
SMITHSONIAN INSTITUTION
WASHINGTON, D.C.

SMITHSONIAN
INSTITUTION

MUSEUM
OF
NATURAL
HISTORY

UNITED STATES NATIONAL MUSEUM BULLETIN 265

The Evolutionary History of the Avian Genus Chrysococcyx

HERBERT FRIEDMANN

Director, Los Angeles County Museum of Natural History
Research Associate, Smithsonian Institution

SMITHSONIAN INSTITUTION PRESS
WASHINGTON, D.C.
1968

Publications of the United States National Museum

The scientific publications of the United States National Museum include two series, *Proceedings of the United States National Museum* and *United States National Museum Bulletin.*

In these series are published original articles and monographs dealing with the collections and work of the Museum and setting forth newly acquired facts in the fields of anthropology, biology, geology, history, and technology. Copies of each publication are distributed to libraries and scientific organizations and to specialists and others interested in the different subjects.

The *Proceedings,* begun in 1878, are intended for the publication, in separate form, of shorter papers. These are gathered in volumes, octavo in size, with the publication date of each paper recorded in the table of contents of the volume.

In the *Bulletin* series, the first of which was issued in 1875, appear longer, separate publications consisting of monographs (occasionally in several parts) and volumes in which are collected works on related subjects. *Bulletins* are either octavo or quarto in size, depending on the needs of the presentation. Since 1902, papers relating to the botanical collections of the Museum have been published in the *Bulletin* series under the heading *Contributions from the United States National Herbarium.*

This work forms number 265 of the *Bulletin* series.

FRANK A. TAYLOR
Director, United States National Museum

Contents

Acknowledgments

The present study is the second in a series which, when completed, hopefully may provide the background for a better understanding of the phenomenon of parasitic breeding in the Cuculidae. The first paper in this series [Friedmann, 1964] dealt with the crested cuckoos, forming the genus *Clamator*. The genus covered in the present paper contains three times as many species as *Clamator* and occupies a much wider portion of the land areas of the Old World. It is the first attempt to study all the glossy cuckoos as a group. In the past the African species have been dealt with by specialists on African birds, the Australian and Malaysian ones separately by other regional students, and the Asiatic ones by still other writers. Until a comprehensive and comparative study of all of the glossy cuckoos was made, it was impossible to compare meaningfully the known facts about the life histories of these birds.

As in the earlier study of *Clamator*, the attempted appraisal of the phylogenetic relationships of the 12 species of *Chrysococcyx* demanded careful examination of large amounts of preserved material of each species. A research grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History enabled me to spend 19 very productive days at the British Museum (Natural History) in London and also to examine the extensive material in the American Museum of Natural History. These two collections comprise by far the bulk of the pertinent material. The specimens in the United States National Museum in Washington were also studied. To the custodians of these bird collections I express my thanks for their cooperation in making these materials available to me.

Museum study specimens were examined to ascertain the nature, the frequency, and the distribution within and between the dozen members of the genus of the types of plumage patterns, plumage phases, and kinds and degrees of variation within these patterns and phases. This survey was made with an eye to any phylogenetic suggestions that might be adduced from the many hundreds of specimens studied.

By correspondence with the unfailingly cooperative curators of their respective collections and, in a few instances, by loans of selected, critical specimens, I have been able to make use of the data on pertinent material in the museums of Bulawayo, Durban, Nairobi, and

Pretoria, in Africa; of Bombay, Singapore, and Manila, in Asia; of Sydney and Adelaide, in Australia; of Berlin, Copenhagen, Genoa, Leiden, Milan, Paris, Stockholm, Turin, and Vienna, in Europe; and of Ann Arbor, Cambridge, Chicago, and Los Angeles, in the United States. To the officials of these museums who have helped me with data or specimens in the past 25 years I offer my thanks. The following individuals also have assisted with contributed field observations, with egg-specimen data, and with other relevant information: S. A. Ali, L. Auber, R. K. Brooke, A. C. Cameron, A. H. Chisholm, G. Duve, T. Farkas, N. Favaloro, N. C. Fearnley, M. T. Goddard, F. Haverschmidt, K. A. Hindwood, A. Hoogerwerf, L. Hyem, M. P. S. Irwin, C. H. Jerome, F. Johnston, R. Kreuger, R. Liversidge, C. J. Marinkelle, A. R. McGill, A. R. McEvey, W. Meise, H. M. Miles, P. Millstein, B. V. Neuby-Varty, J. Ottow, J. Paludan, E. Pike, C. R. S. Pitman, O. P. M. Prozesky, R. A. Reed, E. H. Sedgwick, D. L. Serventy, C. J. Skead, R. H. N. Smithers, G. Symons, R. E. Symons, V. G. L. van Someren, C. J. Vernon, J. G. Williams, and J. M. Winterbottom. Mr. K. A. Hindwood kindly helped me with the nomenclature of Australian birds and also put me in touch with a number of the Australian contributors, whose names are listed above. Others who assisted me in various ways in the past but who will not see this publication are the late E. Ashby, E. C. S. Baker, J. P. Chapin, and A. Roberts.

My personal field experience with *Chrysococcyx*, although limited to three of the four species that occur in Africa, formed my original basic interest in this group and played a contributing role in the present study. This field experience was made possible by grants from the National Research Council, the American Philosophical Society, the John Simon Guggenheim Memorial Foundation, and the Smithsonian Institution.

Permission to reproduce a map (fig. 4) from *Fundamentals of Ornithology* by van Tyne and Berger was granted by the publishers, John Wiley & Sons.

The colored plates of the plumages of the glossy cuckoos were prepared for this publication by Evelina R. Templeton, scientific illustrator of the Los Angeles County Museum of Natural History.

For her patience with endless changes in the manuscript and for her careful typing of the final copy, my thanks are due my secretary, Myrna L. Patrick.

The Evolutionary History of the Avian Genus *Chrysococcyx*

Introduction

The genus *Chrysococcyx* is one of a number of genera of cuckoos that are brood parasites in their reproductive habits. Their phylogeny, differentiation, dispersal, and ethology—all of which are reviewed in a comparative, yet detailed, way for the first time in this paper—are of interest in themselves not only as a special "case history" in the development of parasitism, but also for the light they throw on the broad, general problems of evolution of parasitic reproduction in the cuckoos as a family and in birds in general.

As I pointed out in an earlier paper on *Clamator* (1964) the various genera of parasitic cuckoos reveal divergent paths of development in their mode and degree of specialization as parasites. *Chrysococcyx*, for example, agrees with *Cuculus* in the evicting habit in the early nestling stage, a phenomenon not present in *Clamator;* it agrees with both *Cuculus* and *Clamator* in the habit of host-egg removal by the adult cuckoos from parasitized nests. Among its dozen included species *Chrysococcyx* presents a broad range of host-parasite situations, from those found in species like *malayanus* and *osculans* with only a very small number of regular hosts to those shown by others like *lucidus* (*plagosus*), *basalis, klaas,* and *caprius* with many dozens of host species apiece. *Chrysococcyx* agrees more (but not rigidly) with *Cuculus* than with *Clamator* in the intensity of parasitism on its usual hosts, as measured by the incidence of multiple to single eggs in individual nests of the latter.

Among the most interesting and intriguing biological problems exhibited by the glossy cuckoos are:

1. The atavistic retention of courtship feeding by the adult male with the correlated fledglinglike behavior of the female; 2. the still more atavistic (but not infrequent) fledgling, and even nestling, feeding by adults of these parasitic breeders; 3. the tendency, definitely begun but far from perfected, toward primary differentiation in host selection by sympatric species of the genus; 4. the achieve-

ment of various degrees of similarity to host eggs by the eggs of different species of glossy cuckoos, and the lack of continuity of pattern found in the development of this favorable adaptation in the phylogeny of the genus *Chrysococcyx;* 5. the fact, related to the preceding, that various glossy cuckoos show different degrees of egg morphism or the lack of it (one phenotypic egg); 6. the enormous diversity of migratory behavior in different segments of the genus and even in regional, geographic portions of the total population of some of the species; 7. a remarkable and, apparently, a fairly abrupt change in the plumage patterns of the young; 8. a great intensification of sexual dimorphism in the adult plumage in some species of the genus and not in the others; 9. the fact that the genus shows a multidirectional radiation of differentiation, not one main line of progressive alteration from a presumably earlier, more "primitive" to a later, more "advanced" stage.

As will be seen from the body of this paper, the glossy cuckoos do not reveal any such striking reversal of evolutionary trends as that found among the crested cuckoos. They do present a picture of interest in that they form an ancient group with definite gaps in its composition due to the fact that a number of evolutionary intermediates between current species have long since disappeared without a trace. The glossy cuckoos may be numbered among those cases that are all too numerous in nature but that fail to be reported on in detail since they do not lend themselves to as convincing and as readily accepted reconstructions as do others where the steps between all present species are more easily discerned.

My experience with *Chrysococcyx* in the field is limited to 3 of the 4 African species (the genus contains 12 species in all), and, as will be shown in this report, these African members of the group probably are phylogenetically the more recent species of the glossy cuckoo assemblage. However, over many years, I have compiled, compared, and studied data on all aspects of the life histories of all the included species, including much unpublished material kindly sent me by cooperative and generous observers. The scattering and haphazard nature of many of these discrete bits of data, and the wide range of accurate detail (or lack of it) in many of them has made it difficult to correlate, appraise, and interpret them, and it has therefore become imperative to undertake a careful synthesis and reconstruction of the past history, vicissitudes, and relationships of the group as a whole. Inasmuch as this reconstruction is basic to our evaluation of brood parasitism in the glossy cuckoos, we may now turn to the composition of the group and to their apparent natural arrangement.

The data and their discussion and interpretation are presented in this paper in the following sequence, to give a coherent picture of the evolutionary history of the glossy cuckoos. The morphological differentiation of the group as evidenced by the apparent phylogenetic relationships of the existing forms is presented in detail. Following this, the comparative data on migratory behavior are described to help explain the present geographic distribution of some of the various species of the group. The similarities and the differences in the courtship habits of the species are then considered for the glimpses of past history they reveal. With this background as a basis we then discuss each important behavioral segment of the parasitic habit in the glossy cuckoos, with all the data pertinent to the problem of host selection and its evolution; of host specificity; of egg morphism and its importance as evolutionary material; of the mode of egg-laying by the parasites; of removal of host eggs by the cuckoos; and of the highly specialized relations between the nestlings of the hosts and of the parasites. This is followed by a discussion of all that is known of the eviction of nestmates by the nestling cuckoos and of fledgling feeding by the adults. Both of these behavior patterns are highly significant in the biological history of the glossy cuckoos.

All these data and all the ideas pertinent to them are then brought together and summarized. An appendix provides in its first part a distributional check list of all the members of the genus *Chrysococcyx* and in its second shorter part, brings together the earlier and the more recent knowledge of the plumages of one species, hitherto very inadequately described.

Phylogenetic relationships

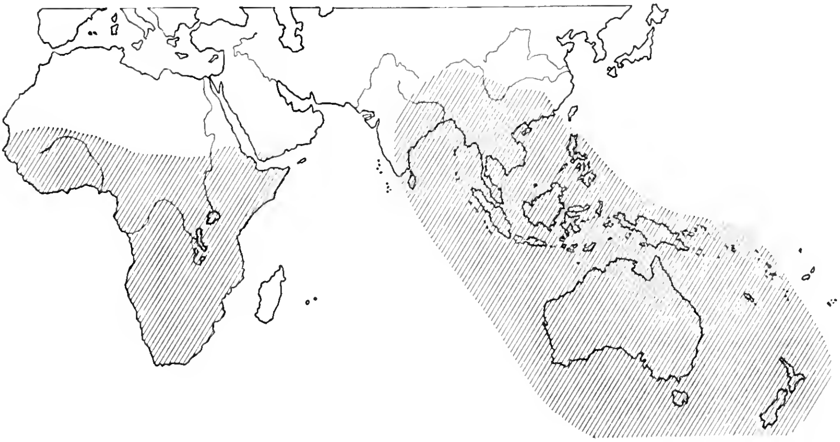


FIGURE 1. Geographic range of the genus *Chrysococcyx*. [Shaded area in the Austro-Malaysian region should be taken to refer to land areas only.]

The glossy cuckoos, with which one nonglossy species, *osculans*, is here united, following Serventy and Whitell (1962, p. 268), form a fairly homogeneous group of small, parasitic cuckoos inhabiting New Zealand, Australia, the East Indies and the islands of the southwest Pacific, southeastern Asia and India, north to the Himalayas, southern Tibet, and Szechwan, and all of Africa south of the Sahara. Within this enormous range the group is represented by 12 species, with a total of some 32 currently recognized species and subspecies: Of these 12 species, 7 (*basalis, caprius, flavigularis, maculatus, meyerii, osculans*, and *ruficollis*) are monotypic while 5 have more than a single form each. Of these 5, 2 (*xanthorhynchus* and *klaas*) have 3 races each, 2 (*cupreus* and *lucidus*) have 4 apiece, while 1 (*malayanus*) has no fewer than 11 subspecies, due no doubt to its occupation of many oceanic islands with correspondingly greater opportunities for the formation of isolated gene pools.

