lay more than one egg per nest.

Cuckoos are often cited as an example of how natural selection produces perfection in trickery, because the cuckoo egg is such a close match of the host egg. In some cases, the match is indeed wonderful. Many of the cuckoos that parasitize babblers lay plain blue eggs so like those of their hosts, in both size and colour, that the only sure way of identifying the cuckoo egg is by its heavier shell. In other cases the match in colour and spotting is impressive, but the cuckoo egg is obvious to the human observer because it is larger and more rounded in shape. This applies to Common Cuckoo eggs in Reed Warbler nests, for example. But in many cases the cuckoo egg looks strikingly different from the host egg. There may be a rough match in colour, but the spotting pattern is clearly different, or there may be no match at all. For example, in South Africa Jacobin Cuckoos lay plain white eggs, quite unlike the spotted eggs of their bulbul hosts, and Red-chested Cuckoos lay uniform dark brown eggs which look nothing like the pale and spotted eggs of their main host, the Cape Robin. This variation is one of the puzzles we will address later on.

Many of the parasitic Old World cuckoos are migrants. Populations of the two species that breed in Europe spend the winter in Africa, south of the Sahara. An early ringing recovery of the Common Cuckoo was reported in a British national newspaper, *The Observer*, on 5 November 1933: 'A cuckoo ringed in a Pied Wagtail's nest near Eton, Buckinghamshire, met its end in a jungle clearing of the French Cameroons, via the arrow of a native.' Many Asian cuckoos migrate south to winter in southeast Asia and the Malay archipelago, while Australian species move north to New Guinea and the Pacific islands. Within Africa, there are often local movements. For example, cuckoos that breed in South Africa may move north to equatorial regions in the non-breeding season.

These regular movements have led to tropical cuckoos being known as 'rain birds', because they arrive on the breeding grounds and sing at the onset of the rains when most host species begin to breed. In Europe, the Common Cuckoo has long been regarded as a harbinger of spring.[6] The oldest secular lyric in English, dating from *c.* 1250, is the cuckoo song:

> Sumer is icumen in,
> Lhude sing cuccu,
> Groweth sed, and bloweth med,
> And springth the winde nu-sing cuccu!

And Edmund Spenser, sometime undergraduate of my College in Cambridge, Pembroke, also linked the cuckoo's arrival to the coming of spring in his sonnet sequence 'Amoretti' (1595).

The merry Cuckow, messenger of Spring,
His trompet shrill hath thrise already sounded.

A traditional rhyme from Norfolk, eastern England, refers to the summer months by the cuckoo's behaviour:

In April come he will;
In May he sings all day;
In June he changes his tune;
In July he prepares to fly;
In August, go he must.

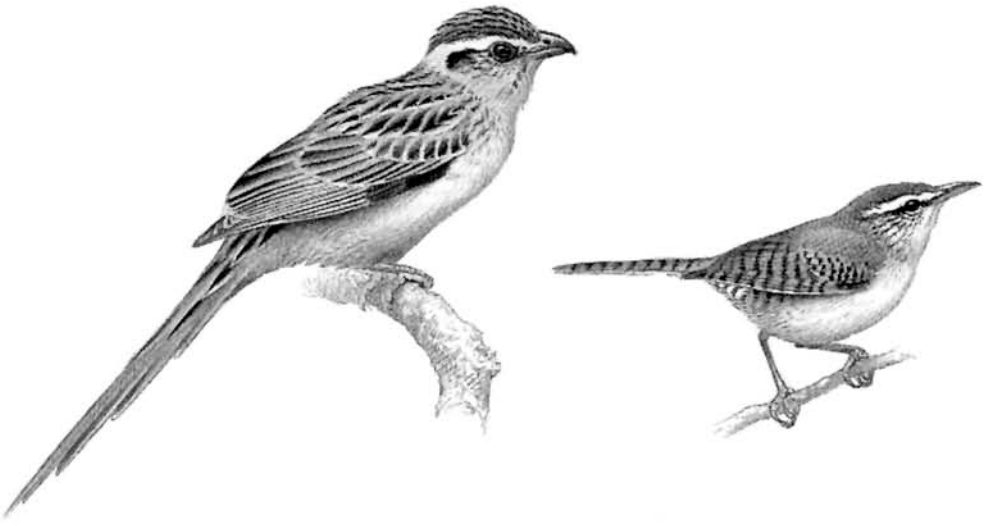
Indeed, so regular is the cuckoo in its activities that it was looked upon as a reliable forecaster of future events. Traditions dating back to Roman times advise lovers, on hearing the first cuckoo in spring, to search under their feet for a hair, for it will be the colour of the hair of their future spouse. The number of calls heard was also said to predict the number of children a couple would have, or how long you would live, or how long you would remain unmarried, and so on. In some parts, it was thought unlucky to hear a cuckoo before breakfast, and hearing the first cuckoo in bed was a sure sign of illness or death. However, good fortune would come if one was heard while out walking, and a child born on the first day a cuckoo calls in spring could expect good luck throughout its life.[6]

In Danish folklore, the cuckoo is said not to have time to build a nest simply because it is kept so busy answering all these questions!