In much of the recent literature one of the Australian species, *osculans*, has been placed in a monotypic genus *Misocalius*, chiefly because it lacks the metallic gloss on the upperparts found in the rest of the species; the four African species (*flavigularis, klaas, cupreus*, and *caprius*) have been kept in *Chrysococcyx*, and the seven Indo-Australian ones (*basalis, lucidus, malayanus, maculatus, xanthorhynchus, ruficollis*, and *meyerii*), in *Chalcites*. These three genera are actually one group, for which *Chrysococcyx*, as the oldest name available, must be used. That they were not merged long ago is probably due to the fact that the included species were dealt with chiefly by regional specialists who did not attempt to study them all together.

Many years ago Sharpe (1873, p. 579) admitted that, were it not for their glossy plumage and small size, he could not separate generically these species from the larger, plain-colored, long-tailed birds of the genus *Cuculus*. Similarly, the genus *Cacomantis* is difficult to separate from either by trenchant characters. Yet each of the three is a "natural" assemblage, and as such each commends itself to generic status in the opinion of all taxonomists with extensive knowledge of, and experience with, these birds. Thus, the species *osculans* which seems like a link between *Cacomantis* and the Indo-Australian section of *Chrysococcyx*, possessing the relatively long bill of the former and the shorter, less graduated tail of the latter, agrees with the latter in its unbarred and unstreaked juvenal-plumage pattern, and therefore is better placed in *Chrysococcyx*.

Even Mathews (1918, p. 337), who kept *osculans* in a separate genus, wrote that its evolution from an ancestral "form of *Lamprococcyx* is presumed, and if it spreads to the wetter districts it is sure to become darker, more glossy and more like a Glossy Cuckoo than the desert bird is. The egg suggests that of the Bronze Cuckoos, while it is recorded that its flight recalls that of these latter birds. . . ." While not defending or criticizing Mathews' assumed evolutionary paths, I cite his statement as further evidence of the close relationship of *osculans* with the glossy cuckoos.

The fact is the genera *Cuculus*, *Cacomantis*, and *Chrysococcyx* are ancient, and, as so often happens in such categories, some have differentiated in the direction of the others, making it very difficult at this late date to distinguish between original similarities or differences and later convergences or divergences. This situation was noticed by Mathews (1918, p. 384), who was a generic "splitter" but who was moved to write that the gradation of the three groups "is very peculiar, as it is marked in most particulars, size, coloration, length of tail, etc.; yet it is possible we see here again instances of convergence, as often met with when dealing with ancient groups. . . . The Bronze Cockoos have been continually separated from *Cacomantis* on account of their bronze coloration and smaller size; but here again some species are dull, while it is obvious that the bronze species are separable into groups and have evolved more or less independently. . . ." Mathews then considered that the African species, which he had looked at only casually, were quite distinct from the Indo-Australian ones, and he assumed that they were derived from a different source, a conclusion I consider improbable. He did conclude that the Malaysian-Australian forms were a complex assemblage and that the best guide to their affinities was to be derived from their plumage changes. Unfortunately, he went on to divide what is here considered one genus, *Chrysococcyx*, into no less than five genera, *Misocalius*, *Chalcococcyx*, *Lamprococcyx*, *Neochalcites*, and *Chrysococcyx*. Had he studied the African forms more thoroughly, he might well have divided *Chrysococcyx* into two genera, recognizing *Lampromorpha* as did many of the African specialists of his time.

Peters (1940) apparently made no careful study of these cuckoos, and he followed the then-current usage by recognizing *Misocalius* for *osculans*, *Chysococcyx* for the African forms, and *Chalcites* for the Indo-Australian species. Berger (1955), on the other hand, investigated the anatomy (pterylosis, wing and leg myology, syrinx, liver, and intestinal caecum) of a number of species of glossy cuckoos, fortunately including representatives of three genera (as then recognized)—*Chrysococcyx* (*cupreus*), *Lampromorpha* (*klaas* and *caprius*), and *Chalcites* (*lucidus*), and he concluded that all were congeneric. He noted that "anatomical similarities further suggest that *cupreus* and *klaas* are more closely related to each other than to either *caprius* or *lucidus*. Though *lucidus* possesses certain anatomical features exhibited by *caprius* (especially the M. iliotibialis and the place of insertion of the syringeal muscles), in most respects *lucidus* is like *cupreus*. Therefore, *caprius* is most unlike the other species of this genus."

Of the 12 species of the group, the breeding habits of 9 are known, and these are all parasitic. The three whose eggs and young have not yet been discovered are *ruficollis*, *meyerii*, and *flavigularis;* it seems safe to assume that these are parasitic as well. In other words, there is no reason to think that any chronological stages in the development of parasitism are to be seen in the members of this genus. Since *Chrysococcyx* is obviously most closely related to other parasitic genera such as *Cuculus* and *Cacomantis,* it is reasonable to conclude that the glossy cuckoos were descended from Cuculinae that were already parasitic. As we shall see, some special refinements of brood parasitism are to be found in certain members of the group and not in others; refinements such as egg similarity to host eggs, restriction of parasitism to a small rather than a large number of host species, and atavistic behavior patterns such as nestling and fledgling feeding. However, since until now all the species of the genus were studied, not as an entity, but almost solely according to geographic occurrence, it was impossible to appraise the significance of differences in refinement, or atavism of portions, of the behavior patterns associated with the annual reproductive cycles of these birds.

The chief intention of my comparative survey of adequate series of specimens of all of the 12 species was to enable me to suggest their most probable phylogenetic pattern, according to which I might then arrange and evaluate the data on various aspects of their biology. The many hundreds of study specimens in the British Museum and in the American Museum of Natural History were carefully examined and compared, but even this ample material failed to suggest with incontrovertible definiteness which particular pattern was the only correct interpretation of the relationships and of the past history of the group. It was impossible to conclude that the incomplete, circumstantial evidence of the present forms of the genus and of their distribution pointed to only one interpretation. Too many—in fact almost all—intermediate stages have long since disappeared in this ancient assemblage. Even the "intuitive" grasp of a complex picture—which actually is usually a result of time-requiring "mental digestion" arrived at without any rigidly logical series of steps, and which results in the generally clarified, or at least correlated, arrangement on which taxonomists so often have come to rely and on which they lay such store (often with sound reason)—has been less neatly precise in the present instance than I could have wished it might be. This factor of uncertainty is an almost universal characteristic of evolutionary or phylogenetic reconstructions, and it is by no means peculiar to the present one. I mention it only because so many times authors either leave it unsaid or minimize it in their effort to advance what seems to them the best, if not the only, possible arrangement of their data.

Within the limitations expressed in this preamble, I will now outline what seems to me to have been the past history, movements, and differentiation of the glossy cuckoos. The group originated in the Indo-Malaysian area, whence it spread to New Guinea, Australia, New Zealand, to the islands of the southwestern Pacific, to Burma, Assam, and India, and thence to Africa. The evidence will be presented in the following pages.

First, I will mention the two major geographical dispersals the group underwent, outlining the reasons for my interpretation. These two great dispersals involved a westward-spreading movement from southern Asia to Africa, and a southern- and southeastward-spreading movement from Malaysia to Australia and New Zealand. The latter was probably much earlier than the former in the history of these cuckoos, but it is not possible to prove this since evolutionary rate of change may have been more rapid in the westward-pushing African stock than in the movement that spread to Australia and New Zealand. In other words, that the present African members of the genus seem more distinct, more divergent from the ancestral stock may be due to more rapid change in a new environment and may not necessarily be an expression of greater age than that evidenced by the lesser degree of morphological change exhibited by the present Australian and New Zealand portion of the group.

That there are no glossy cuckoos in Madagascar and the other islands of the central and western Indian Ocean (Comoros, Mauritius, Reunion, Aldabra, the Seychelles, etc.) suggests that the westward spread of this group from southern Asia occurred after the isolation of Madagascar and the Mascarene Islands from Africa in Pliocene time. The additional fact that two of the African species, *caprius* and *klaas,* have been found in southern Arabia suggests that a more northern route may have been taken. It is equally possible, however, that these southern Arabian birds may be relatively recent émigrés from Africa. Both are known from only a very few specimens—*caprius,* indeed, from a single one, from Arabia—but *klaas* appears to have bred there, according to Meinertzhagen (1954, p. 310).

Similarly, at the other end of the range of the genus, the fact that the birds breeding in New Zealand (*C. lucidus lucidus*) and in southern Australia and Tasmania (*C. lucidus plagosus* and *C. basalis*) migrate incredible distances over the open oceans, sometimes as much as 2000 miles, to the Solomon Islands and to the islands of the Bismark Archipelago, suggests a revealing annual retracing of their ancient ancestral dispersal between their present southern and southeastern breeding areas and their original locus of origin.

The term "locus of origin" must be accepted in a rather loose sense, as we have no way of proving that the islands presently used as wintering quarters were the original homes of these subsequently migratory birds. It so happens that the main areas to which these cuckoos now repair for their nonbreeding season, the Solomon Islands, and, to a lesser extent, the Bismark Archipelago, have no resident or breeding populations of glossy cuckoos. In the complete absence of evidence as to what may have been the case in the remote past, it is not possible to explain this geographical gap or even to ask if there may once have been *Chrysococcyx* populations there. The current absence of local birds may make these islands more readily "suitable" for the New Zealand and Australian migrants, but even this suitability is uncertain. In Africa the populations of the three species of glossy cuckoos that breed in the southern portion of the continent spend the southern winter in equatorial areas that contain resident populations of all three. It may be that the absence of breeding fantail warblers (*Gerygone*) in the Solomons is correlated with the lack of resident glossy cuckoos, for both this favorite host and its parasite occur on Rennell and Bellona Islands.

For the sake of greater coherence and clarity in this review of the history of the differentiation and dispersal of *Chrysococcyx*, discussion will be limited to species. The variations within each species will be treated later as needed. At this point it is sufficient to say that in no case do the infraspecific variations and differentiations throw any doubts on the vicissitudes, here outlined, of the specific taxon of which they are a part.

If we begin with the Indo-Malaysian area as the probable locus of origin of the genus, *C. malayanus* would then seem to be the nearest of the existing species to the original home area, as well as the one most similar to the ancestral stock. As the most wide-ranging of the Malaysian-Australian members of the genus, and as the most polytypic species of the entire group (with 11 races), it appears that *malayanus* may well be the oldest of existing *Chrysococcyx* species. It includes only tropical forms, most of which seem to be nonmigratory as compared with the nearly related species *lucidus* and *basalis*, parts of which are highly migratory. In their review of the subspecies of *malayanus*, Hartert and Stresemann (1925, p. 160) noted that from the Malay Peninsula eastward the races of this species inhabit almost all the islands of the Malay archipelago, east to New Guinea and the Fergusson Islands, and to the tropical portions of Australia. In his discussion of the origin of the avifauna of Timor and Sumba, Mayr (1944, pp. 172, 189) considered *C. malayanus* as one member of the "Banda Sea" element, a group of species of more eastern origin that supposedly came into these islands in Pliocene time. The species is not represented by breeding populations in the Bismark or the Solomon Islands, where no glossy cuckoos are known to breed, and it is also absent from Bali, Lombok, Sumbawa, Flores, and Sumba, as well as from Palawan and the northern Philippines. The race *minutillus* of northern Australia has been treated as a separate species by some recent authors.

It requires no great imagination to see that *lucidus* and *basalis* are closely related to the primordial "*malayanus*" stock. The three species, although quite readily distinguished, are sufficiently similar in appearance to indicate that they are more nearly related to each other than they are to any of the other species of the genus. As we have already stated, *malayanus* has a very wide, discontinuous range involving many islands. *C. basalis* breeds in southern Australia and Tasmania, but winters northward in the Sunda Islands, from Java to Sumbawa, and has been recorded as well from Borneo, Sumatra, the Malay Peninsula, Celebes, the northern Natuna Islands, Kangean Island, and Christmas Island (in the Indian Ocean). *C. basalis* is monotypic. The third species, *C. lucidus*, has four races, being next to *malayanus* in the degree to which it has broken up into geographically differentiated populations. Its breeding range includes the same portions of southern Australia and Tasmania (*C. l. plagosus*) as does that of *C. basalis;* plus New Zealand and the Chatham Islands, and possibly also Norfolk and Lord Howe Islands (*C. l. lucidus*); New Caledonia the Loyalty Islands, New Hebrides, Santa Cruz and Banks Islands (*C. l. layardi*); and Rennell and Bellona Islands (*C. l. harterti*). The last two subspecies are resident; the first two migrate extensively, *plagosus* wintering in the Lesser Sunda Islands, New Guinea, and the Bismark Archipelago, and typical *lucidus* migrating through the Louisiade Archipelago (Woodlark, Misima) to the Solomon Islands and the Bismark Archipelago.

On the whole, *C. lucidus* seems closer to *C. malayanus* than does *C. basalis*, and it may be significant that the eggs of the first two species are fairly similar, uniform olive-bronze to olive-green, occasionally with faint longitudinal streaks (as in *C. m. poecilurus*), while those of *C. basalis* are very different, pinkish white, finely speckled with pinkish red. *C. basalis* also has a bill relatively narrower for its length than does either *C. lucidus* or *C. malayanus*, and it also has more rufous in its rectrices than do the latter two species.

C. malayanus is slightly smaller than either *basalis* or *lucidus* and is usually thought to differ from both in the pattern and extent of the rufous coloration in the tail—all the rectrices in *malayanus* having some rufous, while in *lucidus* the tail has little or no rufous on the next to the outermost pair of feathers and in *basalis* there is no rufous on the outermost pair of rectrices but a considerable amount of this color on the basal portion of the next three pairs. However, this character of rufous coloration in the tail feathers varies considerably within the species *malayanus*, and since *lucidus* (and its races) and *malayanus* (and its numerous subspecies) do not overlap geographically in the breeding season, it may not be too farfetched to ask if they may not be conspecific, representative forms. Thus, within *malayanus*, all the rectrices have rufous in the race inhabititing northern Queensland, *C. m. russatus*, while in *C. m. minutillus* there is no rufous in the outermost pair of rectrices, although there is a considerable amount of this color in the basal half of each of the next three pairs; in *C. m. rufomerus* there is no rufous in any of the tail feathers; in *C. m. malayanus* there is no rufous in the outermost pair, although a considerable amount in the basal portion of the next two pairs.

The species *C. basalis* not only has a narrower bill but also differs in other proportions, such as the longer tail and somewhat longer legs. It also is less bronzy colored above than *malayanus* or *lucidus* and its throat is longitudinally striped or streaked, rather than barred as in the latter two. It is more distinct from either *malayanus* or *lucidus* than they are from each other. Also, that *lucidus* and *basalis* are sympatric is further evidence of their specific distinctness; as said above, however, this geographic argument does not apply to the *lucidus-malayanus* picture.

At this point we come to a much more noticeable morphological differentiation, a change that resulted eventually in the species *osculans*. Here the striking change is in the loss of the metallic, glossy coloration in this bird, which is otherwise a larger relative of *lucidus*, *basalis*, and *malayanus*. The eggs of *malayanus* are said (by North, 1912, p. 28) to approach a chocolate-bronze color at times. It is possibly significant that the eggs of *C. osculans* are a rich chocolate-brown color; this may reflect some phylogenetic connection between the two, *osculans* being a glossy cuckoo that has lost its glossy color but is otherwise an obvious member of the group. However, egg coloration in parasitic cuckoos is too selectively vulnerable and, hence, changeable in the course of evolution to be, in itself, a very trustworthy index of relationship. The most that may be said of *osculans* is that it is more probably related to the other Australian congeners (*lucidus*, *basalis*, and *malayanus*) than to any of the other, geographically more distant species of *Chrysococcyx*.

We now come to two derivative species found in the mountains of New Guinea, *ruficollis* and *meyerii*. The former is, essentially, fairly similar to *malayanus* but has the throat and breast suffused with rufescent. This poses no difficulty in a phylogenetic reconstruction since *malayanus* (especially the subspecies *C. m. russatus*) shows a trend in this direction. *C. ruficollis*, still a poorly known species, occurs in the mountain forests at altitudes of from 2000 to 3300 meters, and occasionally down to 1300 meters according to Mayr (1941, p. 73). Fuller knowledge may reduce *ruficollis* to the status of a race of *malayanus*, as was suggested by Rensch (1931, p. 544) who pointed out that the two species do not overlap in their breeding ranges. Mayr (1932) suggested that the tail pattern of *ruficollis* raised the possibility of its close relationship to *lucidus*, and noted that the solution of this problem must await fuller knowledge of the vocalisms, habits, and eggs of these cuckoos.

The other species, *C. meyerii*, however, is, very distinct. Between it and the stock of which *malayanus* seems to be the least changed representative, there is a gap in the existing evidence. Not only is it more brightly metallic on the upperparts, but the female has a wholly new plumage character, with a bright-chestnut forehead and anterior portion of the crown. This is the only species of the entire genus in which this marked, brightly colored character has developed in the female. The fact that the young of this species is unbanded below is evidence that *C. meyerii* is related to the other Indo-Australian species. It may be noted, at this point, that Iredale (1956, p. 185) has made some comments about this species, which do not tally with the information in his own book. He writes that the immature "is so unlike the adult as to raise suspicion about all the distinctions cited in favour of the separation of these Cuckoos by means of tail coloration. The young bird, figured on Plate XII, Figure 9, shows no bronze above, only a dullish green, while it is whitish below . . .," but the colored figure he gives shows the entire upperparts of the bird from forehead to tail pale chestnut-brown! *C. meyerii* is distinguished in both sexes by a broad chestnut area in the remiges, by its brightly glossy-green upperparts, and by its small size.

C. meyerii is a critical species in the evolutionary vicissitudes of the genus. Not only is it the first expression of a trend toward brilliantly colored forms—a trend that again reveals itself in two species of the Asiatic mainland, *C. maculatus* and *C. xanthorhynchus*—but it is the first species (in this reconstructed phylogeny) that possesses very distinct sexual plumage dimorphism. It is also the last species in our present arrangement to possess the character of largely unmarked, uniformly grayish or brownish ventral plumage in the young, agreeing in this important respect with all the Australasian species and differing from the two Asian and all the African ones, the young of which are very strongly banded over the entire underparts. In some of the Australian and Malaysian species the sides and flanks of the young are banded, but these cross marks do not extend across the breast or abdomen, and even in these species occasional completely unbanded individuals occur (*C. l. plagosus*, Mayr, 1932).

The change of this aspect of plumage patterns, associated as it is with the presence of sexually dimorphic plumages in the adults, is a biologically interesting development and merits further discussion here. Ventral barring as a pronounced pattern is found in the young of *maculatus* and *xanthorhynchus* and of the four African species, while the young of the Malaysian-Australian species have uniform, unbanded underparts from chin to vent. Conversely, the adult males of the latter group show a well-developed trend for crossbars on the underparts, while all but one (*flavigularis*) of the former group do not. In other words, a fairly basic pattern is associated with immaturity in one group and with maturity in the other. The one western exception, *C. flavigularis*, has the barred pattern on the abdomen in the adult-female plumage, and in this respect it forms a significant link between the two sections of the genus.

The biological appraisal of the evolutionary significance of ventral barring is difficult to form. While such barring is characteristic of the young of many other cuckoos of the subfamily Cuculinae, such as the various species of *Cuculus*, *Cacomatis*, and *Cercococcyx*, it is absent from others of such genera as *Clamator*, *Scythrops*, and *Coccyzus*. It is, therefore, not necessarily an immature plumage pattern in itself, although there are many birds unrelated to the cuckoos in which the young are banded, spotted, or streaked, while the adults are relatively free of such markings.

It should be kept in mind that we are discussing here, not an exact replication of a transverse pattern, but a tendency to produce this type of marking. In this connection, the following thoughts might well be mentioned. If, as is widely assumed, the juvenal and immature plumages tend to reflect earlier, more "primitive" phylogenetic stages in the history of a group of species to a greater extent than do the corresponding adult plumages, how are we to understand the reversal of pattern sequence within such a fairly compact group as the glossy cuckoos? One solution of this enigma would be to regard the Asiatic and African species as a genus apart from the Malaysian-Australian ones. This, however, would merely reword the question in terms of two related genera instead of one somewhat divergent group of congeneric species. Also, the plumage patterns of *flavigularis*, as already mentioned, help to bridge the gap. If we were to interpret the presence of strongly barred ventral-plumage pattern in the young as more "ancient" than the absence of such a pattern, we might ask if the Malaysian-Australian species were actually more recent in their origin than the others. Yet this seems most unlikely; we can only conclude that the tendency to produce a barred ventral-plumage pattern in the young was developed at the time that a portion of the ancestral stock began to spread westward to the Asiatic mainland and that this tendency has been retained in all the species that have arisen from that segment.

On returning to our descriptive review of the genus, we come to a gap between *meyerii* of New Guinea and the two Asiatic species, *maculatus* and *xanthorhynchus*. This is a gap both in existing birds and in geography, and it should be made clear that the existing species on the two sides of the gap are related but not necessarily immediately derivative. Both are expressions, similar in some ways and distinct in others, of a trend toward brighter, more glittering plumage. The two species of the Asiatic mainland are closely related to each other, although the adult males are strikingly different in appearance, that of *maculatus* being bright metallic-green above and that of *xanthorhynchus*, bright violet. The females of the two are more alike, but are readily distinguishable; that of *maculatus* has the crown and hind neck between cinnamon and pale chestnut, and the upper parts of the body light, but bright, green with a varying amount of coppery glints and reflections; that of *xanthorhynchus* is bronze-green above, slightly browner on the head and has all the upper wing coverts and many of the dorsal body feathers banded with chestnut. Moreover, the violet cuckoo is slightly smaller than the emerald one. The juvenal plumages and the eggs of the two are very similar. The emerald cuckoo, *C. maculatus*, is a monotypic species, known to breed in the Himalayas from Kuman through Assam, southeastern Tibet and Szechwan, to Hupeh, south to Yunnan, and Burma, migrating or wintering south to India, Hainan, the Malay Peninsula, and Sumatra. The violet cuckoo, *C. xanthorhynchus*, with three races (one of them of uncertain status), occurs from Assam, southwestern Yunnan, and southern Annam, south to eastern Bengal, the Malay Peninsula, Thailand, the Andaman and Nicobar Islands, Sumatra, Lingga Archipelago, Java, Borneo, and east to the Philippines (Luzon, Mindoro, Samar, Cebu, Basilan, and [?] Palawan).

Alone among all the species of glossy cuckoos, the Asiatic emerald cuckoo, *C. maculatus*, has been said to have two distinct seasonal, adult-male plumages. Ticehurst (in Stanford and Ticehurst, 1939, pp. 15–16) was the first to call attention to this matter. He was aware of the fact that in the earlier literature only one plumage was described for the adult male, but he found that not only did the birds undergo a complete postnuptial molt (as is normal for practically all birds), but that in the new plumage the upperparts of the body were, not bright green, but coppery-bronze and that the head, ear-coverts, chin, throat, and upper breast became, not solid bright green, but barred, similar in pattern to the rest of the underparts. He further found that there was a less complete spring molt, whereby the solid green of the breeding plumage was once more regained.

If this species had two distinct, seasonal, adult plumages in the male, this would constitute a real biological disparity, for no such situation is known to exist elsewhere in the genus. Examination of a good series of adult males (41 specimens) in the British Museum partly, but not very convincingly, bears out Ticehurst's findings. It suggests that some of the adult males, presumably, but not certainly, birds in the first adult plumage, tend to be more coppery-bronze and less bright green on the upperparts than do other (older?) birds and that these same individuals tend to have the ventral bars more bronze and less green as well. The appearance of a few white bars on the throat and breast of adult males seems to be almost haphazard (about 20 percent of the specimens showed one to three such marks and these are not all examples taken in any one season). Three examples, however, do show what Ticehurst described. Two were collected at Dibrughur in August 1879 by J. R. Cripps, and one at Bangkok, on January 25, 1923 by Sir W. J. F. Williamson. In them the feathers of the forehead and the foreparts of crown, chin, and throat are dark, bright green, conspicuously barred with white, while the posterior parts of the crown, occiput, back, and rump show a mixture of bright-green feathers with some that are darker and more bluish, but hardly coppery bronze as Ticehurst wrote. This is true for the two Dibrughur specimens, but not so for the one collected at Bangkok. Inasmuch as this barred forehead, chin, and throat condition is shown by only 3 out of 41 fully adult males, it is not certain that they really represent a distinct nonbreeding, adult-male plumage. Since no such seasonal plumage is known for any of the other glossy cuckoos, it would seem safer (but not necessarily more accurate) to consider these birds as examples of partly retarded plumage characters, retaining the bar-producing tendencies of the immature stage beyond their usual duration. Deignan (1945, pp. 164–165) apparently considered Ticehurst's nonbreeding plumage stage uncertain, since he referred to one of his specimens as "completing a molt from the juvenal plumage to one like that described by Ticehurst . . . as the dress of 'the adult male in winter.' "

Further evidence of the close relationship between *xanthorhynchus* and *maculatus* is afforded by four examples of males of the former in early or later stages of molt from the immature to the adult dark-purple plumage. In these four specimens, taken in the following localities: two from Lower Pegu, December 20 and January 11, 1878; one from Bangkok, March 5, 1918; and one from Karen-nee, March 15, 1874. The dark abdominal bars on these specimens are bronze-green as in *maculatus*, although the new feathers of the throat and upperparts are the deep purple normal to *xanthorhynchus*. Furthermore, in the females of both species the ventral bars are very similar, bronze-green in color.