New World Cuckoos

The three parasitic ground-cuckoos from the New World are long-legged and long-tailed birds with brown plumage and short, rufous crests. The Striped Cuckoo (28 cm; 52 g) inhabits scrub, forest edge and open country with scattered trees, and it feeds on insects on the ground and in the vegetation. It was first recorded as parasitic in 1909. The hosts are small passerines with domed nests. The cuckoo's eggs are white, bluish-white or bluish-green. Many of the hosts lay eggs of these colours, so there is likely to be egg mimicry. It may be difficult for the young cuckoo to eject the host eggs from a domed nest. Instead, it has another trick. It is equipped with sharp bill hooks and kills the host young. In 1979, Eugene Morton and Susan Farabaugh first described how a three- to four-day-old cuckoo chick stretched up with its gape open and made biting and twisting movements at anything that touched it. As a result, its nestmates (newly hatched wren chicks) became covered in scars, died from their wounds and were then removed by the host parents.

The two *Dromococcyx* cuckoos were not known to be parasitic until 1914 (Pheasant Cuckoo 36 cm; 80 g) and 1949 (Pavonine Cuckoo 28 cm; 48 g). They are forest birds which feed mainly on the ground on insects and lizards. The hosts are small passerines with either open or domed nests. Neither of these cuckoos' eggs are well known. There are reports of host young disappearing soon after the cuckoo hatches but it is not known how this happens. All these species need further study.

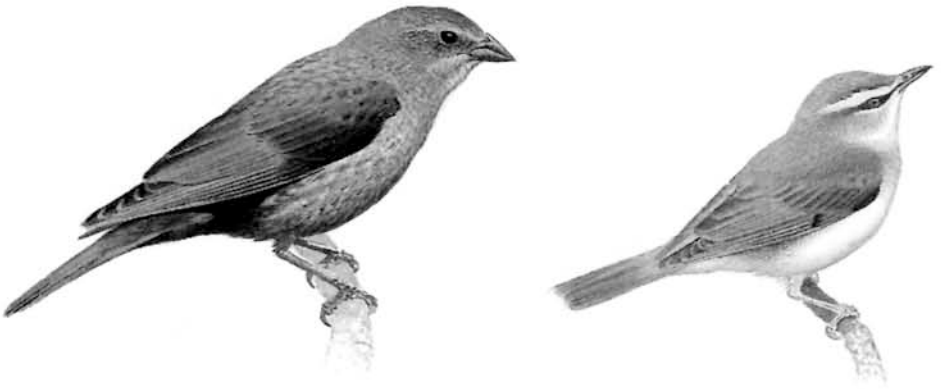


Striped Cuckoo (left) with one of its favourite hosts, the Rufous-and-white Wren.

THE COWBIRDS

Two hundred years ago, it was discovered that cuckoos are not the only parasitic birds.[4] In his book *American Ornithology* (1810), Alexander Wilson described observations of a female Brown-headed Cowbird sitting on the nest of a Red-eyed Vireo. On later inspection, the clutch was found to contain an egg quite unlike those of the vireo. Eight years earlier, in 1802, Don Felix de Azara wrote of the parasitic habits of the Shiny Cowbird in Paraguay and Argentina. The Bronzed Cowbird of central America was added to the list of parasites in 1861.

Then, in 1874, W.H. Hudson's observations in Argentina showed that the Screaming Cowbird was a parasite of the Bay-winged Cowbird. Hudson was so thrilled with this finding that he wrote: 'Today I have made a discovery, and am as pleased with it as if I had found a new planet in the sky. The mystery of the bay-wing's nest . . . found containing over the usual complement of eggs is cleared up.' The discovery was a triumph of careful observation because although the parasite and host young are raised together, the eggs are more or less identical, and the nestlings and fledglings are also almost impossible to tell apart, even though the adults of the two species are so different (**Plate 6d**). Only when Hudson saw some of the fledglings apparently 'undergoing the process of transmutation into another species' did he realize what was going on. He concluded: 'It seems impossible for mimicry to go further than this.'[7] Finally, in 1894 the Giant Cowbird was recorded as a parasite to produce a final total of five parasites out of the six cowbird species.