It may be noted that in the majority of adult males many of the bright-green feathers of the upperparts have vague subterminal dark, but glossy, bluish areas which almost foreshadow the dark violet of *C. xanthorhynchus*. This is also especially the case with the inner and terminal portions of the remiges, which are often dark purple. This all suggests the not very surprising observation that the difference between the violet *xanthorhynchus* and the dark green *maculatus* is not as great as it might seem and that, in an evolutionary sense, it is quite possible to accept a "leap" of such dimensions between two related species. It may be mentioned, at this point, that considerable purplish tinge occurs in adult females of *lucidus* (in the nominate race, *plagosus*, *layardi*, and *harterti*). While these birds have a dull purplish-bronze color, and not deep-violet as in *xanthorhynchus*, they serve to indicate that the difference between purple and green is less great than the visual appearance of the end result (as developed in *maculatus* and *xanthorhynchus*) might suggest. Also, one cannot help but recall somewhat similar suggestive, green-to-purple plumages in some of the African starlings of the genera *Lamprotornis* and *Cinnyricinclus*. Two male *xanthorhynchus*, in the American Museum of Natural History, both marked "adult," show the extremes of coloration, the upperparts, throat, and breast being purplish-coppery in one and deep violet-blue in the other.

At this point in our reconstruction of the past vicissitudes of *Chrysococcyx* we come to the largest and most serious gap in the available evidence, a gap that separates all the eight Indo-Malaysian-Australian species from the four African ones (*caprius*, *cupreus*, *flavigularis*, and *klaas*). So different are the latter group that it is understandable that a superficial glance at them caused Mathews to think they had little in common with their more eastern relatives and to suggest they may have had a quite separate ancestry. However, this in not an acceptable interpretation, and closer study reveals characters common to both groups. As already mentioned, the absence of any glossy cuckoos from Madagascar and the other, smaller islands of the central and western Indian Ocean suggests that the spread of the group from southern Asia to Africa probably took place in Pliocene or post-Pliocene time. It was, however, sufficiently long ago to have permitted not only much differentiation from their eastern ancestral stock but also to have provided the duration and opportunity for the African glossy cuckoos to have formed two subgroups within themselves, one containing the didric cuckoo, *C. caprius*, and the other comprising the remaining three.

As is usual in phylogenetic reconstructions, there is no concrete evidence by which to prove beyond question which of the four present African species is nearest to the original stock that invaded that continent. Careful comparison of all characters, habits, and distribution makes it probable that the invader is the *klaas-flavigularis* section. These two closely related species are more like (or less unlike) the Indo-Australian members of the genus than are either *caprius* or *cupreus*, and of these two it seems that *flavigularis* is nearer to the original émigré stock to Africa than is *klaas*. This is, admittedly, as in all such evolutionary conclusions, a judgment rather than a proven fact, and because of its nature as a considered opinion it is essential that the evidence be given in detail at this point.

The yellow-throated cuckoo, *C. flavigularis*, is a monotypic, very inadequately known, rarely observed, and seldom even collected bird of the west African forest area. Because of its relative rarity in collections, with a resulting paucity of observations on what may be learned from the examination of specimens, *C. flavigularis* merits discussion in some detail here. It is certainly the least known and least adequately reported of the African members of the genus, and it may well be less known than any of the Indo-Australian forms as well. It is restricted to the forests of equatorial Africa, from Sierra Leone in the west, to the Congo-Uganda border in the east, and south to southern Cameroon and the forests of the lower Congo and of the Kasai area. Although it is wholly restricted to the true forest and does not venture out into the tree-dotted grasslands where its close relative *C. klaas* is found, the latter invades the outer fringes of the denser forest enough so that the two species are occasionally sympatric. Curry-Lindahl (1960, pp. 111–112) found the two together in the forest at Lwiro, in the eastern Congo. The fact of sympatry is evidence of the fully established specific independence of the two, a fact which had not been questioned by anyone in the meager literature of *flavigularis*, but which may be stressed here nonetheless.

In its character of barred underparts in the female and of barred abdomen in the male, *flavigularis* seems somewhat intermediate between the other African glossy cuckoos, where this ventral barring is purely a character of immaturity, and the Asiatic species, *maculatus* and *xanthorhynchus*. It cannot be proved, at this late date, whether the stock presently represented by *flavigularis* was the original invader of Africa from the Orient, or whether its ventral barring is merely a reappearance or a perpetuation of a basic pattern in the old *Chrysococcyx* stock, using that generic name in the broad sense. The species *flavigularis* further agrees with the two mainland Asiatic species in having the bill and feet yellow, not dusky as in its nearest African relative, *klaas*. In as far as it may be possible to postulate an evolutionary sequence from the circumstantial evidence of the contemporary, surviving components of the genus, *flavigularis* may seem to be closer to the original stock that came from Asia to Africa than is any of its other African congeners. Actually, in its ventral barring *flavigularis* has the pattern more narrowly and finely developed than any of the Indo-Australian forms, and even suggests the finely barred pattern of some species of *Cacomantis* (such as *sonnerati*). This point is of suggestive interest, as one cannot wholly dispel the possibility that *Cacomantis*, or some similar stock, may have been the remote ancestor of the glossy cuckoos as a group.

That *flavigularis* is a bird of the West African forest belt is, if anything, what one might expect of a descendant of an originally south Asiatic stock, as most of the Asiatic "relicts" in Africa are found in precisely that area. Admittedly, this is hardly a bit of evidence in itself, but it is worth mentioning because, in a case where so little of the past history of a group may be sensed convincingly from tangible data, even a slight corroborative suggestion is welcome. Whether it represents the primordial stock closely or not, *flavigularis* has remained a strictly sylvan entity like its Asiatic progenitor, and like *maculatus* and *xanthorhynchus* it is difficult to see, to watch, and to collect.

We have already mentioned that *C. klaas* is quite obviously the nearest relative to *flavigularis*, and the closeness of the two will be shown even more in the following discussion of their plumage characters. Especially interesting evidence for this close relationship is afforded by the fact that occasionally *klaas* may produce a female plumage quite similar to that of *flavigularis*. This is certainly not frequent or usual, but it does happen. It is illustrated by a female *klaas* in the British Museum (B.M. 78–12–31–325), *ex* coll. R. B. Sharpe, who got it from Layard from South Africa. It is fortunate that this particular specimen came from an area where no question of its being *flavigularis* could possibly arise, thereby eliminating any question as to its correct identification. This revealing example differs from other young or females of *klaas* in having the entire underparts from chin to upper abdomen and sides pale buffy, narrowly barred with dusky earth-brown, almost as in young or female *flavigularis*, but with the wavy bars more widely spaced and with the middle of the lower abdomen and the under-tail coverts whiter and less barred. It has the wavy crossbars narrower than in any other of several hundred examples of *klaas* examined. It is definitely a female *klaas*, although it shows a surprising trend in the direction of female or juvenal *flavigularis* in the pattern of the underparts. On the top of the head, nape, upper back, and rump it is almost uniformly dull coppery-brown, the scapulars and upper wing coverts bright green barred with cinnamon as in other females of *klaas*. Female *flavigularis* usually have a bronzy wash over the copper-brown of the upperparts, and are usually less brownish, more bronze than in *klaas.*

Another similarity between these two species is the bright green gorget on the sides of the throat in adult males of the two. The fact that the chin and middle of the throat in males of *flavigularis* is bright yellow may be looked upon as a "step" that "ties it in" between *klaas* and *cupreus,* and it is of interest to find that in both *flavigularis* and *cupreus* the yellow fades to white in post-mortem changes in old specimens suggesting an identity in the chemical nature of the pigment in the two.

Some notes on the actual plumage of *flavigularis* based on study of specimens, and comments on what some other authors have written about this species may now be given. Aside from the recorded differences between *flavigularis* and *klaas* in the plumages of females and juvenals, and of the chin and throat color and that of the abdomen, in the males, it may be said that the upper parts of males of *flavigularis* have more coppery-bronze tones than do those of *klaas.* At this point, it may be well to correct one detail in the description given by Mackworth-Praed and Grant (1957, p. 512), who write that the underparts of the body of *flavigularis* are narrowly barred with dark green; it would be more accurate to say it is marked with brown bands with not more than a slightly greenish-bronzy wash.

The tail pattern in *flavigularis* is unique; the two median rectrices are uniform purplish-coppery color, the next pair dark brown glossed with coppery and with white tips and broad, white outer margins to the basal three-quarters of their outer webs; the remaining three pairs are pure white with a subterminal bar of blackish-bronze, the bars becoming narrower centrifugally. In *klaas,* on the other hand, there is no white on the four median rectrices, and the three outer pairs are white with five or six narrow, incomplete dark bars.

Shelley's colored plate (1879, p. 679) accompanying the original description of *flavigularis* shows the bird as having superciliary streaks and the ear-coverts a bright purplish-copper color; these characters are certainly not present in the adult males I have examined. An adult male from River Ja, Cameroon, in the British Museum (B.M. 1911–5–31–119) has the entire top and sides of the head, upper back, lower back, and upper wing coverts a dark bronze-green, quite devoid of any "fiery copper" or "lilac bronze" mentioned by Shelley. Bannerman (1953, vol. 1, p. 583) also gives an inaccurate picture when he writes that *flavigularis* "has not the brilliance in the plumage of the other Golden Cuckoos, the upper side appearing in both sexes more of a purplish bronze . . . ." It is darker green, less glittering but hardly purplish-bronze.

It seems correct, however, to agree with Shelley's conclusion that the *klaas* is the closest living relative of *flavigularis*, and it is reassuring to find that specimens of the latter show this all the more by lacking the excessive coppery or purplish hues described by Shelley when he first made the species known.

In his study of the African glossy cuckoos other than *flavigularis* (which apparently was not available to him at the time), van Someren (1925, pp. 660–662) correctly concluded that *klaas* was more nearly related to *cupreus* than to *caprius*. He listed 10 characters in proof of his conclusions, and we may now review them with *flavigularis* in mind.

1. There is little gold or bronze in the dorsal green color of *klaas* and *cupreus*, while there is much of this in *caprius*. In this respect *flavigularis* agrees with *klaas* but is even duller.
2. Both *klaas* and *cupreus* have a "frosted" appearance in their dorsal feathers, while *caprius* has a smooth, silky appearance. In this regard *flavigularis* has neither.
3. In the adult male *klaas* and *cupreus* have metallic green feathers on the sides of the throat, and *caprius* does not. Here *flavigularis* agrees with the first two.
4. The outer tail feathers of juvenal and female *klaas* and *cupreus* are always white with a few dark bands, while in *caprius* they are always dark with white spots. Again *flavigularis* agrees with *klaas* and *cupreus*.
5. The females of *cupreus* and of *klaas* are always barred on the underside (*flavigularis* even more so); not so in *caprius*.
6. The juvenal plumage of *klaas*, *flavigularis*, and *cupreus* are transversely barred from chin to vent; longitudinally streaked, especially on chin, throat, and breast in *caprius*.
7. The backs of young *cupreus and klaas* are similar in "style of coloration," but not in *caprius*. Just what this means is not clear, but *flavigularis* is much more like young *klaas* than *caprius* above.
8. The form of the bill in *klaas* approaches that in *cupreus*, not in *caprius*. Unfortunately no indication is given as to the differences in bill form in the three, and I can find nothing in *flavigularis* that differentiates it in this respect from any of them.
9. In the scapulars the color is more concentrated toward the tips of the feathers, less extended basally, in *klass* and in *cupreus* than in *caprius*. This is at best a small difference, but in it *flavigularis* agrees with the first two species.
10. The barbules are broad in *klaas*, *flavigularis*, and *cupreus*, and relatively narrow in *caprius*.

From this list of 10 "characters" it becomes evident that *flavigularis* and *klaas* are closely related. The green gorget on the sides of the throat in the adult males of the two is a striking item of similarity, and bridges the gap between them to the extent that the evolutionary history of *klaas* requires little imagination to unravel.

The two remaining species, *caprius* and *cupreus*, are very different from each other. The former is a common, widespread bird of the open bush and tree-dotted grasslands, and the latter is much more of a forest dweller. As we have already seen from van Someren's tabulation of characters and also from Berger's (1955) internal anatomical studies, *cupreus* is closer to *klaas* than to *caprius*, which is rather divergent from both. In an evolutionary sense, however, neither poses any real difficulties of interpretation. They are both "climax" species of the African section of the genus, just as in their ways *meyerii* and *ruficollis* are in New Guinea and *osculans* is in the drier parts of Australia.

Furthermore, it may be pointed out that the plumages of the young birds and of the adult females of the African *klaas*, *cupreus*, and *caprius* are fairly similar in general pattern to those of corresponding stages of the Asiatic *maculatus*. The yellow-bellied emerald cuckoo, *C. cupreus*, has become differentiated into four geographic races; the didric cuckoo, *C. caprius*, has remained monotypic. Both have migratory populations in southern Africa and resident ones (as far as we know) in equatorial Africa.