Female Brown-headed Cowbird (left) and one of its many hosts, the Red-eyed Vireo.

The cowbirds are members of the family Icteridae, the New World blackbirds, which includes 96 species. Apart from five cowbirds, all the rest raise their own young. The icterids are among the dominant species in savannahs, grasslands and marshes of North and South America. Many species have adapted to land modified by humans, especially farmland and pastures with cattle. As a result, some of the cowbirds, in particular, have spread dramatically in the last few hundred years. Icterids often feed by probing their bills into the ground, vegetation or crevices, and gaping to expose food under the surface. They are mainly insectivorous, but also eat fruit and seeds. They may gather in large mixed-species flocks in the non-breeding season. Many icterids, including the parasitic cowbirds, have glossy black plumage (**Plates 5a, 6a**). Females are often less glossy or brown.

Two of the parasitic cowbirds are specialist parasites of other icterids. The Screaming Cowbird (18–21 cm; 50–60 g) is highly specific and almost always only parasitizes the Bay-wing Cowbird (18 cm; 45 g). The Giant Cowbird (31–34 cm; 162–219 g) parasitizes just oropendolas and caciques. The other three cowbirds are generalists, parasitizing a variety of passerine species but including other icterids among their favourite hosts. The Brown-headed Cowbird (16–18 cm; 40–50 g) exploits more than two hundred hosts in North America and the Shiny Cowbird (18–21 cm; 45–55 g) also exploits more than two hundred hosts in South America. The Bronzed Cowbird (19–21 cm; 57–67 g) in central America has more than 70 hosts.[8]

The female cowbird often punctures or removes some host eggs before laying, and usually lays just one egg per host nest, though she may lay two or more and some host nests are parasitized by more than one female. The eggs of the Screaming Cowbird are very like those of their host and those of the Giant Cowbird are often a good match of the oropendolas' and caciques' eggs. By contrast, the eggs of the three generalist cowbirds are usually quite unlike those of their hosts (**Plates 5b, c and 6c**).

THE HONEYGUIDES

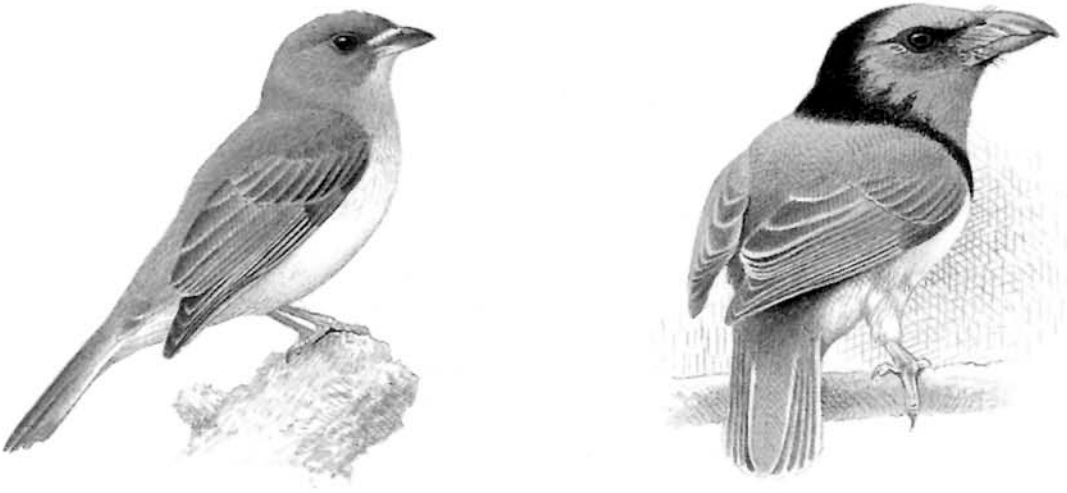
The honeyguides comprise seventeen species in a separate family, the Indicatoridae. Their closest relatives are the woodpeckers (Picidae). Fifteen species of honeyguide are confined to Africa, south of the Sahara, while the other two are Asian. They are small, inconspicuous birds of forest and open woodland, with olive, grey or brown plumage. They vary in length from 10 to 20 cm and in weight from 10 to 55 g. The bill is short and stout in most species but the three *Prodotiscus* are flycatcher-like and have fine, pointed bills. All the species feed on insects but the characteristic peculiarity of the family is that they also eat wax, taken from active or abandoned bees' nests or from the exudate of other insects. The wax is digested with the help of special bacteria that live in the bird's gut.[9]

In Africa, two species (the Greater and Scaly-throated Honeyguides) guide large mammals to bees' nests and this is the source of the family name. The followers are usually Honey Badgers or Man, but baboons may also be involved. The bird sits nearby while the mammal breaks open the nest, and then it feeds on any comb that remains. Honeyguides eat both bee larvae and the wax, but not the honey itself. This is a remarkable example of cooperation between the honeyguide, which can find the bees' nests but cannot break them open, and mammals, which can gain access to the nests but have difficulty in locating them.

Honey gathering by humans is depicted in rock paintings made 20,000 years ago, so the relationship between honeyguides and Man may well be an ancient one. It has been particularly well studied in Kenya, where the Boran people find honey by following the Greater Honeyguide.[10] Both parties benefit: the average time for a Boran to find a new bees' nest is nine hours if he searches alone, but just three hours with the bird's help, while 96% of bees' nests are accessible to the birds only after humans have opened them with tools. The humans' use of smokey fire to calm the bees' aggression reduces the chance that the birds get stung too.

The Boran and honeyguides have developed a remarkable way of signalling to each other.[10] The Boran whistle (**Plate 7b**), and if there's a honeyguide nearby that knows the whereabouts of a bees' nest, it approaches and flies about restlessly, emitting a persistent call 'tirr-tirr'. It then disappears in the direction of the nest, probably to check its position, and after a while it returns. The time of this 'first disappearance' tells the Boran how far away the nest is – the shorter the time, the closer the nest. The bird then makes short flights towards the nest, waiting to make sure that the Boran are following. The Boran whistle to tell the bird that they are on the trail, and as soon as they catch up to within 5–15 m, the bird flies off again, calling and spreading its white outer-tail feathers, which make it more conspicuous. As bird and humans approach their quarry, the bird makes shorter and shorter flights, and when they arrive it changes its call and circles the nest. The Boran claim that when nests are very far away (more than 2 km) the birds encourage them to follow with deceptively short flights which indicate 'there's not far to go!'. This wonderful interaction with Man, once common in many parts of Africa, is now disappearing because of cultural changes in tribespeople, especially the use of alternative sources of sugar and the loss of local knowledge and skills.

The first discovery of brood parasitism in honeyguides was in 1867 and all of the



Lesser Honeyguide (left) and one of its hosts, the Black-collared Barbet.

11 species whose breeding habits are known are parasitic.[4] The main hosts are hole-nesting species, especially other members of the Order Piciformes, the woodpeckers and barbets, together with hoopoes, woodhoopoes, kingfishers, bee-eaters and starlings. However, the *Prodotiscus* honeyguides parasitize open-nesting hosts, such as flycatchers, warblers and white-eyes.

The female honeyguide lays one egg per host nest, sometimes after she has punctured or removed one or more host eggs. The eggs are white, like those of their hole-nesting hosts (**Plate 7a**). This is likely to reflect the honeyguides' own ancestry as hole-nesters, rather than a newly evolved adaptation for tricking their hosts. In the *Indicator* honeyguides, the young parasite has sharp bill hooks with which it

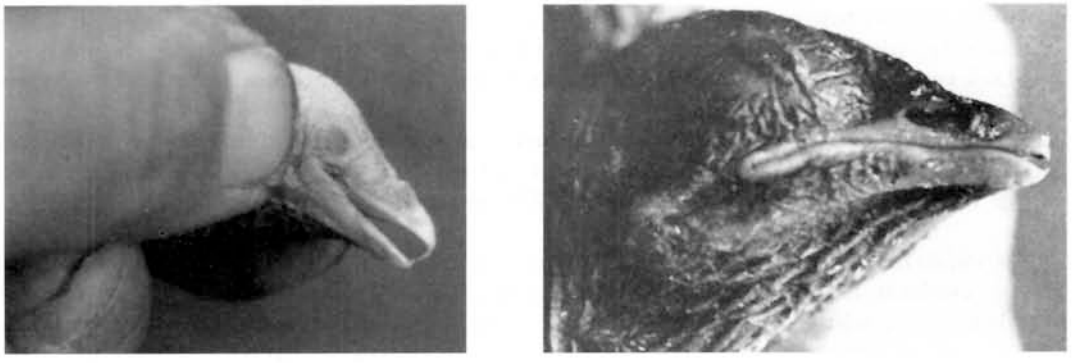


Figure 2.2 Parasitic chicks with lethal weapons.
Left: The bill hooks of a nestling Lesser Honeyguide (photo by Robert B. Payne).
Right: Bill hooks of a nestling Striped Cuckoo (from Morton & Farabaugh 1979).