To round out this discussion of plumages it may be noted that the genus *Chrysococcyx* reveals a tendency to produce rufescent coloration, both as a part of the normal plumage patterns of many of its component species and also as an occasional, complete color phase. Rufescent or hepatic plumage phases occur in different degrees of frequency in a number of genera of cuckoos. This plumage, however, has been found only in immature birds and has been described in the European cuckoo, *Cuculus canorus canorus*, by many authors. It also occurs in the closely related yellow-billed cuckoo of Africa, *Cuculus canorus gularis*, but has not been noted in the other African species of the genus (*solitarius* and *cafer*) or in the Australian *Cuculus pallidus*. Enough examples of these three species have been preserved in collections to make the absence of an hepatic phase a well-established fact. I am not aware of such a rufescent plumage in the young of the Asiatic species of *Cuculus*, but here further search may reveal it.

In the genus *Cacomantis* rufescent plumage is the regular, not the unusual or sporadic coloration. In view of the close phylogenetic connection between it and *Chrysococcyx*, it is suggestive to find this trend well developed there. It is possible to think of this situation as a basic one from which the occasional rufescent tendencies of the glossy cuckoos may have stemmed.

In the glossy cuckoos an hepatic plumage has been noted in two species, the violet cuckoo, *C. xanthorhynchus*, and the didric, *C.*

caprius. In the former species Hume (1875, p. 81) described an immature bird from Upper Pegu with the entire head, neck, chin, and throat pale, rusty rufescent with broad blackish-brown streaks and with the upper parts of the body hair brown. In the British Museum collection I examined a young example of this species (B.M. 82-1-20-989) from Thayetingo that had the entire head, above and below, cinnamon with longitudinal blackish streaks, reminiscent of *Cacomantis*. In the didric cuckoo the hepatic phase has been noted so far only in a few immature females. Such birds are almost wholly bright cinnamon above on the head, nape, back, wings, and tail; the feathers of the back and wings and the upper tail coverts have some greenish crossbars, and the rectrices, greenish-black ones.

In the case of still another glossy cuckoo, *C. klaas*, we find that the females usually have some mixture of coppery-bronze on the top of the head and the upperparts of the body and tail, but this varies, apparently individually. Whether this may be looked upon as a vestigial or, conversely, as an incipient, hepatic morphism is not clear.

It is necessary to stress that the term "plumage phase" is obviously not the same in its implications in the cuckoos as in, for example, the owls of the genus *Otus*. In the latter birds the phase persists throughout the life of the individual and not only for the duration of its immature stage.

The variable extent to which rufescent coloration normally occurs in the tail feathers is a well-known character by which museum taxonomers have long "keyed out" races and species of Australasian glossy cuckoos. Thus, in *C. malayanus* we find the following racial differences in this regard: some rufous on all the rectrices in *russatus;* none or little on the outermost pair of rectrices but considerable on the next three pairs in *minutillus* and *poecilurus;* none on the outermost pair but some on the next two pairs in *malayanus*. In the related species, *C. lucidus*, the nominate, New Zealand race and the New Caledonian subspecies, *harterti*, have no or very little rufous on the next to the outermost rectrix, while the south Australian and Tasmanian race, *plagosus*, has a considerable amount of this color on the inner web of that feather. In the allied *C. basalis* the basal two-thirds of all but the outermost and the median pair of rectrices are rufous. The tendency to produce rufescent pigment in parts of the rectrices appears also in the females of the African species, *klaas* and *caprius*.

The one place in the whole genus *Chrysococcyx* where the most striking and most definite (invariable) production of this rufous color has taken place is in the New Guinea highland species, *C. meyerii*, in which the adult female has a bright-chestnut rufous patch on the forehead and fore-crown, while the male has this area bright, shining green. This unique pattern is quite different from anything found in the rest of the group, but in a large, overall view it may be looked upon as an intensified but morphologically restricted expression of what may have been a basic but unformulated tendency to produce rufescent coloration in the *Chrysococcyx* stock. In this species the basal half of the remiges are rufous, a condition not found in any other member of the genus.

The other color character that shows much irregular variability in the glossy cuckoos is the purplish or coppery-purplish tone that appears at times to replace to a greater or lesser extent the greenish color. This occurs as a relatively minor, subspecific character in *C. lucidus*, in which the Australian race *plagosus* has the top of the head and back of the neck purplish-bronze, instead of green as in the typical New Zealand birds. The distinction between green and purple becomes very marked, and the colors themselves are greatly brightened and intensified in the two closely related Asiatic species, *maculatus*, with glittering emerald plumage, and *xanthorhynchus*, where the purple has been strengthened into a deep violet.

In this connection, we may recall that many years ago Walden (1874, pp. 137–138) described a male *xanthorhynchus* molting into the deep amethystine color of the adult plumage. He noted that some of the feathers of this individual "appear to have changed from green to amethystine without having been moulted. Thus the basal part of one of the median rectrices is more or less green, while the remainder is of a mixed amethystine and greenish hue. Its fellow rectrix, a new feather not fully grown, is coming in of a pure amethystine colour. Several of the upper tail coverts are green at their base . . .". Walden concluded that the old feathers could change from green to purple through abrasion or by fading, but this remains to be demonstrated.

Inasmuch as a number of digressions from the presentation of the relationships of the existing species have been permitted in the above survey, it may be well to recapitulate the whole history of the genus very briefly. It appears that there were three major branchings of evolutionary lineages in the history of the glossy cuckoos, with considerable but less striking speciation in the stock prior to the first, between the first and the second, between the second and the third, and after the third of these major changes. In the original stock, the closest living representative of which is *malayanus*, relatively small morphological divergences resulted in what we know today as *lucidus*, *basalis*, and *ruficollis*, and, with a greater degree of superficial change, *osculans*. Then came the first branching, characterized by a trend toward much more brilliant iridescence in the male and toward sexual dimorphism in the adult plumage. The result of this we see today in *meyerii* of the highlands of New Guinea. This trend was continued in the development of the two species of Asia, *maculatus* and *xanthorhynchus*, and, later, in that of the four African species. However, between *meyerii* and the Asian and African forms a new, important character arose, involving a remarkable change in the pattern of the ventral plumage in the young. In all the species from *malayanus* through *meyerii*, the young have the midventral underparts unmarked, uniform, pale brownish or grayish; in the young of the Asiatic and African species the underparts are heavily crossbarred. From the early stock with this character two species, *maculatus* and *xanthorhynchus*, evolved. In spite of their external, visually great difference (green in the one and violet in the other) they are closely related forms.

At this point there is a great gap in the picture, the four African species being quite different from the Asiatic and Australian ones, but of these four, *flavigularis* and *klaas* seem not too distantly related to *maculatus*, and, as we have seen, they possess so many characters in common with *cupreus* that it becomes evident that they too are closer together in their phylogeny than their very distinct plumage patterns might suggest at first sight. Similarly, *caprius*, while differing in a greater number of details from each of the other three African species than they do from each other, is not more than another very distinct species of the same genus, the ancient steps leading to which have long since disappeared.

On the whole, *flavigularis* and *cupreus* are largely sylvan in their choice of habitat, *klaas* is more a bird of the open, tree-dotted bushveldt (although it does enter into the peripheral forest zones), while *caprius* is an open-country bird. The two Asiatic species, *maculatus* and *xanthorhynchus*, and to a very large extent, *klaas*, are parasites on sunbirds, while *caprius* is much more inclined to use the nests of a great variety of weaverbirds as repositories for its eggs, although it does utilize sunbirds as hosts at times, just as *klaas* occasionally parasitizes weavers. Nothing is known of the host choice of *flavigularis;* those of *cupreus* include weavers, shrikes, flycatchers, warblers, wagtails, and sunbirds, a most heterogeneous assemblage.

The external morphological characters most involved in the series of changes are the following: 1. The degree of iridescence in the plumage, which is only moderately well-developed in *malayanus*, *lucidus*, *basalis*, and *ruficollis*, almost entirely lost in *osculans*, and highly developed in the remaining species, with its acme of development in *cupreus*. 2. The amount and distribution of rufous coloration in the tail feathers in the species forming the earlier part of the history of the group—*malayanus*, *lucidus*, *basalis*, *ruficollis*, and *meyerii*. 3. The change from unmarked to a heavily barred ventral-plumage pattern in the young; unmarked in *malayanus*, *lucidus*, *basalis*, *osculans*, *ruficollis*, and *meyerii;* heavily crossbanded in the others. 4. Sex dimorphism in the adult plumages, well developed in the species beginning with *meyerii*, on through *maculatus* and *xanthorhynchus*, and the four African species (where it is less striking in *caprius* than in the other three). 5. The relative length of the tail, longest in the African species, with its maximum in *cupreus*. 6. Total size, smallest in *meyerii*, largest in *osculans*, *cupreus*, and *caprius*. 7. Differential width of the bill, as exemplified in the sympatric Australian species, *lucidus* and *basalis*.

There are also, as we shall see later in this study, remarkable changes in the coloration of the egg shells; here the picture is incomplete because we still have no information about the eggs of three of the species, *ruficollis*, *meyerii*, and *flavigularis* (to say mothing of the eggs of some of the races of some of the other species).

One point calls for some further clarification. In this summary the results of the study have been outlined as if the relative chronology of the species is certain and simple. It is not, and I must emphasize the speculative, inferential aspect of these conculsions. To make the reconstructed picture of the history of the group more comprehensible to the readers of this report, personally unfamiliar with these birds, it has been necessary to minimize the tentative nature of some of the steps involved. The reader must be aware of the difference between verbal presentation and scientific proof. On the other hand, the circumstantial evidence of the current 12 members of the genus *Chrysococcyx* points to the arrangement here outlined. A diagrammatic representation of their relations, given below, suggests a certain amount of multidirectional radiation, or cladogenesis, not a simple progression from "primitive" to "more advanced."

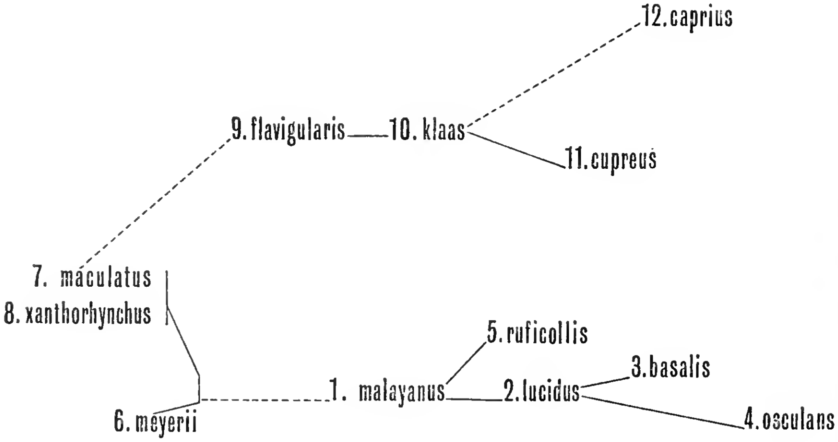


Figure 2. Apparent relationships within the genus *Chrysococcyx*.

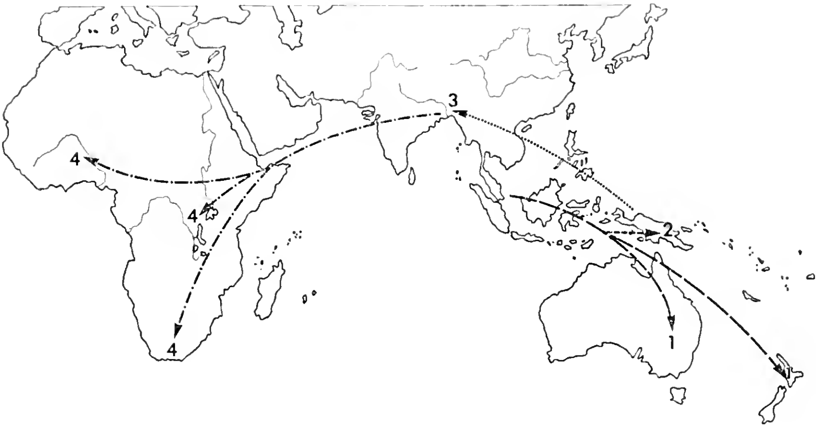


FIGURE 3. Probable evolutionary dispersals of *Chrysococcyx*: 1. dispersal, from Malaysian area to Australia and New Zealand, facilitating the differentiation of *lucidus, basalis, ruficollis,* and *osculans*; 2. secondary movement, to New Guinea with the development of *meyerii*; 3. third dispersal, to southern Asia with the development of *maculatus* and *xanthorhynchus*; 4. fourth dispersal, to Africa with the differentiation of *flavigularis, klaas, cupreus,* and *caprius.*

Migratory behavior

In an evolutionary study such as this, migratory behavior poses two separate problems. The first is the evolution of migration paths and habits within the group; the second has to do with the effects of seasonal movement on further evolution within the members of the genus. A number of authors have emphasized the role migratoriness plays in gene dispersal and have stated that it tends to reduce the chances for subspeciation by mixing up the populations from several breeding areas while in the common nonbreeding, "wintering" grounds each year. Mayr (1963, pp. 417–418) has mentioned the high incidence of monotypic species in the migratory North American warblers, Parulidae, as a case in point. He has also noted that the equally migratory buntings, Emberizidae, on the other hand, show great geographic—or racial—variability, but suggested that this may be due to the fact that they are ground-living birds, perhaps more critically exposed to selective pressures by predators and by microclimates than are the largely arboreal Parulids. The glossy cuckoos are largely arboreal, but they do not present a clear correlation of monotypy with migratoriness or, on the other hand, of polytypy with sedentariness. Thus, three species (*ruficollis, meyerii,* and *flavigularis*) are monotypic and nonmigratory; four others (*basalis, osculans, maculatus,* and *caprius*) are monotypic and migratory; the most highly polytypic species (*mal-*

ayanus) is nonmigratory; one (*lucidus*) is polytypic with two of its four races migratory and two sedentary; two others (*klaas* and *cupreus*) are partly migratory and slightly polytypic; the remaining one (*xanthorhynchus*) is polytypic, but its migratoriness, although not yet known, seems slight and partial.