lacerates and kills the host nestlings, which are then either trampled into the nest lining or removed by the host parents. It is remarkable that this same weapon has evolved independently in honeyguides and New-World ground-cuckoos. Young *Prodotiscus* honeyguides are also apparently raised alone, but it is not known how the host young die.

THE PARASITIC FINCHES

The African parasitic finches include all nineteen species in the genus *Vidua* plus one odd bird, the Cuckoo Finch. The *Vidua* finches are usually classified as grassfinches, Estrildidae, which includes 130 other species, none of which are parasitic. The Cuckoo Finch is traditionally assumed to be more closely related to the weavers, Ploceidae. However, recent genetic studies show that the Cuckoo Finch and the *Vidua* finches are each other's closest relatives, and that they form a distinct group most closely related to the Estrildidae. These results suggest that brood parasitism evolved just once in the African finches, from an ancient estrildid-like ancestor.[11]

The *Vidua* finches are birds of grassland and open woodland and they feed on small seeds of annual grasses that have dropped to the ground. In the non-breeding season they gather in large flocks. Their parasitic habits were first discovered in 1907.[4] They all parasitize other estrildid finches, smaller than themselves, and most specialize on just one host species. Three groups of *Vidua* can be distinguished.[12] In all three groups, the females and non-breeding males are sparrow-like in plumage.

- The indigobirds (10 species) are all similar in size (11 cm; 13–16 g) and appearance. Breeding males are black. The species vary in the colour of their gloss, which may be green, blue or purple, and in the colour of their bill and feet. Their hosts are firefinches and twinspots.
- The paradise whydahs (five species) are larger (15 cm; 19–22 g) and breeding males appear larger still because they have an enormous tail that adds an extra 15–22 cm to their length. The tail is formed through elongation of the central tail feathers, which are flattened and twisted vertically. The breeding males have black upperparts with a yellow collar and belly and a chestnut breast. Their hosts are pytilias.
- The waxbill whydahs (four species) are intermediate in size (12 cm), and the breeding males also have long tails, which adds an extra 20–22 cm to their length, but the tails are narrower. They parasitize waxbills.

All *Vidua* finches lay white eggs, like those of their hosts (**Plate 7c**). This is unlikely to be evolved mimicry but rather a reflection of shared ancestry, because all estrildids have white eggs. The female parasite apparently does not remove any host eggs, and usually lays just one egg per host nest. Unlike most cuckoos and the honeyguides, the young parasite does not kill or eject the host young. Instead, they are all raised together and the parasite chick shows remarkable mimicry of the mouth colour and gape spots of the chicks of its particular host species (**Plate 7d**).

Male and female Shaft-tailed Whydah and their host, the Violet-eared Waxbill.

As we shall see in chapter 13, this is a case of evolved mimicry because parasites and hosts have speciated independently.

The Cuckoo Finch (13 cm; 21 g) differs from the Vidua finches, both in appearance and parasitic habits. The male is bright yellow and the female is streaky brown. It inhabits open grassland, especially near damp areas. It was discovered to be a parasite in 1917.[4] It is not tied to one host but parasitizes various species of small *Prinia* and *Cisticola* warblers. The Cuckoo Finch egg tends to mimic the host eggs, being pale bluish-white with red speckles. Assuming the parasite's ancestor was an estrildid-like bird with white eggs, this is likely to reflect evolved mimicry. The laying of a parasitic egg is usually accompanied by the disappearance of one or more host eggs, so the female Cuckoo Finch probably removes a host egg or two, though this has not been observed directly. Also in contrast to the *Vidua* finches, the Cuckoo Finch chick is strikingly different from the host chicks and there is no mimicry of gape colour. The parasite chick does not evict the host young, but it outcompetes them for food and usually no host young survive to fledge.[13]

A Parasitic Duck

The final specialist brood parasite is a duck from South America, the Black-headed Duck, which breeds on freshwater marshes and parasitizes another duck, the Rosy-billed Pochard, two species of coots, and several other hosts too, including gulls and