In the tropics migration of more than very local movement is indulged in by relatively fewer kinds of small land birds than is the case in the temperate areas. Cuckoos, as a family, are among the most migratory of land birds, and in the glossy cuckoos, which are primarily tropical in their distribution (although extending into southern, subtropical areas or even south-temperate regions in New Zealand, southern Australia, Tasmania, and southern Africa), we find every conceivable degree of migratory behavior, from none at all to some of the most outstanding geographic movements known, involving twice-yearly flights of more than 2000 miles nonstop over open seas.

Something of the degree to which migratory behavior occurs in the cuckoos may be realized by a few statements culled from the literature. In New Zealand Hutton (1900, p. 215) noted that the only regular summer visitors (i.e., breeding visitors) to New Zealand are the two parasitic cuckoos that occur there (*Chrysococcyx lucidus lucidus* and *Urodynamis taitensis*). All the other small land birds that breed in those islands are completely sedentary inhabitants of their individual habitats. A few years later W. L. Sclater (1906, pp. 14–21) estimated that, of the 814 species of birds then known to occur in southern Africa south of the Zambezi, 731 were resident and only 21 were considered to be African migrants, as distinguished from Eurasian winter visitors. Of these 21, no fewer than 9 were cuckoos (all parasitic).

Aside from emphasizing that as a family cuckoos are prone to migratoriness, these observations also strongly suggest that the cuckoos came to these southern-subtropical and temperate areas from the tropics and that they did not originate in those breeding areas that they still annually desert during the nonbreeding season. In other words, their present "wintering" ranges give us some suggestive clues as to the areas from which the birds long ago extended their distribution. However, it must be stated by way of caution that this idea, if followed too literally, could present some difficulties that cannot be explained in terms of the contemporary picture. Thus, *C. lucidus lucidus* of New Zealand migrates to the Solomon Islands for its "winter" season. If we were to assume from this that *lucidus* was originally a Solomon Islands bird, we would have to explain why neither it nor any other glossy cuckoo breeds in those islands today. The climate, the vegetation, the presence of potentially suitable hosts (although there are no *Gerygone* warblers, there are fantails, *Rhipidura*—used as a host by *C. malayanus russatus*—and a number of

Meliphagids) are all such as would make the islands suitable for the glossy cuckoos. It is not easy to account for their disappearance as breeders in the Solomons, as would be necessary if we were to assume that they once were there.

On the other hand, Fell (1947, p. 513) took the opposite view and considered that if the southern, breeding range of *C. l. lucidus* and *C. l. plagosus* were considered to be the old home of the two subspecies, then their present migration routes, corresponding as they do with the southeast trade winds, might be looked upon as a consequence of the direction of these strong air movements. He went on to suggest that one might consider the ancestors of these birds (typical *lucidus*) to have been sedentary New Zealand birds, just as two other races of the species (*layardi* and *harterti*) are sedentary to this day, "and that the migratory habit arose as a consequence of recent glacial conditions rendering New Zealand inhospitable in winter. A similar history might have occurred in Tasmania . . . ."

It still seems to me more probable that the southern races of *lucidus* were tropical in origin and then spread southward to their present breeding ranges from which they returned to lower latitudes each year. To say, as Fell does, that New Zealand is inhospitable in the winter can only mean that it is inhospitable to a tropical or semitropical bird.

Before discussing the migratory habits of each of the glossy cuckoos it is necessary to recall that in the case of parasitic birds such as these the adults may leave the breeding area long before the young of the year and that the latter have little or no contact with the former until they meet in the "wintering" grounds. In other words, the birds of the year cannot possibly have any guidance, either directly or indirectly, from older individuals of their own kind. Thus, Dove (1925, pp. 43–44) noted that in Tasmania the adults of *C. lucidus plagosus* and of *C. basalis* leave for the north about the end of February, but that the young of the year remain well into April. In discussing the New Zealand nominate race of *C. lucidus*, Mayr (1932) was moved to write that "the migration of this species is very amazing, and requires a perfect functioning of the entire 'instinct' apparatus. . . . On the average the young birds depart . . . later than the adults. Nobody shows them the migration route, as their foster parents (*Gerygone* and *Rhipidura*) are sedentary. . . ."

One other aspect of migratoriness should be mentioned before we review the picture in each species of *Chrysococcyx*. We shall see that in a number of these species part of the population is migratory and part is not. In the case of three African species, *klaas, cupreus,* and *caprius,* that breed in South Africa as well as in the equatorial portions of the continent, the southern populations are definitely migratory while their more northern relatives are not. Inasmuch as there is no evidence that the more meridional breeders are ecologically or geographically separated from the more northern ones, it is not possible to assume that they are isolated into nonintercommunicating gene pools. Because of this it becomes necessary to describe migratory behavior in these species as partial. As pointed out in my earlier study of a very similar situation in the crested cuckoos of the genus *Clamator* (Friedmann, 1964, p. 76), partial migration is a term used originally for European and North American species in which some individuals are regularly migratory while others, breeding in the same area, are nonmigratory, resident birds. Strangely enough, the tendency toward migratoriness is not necessarily constant throughout successive years of the life of an individual bird, and apparently it is not necessarily an inherited character. This opens the way for a species to increase its range by the migratoriness of some of its members, who the following season or in the following generations become sedentary in their recently established areas of occupancy.

The above considerations lead directly to, and help to elucidate, the situation as we find it in the first species to be examined, *C. malayanus*. This cuckoo, with 11 subspecies, ranges from the Malay peninsula, from Patani southward, Sumatra, and the Philippines (Negros, Mindanao, Basilan, Tawi Tawi, Bongao), Java, Borneo, Celebes, the Lesser Sunda Islands, Babar Island, Biak, the western Papuan Islands (Weigeu, Misol), New Guinea, the Aru Islands, Vulcan, Dampier, and Fergusson Island, to the Moluccas (Halmaharea, Ternate, Buru, Ceram, Goram, Amboina), the Tenimber and Kei Islands, to northern Australia (Cape York peninsula, Arnhem Land, the Kimberly district of northwestern Australia, and northern Queensland). In most of that range it is, so far as known, nonmigratory, but there is some reason for thinking that one population, the race *minutillus* (northwestern Australia, Arnhem Land, and northern Queensland) may be partly migratory. Mayr (1939, pp. 128–129) and Deignan and Amos (1950, pp. 167–168) have shown that specimens obviously referrable to *minutillus* have been taken on the islands of the Lesser Sunda and the Molucca group (where there are resident races), *rufomerus* in the Lesser Sundas, and *crassirostris* in the Moluccas. It is known that *minutillus* is present throughout the year in its known breeding area of northern Australia, where specimens have been taken in all months of the year except August and September, and there is no reason for doubting that, if search were made, they would be found in those two months also. The existence of *minutillus* specimens from the Lesser Sunda Islands, taken in February, April, May, August, September, October, November, and December, raises a question as to what evidence there really is for migratory behavior in this race. It cannot be resident in these islands sympatrically with *rufomerus*, or in the Moluccas along side of *crassirostris*, and still be a race of the same species. Deignan has suggested that it might be necessary to consider *rufomerus* and *crassirostris* as a separate specific group, but this seems unlikely, since the only diagnostic character they have in common and in which they differ from the other forms of *malayanus* is a deep, metallic, bluish-black subterminal area on the central tail feathers.

It would seem (and present knowledge does not permit a stronger word) that *minutillus* may be partly migratory, that these wandering individuals are not breeding birds in the areas to which they roam, or, less likely, that *minutillus* may have achieved a status of genetic distinction enabling it to "invade" the ranges of *rufomerus* and of *crassirostris* without danger of phenotypic swamping. Actually, the whole history of *C. malayanus* with its high degree of geographic morphism suggests that it must have been a geographic "expander" or migrant, but that its members remained as sedentary "founder" groups in the various islands it had encompassed in its expansion.

In *C. lucidus* we have another polytypic cuckoo, with four races, two of which are highly migratory (*lucidus* and *plagosus*) and two resident where found (*harterti* and *layardi*). Much is known of the movements of the two migratory races, as may be seen from the following summary, based largely on the data supplied by Mayr (1932) and more recently and more fully by Fell (1947). The accompanying map is from Van Tyne and Berger (1959, p. 185) based on Fell's report.

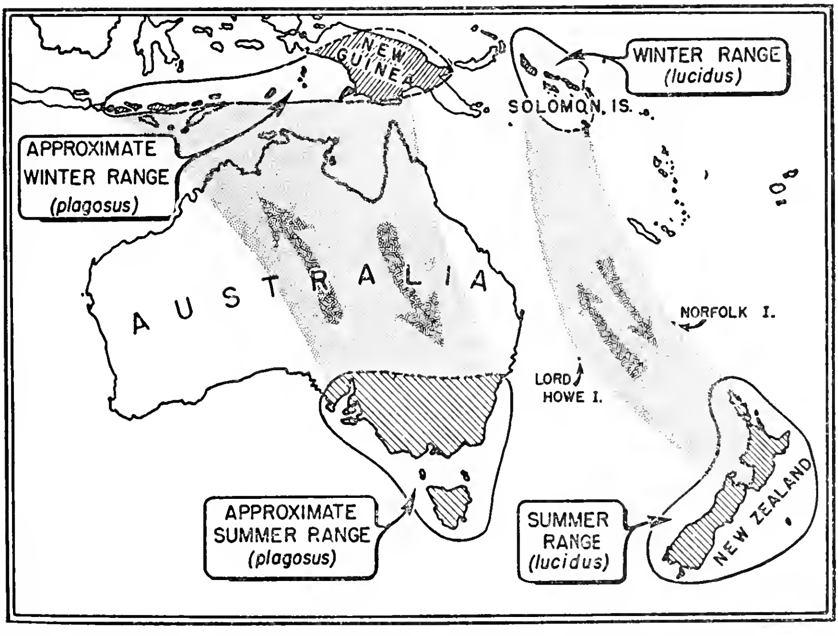


FIGURE 4. Migration of two races of *Chrysococcyx lucidus* (*ex* Van Tyne and Berger)

Typical *lucidus* breeds in New Zealand and Chatham Islands, possibly on Norfolk and Lord Howe Islands, but the detailed data all have to do with New Zealand. The birds begin to leave there late in January with the main migratory exodus in February, a few stragglers delaying their departure until March and even early April, with occasional wintering birds left behind. They begin to return there in mid-September, with the bulk of the birds arriving in October and the latest definite migrant record being November 5. Their nonbreeding grounds are in the Solomon Islands, where the earliest arrivals have been reported on March 16 and the latest departures on September 25. Their migration route, however, is not yet known with certainty. Mayr (1932, pp. 2–5) wrote that "on their way from New Zealand to the Solomon Islands these birds could travel either via New Caledonia and the New Hebrides, or via the Australian coast and eastern New Guinea. For the former route, which would be nearer and more direct, there is no evidence. All the specimens collected in New Caledonia and the New Hebrides are *layardi*." Fell (1947, p. 512) wrote that the data available to him indicated that birds leaving New Zealand in February, March, and April flew " . . . northwest from various headlands across the Tasman Sea via Norfolk or Lord Howe Islands, and then northward to the Solomons. The complete lack of specimens from New Caledonia and New Hebrides, although other subspecies are well known there, seems to show that the New Zealand subspecies cannot normally use that route, if ever. Fig. 7 shows the suggested route as also that probable for the Tasmanian subspecies *C. l. plagosus*, which winters in islands from Lombok to New Guinea. The routes of the two subspecies are roughly parallel, *C. l. lucidus* being displaced about 25° east of the other. The routes seem to correspond roughly with the direction of the South-east Trade Winds. It seems then that the cuckoos are wind-borne from their respective southern breeding lands to their tropical wintering places—and on the return flight are headed into the wind. On neither flight do they fly across the wind . . . ." Van Tyne and Berger's map (fig. 4) shows an amazing direct migration path over 2000 miles of open ocean. While Fell's statement is correct as a general statement, this does not rule out the possibility of some individuals of typical *lucidus* migrating by way of New Caledonia. As a matter of fact, there is one such record, recently reported. Galbraith and Galbraith (1962 p. 35) found that one of Layard's old specimens from Ausevata, New Caledonia, collected on April 26, 1877, is *lucidus* and not, as previously assumed, *layardi*.

The race *plagosus*, which breeds in southern Australia and in Tasmania, winters in the Lesser Sunda Islands (Lombok, Flores, Wetar), in New Guinea, and in the Bismark Archipelago. Its migratory path apparently covers a broad front across much of Australia to New

Guinea and the islands to the west of it. Because it does not cross great expanses of open water its migration may seem less spectacular than that of typical *lucidus*. Yet it would seem likely that much of the vast expanse of the arid country of the Australian interior would offer little to a bird of passage and that *plagosus* may well cover much of it without pausing.

The other two races of *C. lucidus* are nonmigratory, *C. lucidus layardi* in New Caledonia, the Loyalty Islands, New Hebrides, Banks and Santa Cruz Islands; *C. lucidus harterti* in Rennell and Bellona Islands.

The next species, *C. basalis*, is highly migratory. It breeds in Tasmania and southern Australia and "winters" in the Sunda Islands from Java to Sumbawa, but has been recorded also from the Malay Peninsula, Sumatra, Borneo, the Natuna and Kangean Islands, Christmas Island (in the Indian Ocean), and Celebes; it has been noted on migration in the Aru Islands and in the Cape York Peninsula. It appears from the above that it veers generally farther to the northwest in its northern, postnuptial journeying than does *C. lucidus plagosus*, with which it is largely sympatric as a breeder.

Since the next species, *C. ruficollis*, is nonmigratory, we pass on to the following one, *C. osculans*, which is at least partially migratory. The literature on this point gives the impression that, at least in southern Australia, the bird does definitely leave its breeding range at the end of the season, returning there at the start of the next one. Gilbert (1935, p. 22), wrote that in New South Wales the black-eared cuckoo was regularly and "completely migratory." By "completely" he apparently intended to convey the thought that its migration was more definite and obvious to the local observer than was that of *basalis* and *lucidus* (*plagosus*), both of which species he described as incomplete, but regular, migrants. Peters (1940, p. 28) was unable to learn much about *osculans*, writing that the extent to which it is migratory was uncertain, but noting that it had been recorded from the Aru and Kei Islands and from Batjan. It appears to "winter" in the Moluccas, according to van Bemmel (1948) and Mayr (1953), also to a considerable extent in northern Australia. Being essentially a bird of drier areas than the other species of *Chrysococcyx*, it may winter as well in parts of central Australia, where its presence would be undisclosed since there are no observers to report it.

The New Guinea mountain species, *C. meyerii*, is apparently nonmigratory, even in an altitudinal manner. Coming now to the two Asiatic species, *C. maculatus* and *C. xanthorhynchus*, the former is definitely migratory, the latter possibly slightly or only partly so, Even where *xanthorhynchus* is migratory, its movements are largely unrecorded. The little emerald cuckoo, *C. maculatus*, breeds in the highlands from Kumaon through Assam, southeastern portions of Tibet, and Szechwan to Hupeh, and south to Burma, Yunnan, and Annam. It has been recorded in winter or on migration in India, Hainan, Cochinchina, the Malay Peninsula, and Sumatra. The violet cuckoo, *C. xanthorhynchus*, occurs from Assam, southwestern Yunnan and southern Annam, south to eastern Bengal, the Malay Peninsula, Siam, Cochinchina, the Andaman and Nicobar Islands, Sumatra, the Lingga Archipelago, Java, Borneo (including Banguey Island), the Natuna Islands, and the Philippines (Luzon, Mindoro, Samar, Cebu, and Basilan, possibly Palawan). Being a small bird of the treetops, it generally goes unobserved; several observers have told me that it was only occasionally that they found or collected this cuckoo.

These two small, brilliantly colored cuckoos seem in every way so closely related that it is somewhat unexpected to find that they differ as they do in their migratory behavior. It seems that *xanthorhynchus*, with a geographic race, *amethystinus*, in the Philippines, and another possibly dubious one, *bangueyensis*, on Banguey Island off the north shore of Borneo, may originally have been more of a geographic expander than *maculatus*, but that its outlying populations became sedentary and, in time, became subspecifically differentiated.

The yellow-throated cuckoo, *C. flavigularis*, is a nonmigratory bird of the western African forests. The other three African species are all partly migratory—regularly so in their southern populations, all of which regularly desert their South African breeding areas at the close of the season and pass the nonbreeding months in the tropical portions of the continent.

Of the remaining three African species, *C. klaas* is the least consistent in its migratoriness. The didric, *C. caprius*, and the yellow-bellied emerald, *C. cupreus*, have very definite dates of arrival and departure in Africa south of the Zambesi, but *klaas* is considerably less precise. Thus, Clancey (1964, pp. 221–222) wrote that in Natal and Zululand *klaas* was "almost wholly migratory, the majority only on the southern breeding grounds between the months of September and April . . .," but that many overwinter there. Similarly, Benson (1940, p. 402; 1942, p. 212) was aware of even a greater percentage of overwintering individuals in Nyasaland, which caused him to conclude that in that country *klaas* had no regular migration. In eastern equatorial Africa, in Kenya and Uganda, Jackson (1938, pp. 503–509) concluded that *klaas* was subject to partial or local migration. Although it is not clear from his account if part of his apparent uncertainty of the bird's local seasonal movements was due to the annual arrival of "wintering" birds from South Africa, this might have been the case. Farther north, in Ethiopia, Benson (1942, p. 212) found *klaas* to have no regular migration, as contrasted with *caprius*. White (1965, p. 186) summarized the data by calling the species "largely resident, but evidence of migratory movements in some areas . . . ."

Klaas's cuckoo has been divided into three races, but one of these, *arabicus*, known from very slight and unsatisfactory material, is only doubtfully distinct; the other local race, *somereni*, from coastal northern Kenya, seems more valid, but it is yet to be agreed upon by all students of African ornithology. White (1965, p. 186) recognizes neither *arabicus* nor *somereni*. A widely distributed species such as *klaas*, largely resident in much of Africa from Senegal east to the Sudan, Ethiopia and Somalia, south to Angola, Southern Rhodesia, and the eastern Cape Province, might have become differentiated into local races with minor morphological characters, but it has not; *somereni* of north Kenya coastal belt is the only (and small) segment of the total continental population that has become even slightly different (more pronounced white edgings on the wing feathers). Its uniformity can, however, hardly be attributed, even to a small degree, to the partial migratoriness of Klaas's cuckoo.

From the phylogeny suggested earlier in this report of the species of glossy cuckoos, it would seem probable that *klaas* was originally a forest bird like its close relative *flavigularis*. Its extension throughout the bushveld and the tree-dotted parklands of much of Africa was a secondary expansion. Only in the southern part of that expanded range has it encountered seasonal changes marked enough to encourage migratoriness.

The other two African glossy cuckoos, *cupreus* and *caprius* are essentially similar in their seasonal movements to *klaas*, but, in *caprius* particularly, their migration is more definite. Certainly in areas south of the Zambesi the birds are present only in the breeding season, arriving in October, and leaving in late April or early May. In Natal Clancey (1964, pp. 220–221) found *cupreus* and *caprius* to be summer residents (October to April) wintering in equatorial Africa, with *caprius* arriving slightly earlier than *cupreus*. In other parts of Africa there are movements correlated with the rainy season. In my earlier account (1949a, pp. 154–156) I noted that *caprius* was reported as present in Sierra Leone only during the rains, arriving late in April, and that in northern Nigeria its arrival was noted at the beginning of the rains late in May. In Darfur *caprius* arrived in June and remained until September; in Ethiopia it was also noted to occur only during the rains, all birds having departed by the end of May. All this suggests that the didric population of northeastern Africa shifts about, to what location no one knows, at the time when the southern breeding birds are flying northward. In Nyasaland it is a local migrant, and in Zanzibar the resident population is increased by an influx of birds in October and November.

The migratory movements of *klaas*, *cupreus*, and *caprius* offer no suggestive hints as to their respective loci of origin, except that they began in the tropical areas of Africa, not in the southern part.

Premigrational swarming has been reported for two of the glossy cuckoos. Chisholm (1935, p. 257) wrote of *C. basalis* that it has been known to assemble in loose flocks of hundreds of individuals at Cape York late in summer, "apparently bound for northern islands . . . ." Ayres (1884, p. 224) was informed that toward the end of summer in South Africa didric cuckoos (*C. caprius*) "were to be found in hundreds along the Rhinoster river, near Cronstadt, where they were doubtless collecting to migrate . . . ."

Courtship behavior

The courtship behavior of the glossy cuckoos has an evolutionary interest in that it involves an atavistic behavior pattern that can hardly be looked upon as other than a vestige of a distant past when the primordial, ancestral cuckoo stock was not yet parasitic in its breeding. The courting male has the habit of feeding the courted female as if she were a fledgling, and the hen, in turn responds like a young bird with fluttering wings and ruffled body plumage. This pattern has been noted in four species—*lucidus*, *klaas*, *cupreus*, and *caprius*, and since the first is fairly far removed from the other three within the phylogeny of the species of *Chrysococcyx*, it may be assumed that some of the other species will be found to have the feeding pattern as well. In any event, there is no sign, nor is there any reason to expect one, of an evolutionary development of this ethological trait within the genus. It can only be looked upon as an ancestral habit occasionally coming to the surface in these cuckoos. That it appears to be more frequent in this group than in other genera of cuckoos is to be connected with the fact that the glossy cuckoos are also more given to feeding their fledged young than are other parasitic species. (*Cuculus pallidus* is known to feed fledglings of its own kind, but other species of *Cuculus* have not been reported doing so.)

To give some idea of how closely this courtship behavior parallels that of fledgling feeding, we may take the observations of Haydock (1950, p. 150) on the yellow-bellied emerald cuckoo, *C. cupreus*. He saw a female perched on a bare branch of a largely defoliated tree, which circumstances made observation much easier. A male was perched on a branch a little higher up, calling loudly. He then flew down to the female, and, with wings drooping and tail raised almost vertically, he bowed and bobbed up and down in front of her and then presented her with a large hairy caterpillar, transferring this directly from his bill to hers. She accepted and swallowed this gift, the cock bird calling loudly with his head held well back while she did so. The entire performance was repeated shortly afterward, and then coition was attempted but was not accomplished successfully.

In the case of *C. klaas*, Winterbottom (1939, p. 716) wrote that he watched a pair of these cuckoos in Northern Rhodesia (now Zambia). "The male, at least three times while we were watching, caught insects, which it gave to the female. It seemed in a very excited state, and hopped about her with a good deal of posturing, in which the tail played a great part, now lifted aloft like a Wren's, now depressed and held sideways, but remaining silent . . . ."

Beven (1943, p. 237) recorded similar behavior in the didric, *C. caprius*, at Oudsthoorn, South Africa, on October 10. He noted that the cock bird gave its usual call which was answered by the hen, the latter becoming more insistent and frequent as the cock came closer. This was seen a number of times, and each time the male brought and offered caterpillars to the female. On one occasion the cock had to wait with a caterpillar in his bill while the hen was still attempting to swallow one he had given her previously. Jackson (1938, pp. 500–502) also saw a male didric feeding a female several insects. "On each occasion, after presenting it, he faced the female with tail expanded and erect, and bowed to her several times, first to one side and then to the other . . . ."

Watson and Bull (1950, p. 226) noted courtship feeding in *lucidus* in New Zealand, and even suggested that Hursthouse's 1944 record may have been a courtship affair and not a fledgling being fed by an adult as originally described. Fitzgerald (1960, pp. 9–10) has given other instances of courtship feeding in this cuckoo.

Inasmuch as it is not known how regularly and in what quantity male glossy cuckoos offer food to their courtship partners, it is not possible to estimate the nutrient quota involved for the hens. Royama's recent studies (1966) suggest that in some passerine species, especially the great tit and the blue tit, the food supplied by the male is an important supplement and plays a role in enabling the hens to produce their eggs. The present lack of information causes me to question whether a similar importance exists in the glossy cuckoos, but the possibility should be mentioned. Even if courtship feeding may act as an added source of nutriment to the egg-producing hen, the behavior that underlies the habit is still to be looked upon as atavistic.

While courtship feeding is the most interesting and the most revealing aspect of courtship behavior in the glossy cuckoos, it is by no means the only one. Sedgwick (1955, p. 254) commented on a "communal" display of *C. lucidus*, involving three birds on one occasion and five on another, and consisting of a "slow pursuit through the crown of the tree and a rather slow raising and lowering of the wings, often not in perfect synchronization, giving an impression of alternation or an attempt to balance."

Similar communal display antics have been described for *C. lucidus* by Edgar (1960, p. 134), by Fitzgerald (1960, pp. 9–10), and by Watson and Bull (1950, p. 226), while Mathews (1918, p. 358) quoted his correspondent Mattingley to the effect that he had noted six or seven males simultaneously courting a single female, but not in a pursuit flight like the cases described above. Mattingley noted that the cock bird stretches its wings and then leans forward so that its metallic-green back feathers show up clearly; "should the bird be in the sunlight, the colour of its green back is most vivid, and appears like shot silk. . . ." A somewhat similar, but also different, courtship pose is taken by the male of *C. klaas*, according to Winterbottom (1939, p. 716), who wrote that the ordinary display is given high up in trees, and therefore is seldom witnessed. He saw a male, perched about a foot from a hen, go through a series of twistings of the body from side to side without moving its feet, with wings partly spread and drooped, and with the tail partly spread. Here again it would appear that the sideways movement of the courting male is a device for catching the sunlight on its glossy feathers and making them shine during the performance, like the more vertical movements of *C. lucidus*. It is nothing new, but yet serves as a cause for perennial consideration that special plumage colors are related to special movements by which they are utilized in the ethology of their wearers.

Features of brood parasitism in Chrysococcyx

Host selection and its evolution

In our discussion of the phylogenetic relationships of *Chrysococcyx* to *Cacomantis* and *Cuculus* it was pointed out that the glossy cuckoos probably developed out of the stock of which these groups are the present representatives and that these genera are very similar in many ways. It is not surprising, therefore, to find that their host preferences are fairly similar also. This is particularly true for *Chrysococcyx* and *Cacomantis*. The hosts chosen by both are small, insectivorous, passerine birds, and not a few of the species used are parasitized by cuckoos of both genera. It is true that there have been reported a very few instances of glossy cuckoos depositing their eggs in nests of mousebirds, kingfishers, barbets, and woodpeckers, but some of these may be erroneous, or, at best, may be looked upon as unusual, if not accidental, host choices.

In areas where there are a number of kinds of parasitic cuckoos with a considerable range in body size, as is true throughout the entire range of *Chrysococcyx*, it might be expected that the small species, such as the various glossy cuckoos, would tend to parasitize relatively small birds and that larger cuckoos (*Cuculus*, *Clamator*, *Urodynamis*, *Eudynamis*, etc.) would utilize primarily the nests of larger hosts. In a very general way this is what we find, but in Asia and Australia the presence of cuckoos of intermediate size of the genus *Cacomantis* does complicate the situation to some extent. Still, it may be said that there is a general tendency for size correlation between hosts and parasites, although the limits are by no means rigid or constant. This is different from what may be observed in Europe, where *Cuculus canorus*, having no competition from other cuckoos, utilizes a great range of small fosterers, many of them as small as the smallest hosts of the small glossy cuckoos.

In Africa the glossy cuckoos (*caprius*, *cupreus*, and *klaas*) overlap relatively seldom with the larger cuckoos of the genera *Cuculus*, *Clamator*, *Pachycoccyx*, and *Cercococcyx* in their choice of hosts. Strangely enough, the fosterers most frequently serving both *Chrysococcyx* and *Cuculus* are the wagtails, *Motacilla*, and these birds are the only ground-nesting species used with any regularity by the glossy cuckoos. The African glossy cuckoos use primarily species of weavers, sunbirds, warblers, and flycatchers, and relatively seldom parasitize babblers, thrushes, shrikes, and (except for *Chrysococcyx cupreus*) bulbuls, to say nothing about hole-nesting starlings and such larger birds as piapiacs and crows, used extensively by *Clamator glandarius*.

In India, Burma, Siam, and Malaysia, the glossy cuckoos (*maculatus* and *xanthorhynchus*) do overlap in their host choice with *Cacomantis merulinus* (less so with *Cacomantis variolosus*), while in Australia they (*lucidus*, *basalis*, *malayanus*, and *osculans*) find themselves in regular and apparently not unequal competition for many of their usual hosts with several species of *Cacomantis* (*variolosus*, *pyrrhophanus*, and *castaneiventris*), also with *Cuculus pallidus*, and, in New Zealand, even with *Urodynamis taitensis*. To take but a single recent study of the situation in Australia, Rowley (1965, pp. 274–275) found the blue wren, *Malurus cyaneus*, to be parasitized by no less than six species of cuckoos, three glossy cuckoos—*lucidus* (*plagosus*), *basalis*, and *osculans*, by two species of *Cacomantis* (*pyrrhophanus* and *variolosus*), and by *Cuculus pallidus*.

Lest it may seem that excessive use of a single host species by multiple parasites be self-defeating to the extent of seriously depleting the host population, we may recall McGilp's paper (1929, p. 298) in which he discussed a situation "where the Spotted Scrub-Wren (*Sericornis maculata*) [sic] is the foster-parent of several species of Cuckoo. I have worked this area for 10 years, and although hundreds of Cuckoos have been reared during that period, I cannot see that the *Sericornis* has diminished in numbers. In July and early August 75 per cent of the Scrub-Wrens' nests contain one or more eggs of a Cuckoo; later on in the season no Cuckoo eggs are noted. It appears to me that *Sericornis* . . . rears a brood of its own to keep up their numbers. *Sericornis*, in my experience, does not resort to the habit of the Blue Wren (*Malurus*) of embedding the Cuckoos' egg [in the lining material, thus preventing the hatching out of the imposter's egg]."

To turn now to the problem of competition for hosts between the various members of the genus *Chrysococcyx*, obviously more similar to each other than they are to such different, although closely related genera as *Cuculus* and *Cacomantis*, we may note that in areas where two or more species of glossy cuckoos are sympatric as breeders there is a considerable overlap in their host lists. Thus, in southern Asia *maculatus* and *xanthorhynchus* utilize many of the same fosterers; in Africa *caprius* and *klaas* overlap, but on the whole the former is much more prone to use weavers as hosts while the latter uses sunbirds and warblers primarily. The yellow-bellied emerald cuckoo, *C. cupreus*, is apparently, so far as present knowledge goes, an indiscriminate user of both groups of hosts but also lays often in the nests of a bulbul, which the other two do not. Thus, weavers, Ploceidae, account for 78.5 percent of all host records for *caprius* and only 13 percent for *klass*, with 35 percent for *cupreus;* warblers and flycatchers, Sylviidae, account for only 9.5 percent for *caprius* as compared with 47.5 percent for *klass*, and with 15 percent for *cupreus;* sunbirds, Nectariniidae, comprise only 5 percent of the host records for *caprius*, 30 percent for *klass*, and 15 percent for *cupreus*. To these last figures may be added the statement, made orally to me by Pitman, that in his very extensive experience in Uganda he found sunbirds to be the most frequent, almost the "regular," hosts of *klass* and very seldom of *caprius*.

In Australia *basalis* and *lucidus* (*plagosus*) overlap very considerably in their host choices, more than half of their fosterers being parasitized by both species, but they do exhibit some differences in that *lucidus* is largely given to laying in spherical or domed nests rather than open ones, while *basalis* uses all types equally. Thornbills of the genus *Acanthiza* are the most frequently used hosts of *lucidus* (*plagosus*), and, while they are often used by *basalis* as well, the latter cuckoo is more partial to wrens of the genus *Malurus*. About 30 percent of all host records of *lucidus* (*plagosus*) is with species of *Acanthiza*, in *basalis* about 15 percent of the records involves thornbills, while *Malurus* accounts for nearly 30 percent.

In the pages that follow are enumerated the known hosts of all the glossy cuckoos. These data, together with the facts presented elsewhere in this report as to the degree to which host specificity has developed and the degree to which host-egg resemblance has become marked, form the relatively meager body of information that we may interpret as evincing evolutionary trends toward progressive heterogeneity in host fixation among the various species of the group. To meet the need for convenient terms by which to express these variations of host selection, I proposed the following. Alloxenia (with alloxenic as its adjective) may be used to describe cases where each species of parasite uses different host species; homoxenia (with homoxenic as its adjective) may be used for those cases where two or more kinds of parasites make use of the same host species (1967, p. 175).

We are apt to think of *Cuculus* as having gone very far in adaptive host-egg resemblance, but this is mainly because of the development of host-specific "gentes" in one species, *Cuculus canorus*. Certainly other species of the genus do not show anything of comparable evolutionary intensity, and it is to these less specialized parasites that the glossy cuckoos may be compared.

Thus, it appears that *malayanus* is to a large degree bound up in its reproductive pattern with *Gerygone* warblers, and that *osculans* has come to specialize markedly on the speckled warbler, *Chthonicola sagittata* (with the eggs of which its own have close similarity) and to a lesser extent on the redthroat, *Pyrrholaemus brunneus* (to the eggs of which its own bear a fair but less precise resemblance). While it has been claimed by Baker and others that the eggs of *maculatus* and of *xanhorhynchus* indicate adaptive accommodation to sunbird hosts, particularly *Aethopyga* and *Arachnothera*, these eggs are not as highly peculiar in their coloration as are those of *osculans*, and therefore permit one to think their specialization may have been a matter of finding hosts with fairly similar egg types rather than of developing an adaptive pattern in themselves.

The ease with which species such as *lucidus* and *basalis* have been able to make use of the nests of recently introduced, nonnatural hosts as *Passer domesticus, Fringilla coelebs, Carduelis carduelis,* or *Turdus merula* argues against their having evolved rigid, or even fairly obligatory, host preferences. As may be seen in the following accounts of the several species of glossy cuckoos, there is evidence for some host adaptation, but, with the exception of *osculans,* the adaptation has not gone very far in a morphological sense. In the relatively "advanced" African species, *caprius* and *klaas,* there is strong indication of adaptive egg morphism to several divergent hosts, implying an underlying fixity of host selection, which development is not to be seen in what is known of the more "primitive" *malayanus, lucidus,* and *basalis* groups.

C. malayanus.

Host choices are known for less than half of the subspecies of this cuckoo. In the case of three of them, only warblers of the genus *Gerygone* have been reported thus far, and it is likely that these birds are the most frequently used hosts. However, more complete knowledge may reveal a less rigidly obligate dependence on *Gerygone* than is suggested by the current data (e.g., in the northern Australian and New Guinea races of the cuckoo, *russatus* and *minutillus*, it is known that fantails and honeyeaters also serve as hosts). However, in the case of *russatus*, where more observations have been put on record than with *minutillus*, while 4 of the 11 fosterers are species of *Gerygone* these 4 account for more than two-thirds of all host records, with no fewer than 11 records for *G. magnirostris* and 5 for *G. palperbrosa*. The former of these two species is also known to be the chief host of the cuckoos of the subspecies *minutillus*.

The total reported fosterers are listed below.[1]

Host	Race of *Chrysococcyx malayanus**				
	malayanus	*russatus*	*minutillus*	*albifrons*	*poecilurus*
Gerygone magnirostris		X	X		X
Gerygone brunneipectus		X			X
Gerygone palpebrosa		X	X		
Gerygone olivacea			X		
Gerygone flavida		X			
Gerygone sulphurea	X			X	
Heteromyias cinereifrons		X			
Rhipidura setosa		X			
Malurus melanocephalus		X			
Malurus amabilis			X		
Cyrtostomus frenatus		X			
Gliciphila fasciata		X	X		
Meliphaga lewinii		X			
Meliphaga fasciogularis		X			

*No hosts yet known for the other races of this cuckoo.

---

[1] For pertinent published data see: *C. m. malayanus*—Bromley 1941, pp. 140–146; Hoogerwerf 1949, p. 91; Makatsch 1955, p. 188; North 1895, p. 39; 1912, p. 28; *C. m. russatus*—Barnard 1926, pp. 6–7; Cayley 1950, p. 69; Chisholm 1925, p. 164; Le Souëf 1898, p. 59; Macgillivray 1914, p. 163; Mack 1930, pp. 302–303; Makatsch 1955, p. 189; Mathews 1918, p. 366; Schönwetter 1964, p. 571; White 1915, p. 152; *C. m. minutillus*—Barnard 1914, p. 43; Campbell 1901, pp. 584–585; Cayley 1950, p. 70; Le Souëf 1898, p. 59; Makatsch 1955, p. 189; Mathews 1914, p. 116; North 1895, p. 39; Schönwetter 1964, p. 571; White 1915, pp. 153–154; *C. m. albifrons*—Bartels 1925, pp. 54–61; Hoogerwerf 1949, pp. 91–92; Makatsch 1955, p. 189; Schönwetter 1964, p. 570; *C. m. poecilurus*—Dodd 1913, pp. 190–191; Makatsch 1955, p. 189; Rand 1942, p. 313; Schönwetter 1964, pp. 570–571.

C. lucidus.

The various races of this cuckoo are so unequally well known that it seems advisable to list their known hosts separately. At this point, however, it may be stated that all the known fosterers of its various geographic segments are small insectivorous birds and that the little warblers comprising the genus *Gerygone* appear to be the most frequently chosen hosts. Fantails, robins, sunbirds, and honeyeaters are also used, and even the introduced house sparrow, chaffinch, and blackbird are occasionally parasitized in New Zealand.

C. lucidus lucidus.

The nominate New Zealand race of the shining cuckoo has been found to parasitize eight native and three introduced species of birds.[2] From the literature and the unpublished records kindly sent me by their observers I have been able to amass some 58 cases of parasitism, no fewer than 40 of which involved *Gerygone igata*, which must, then, be considered the primary host. In this connection it may be noted that in Australia the allied cuckoo race, *C. l. plagosus*, also uses *Gerygone* warblers but less frequently than it does thornbills (*Acanthiza*).

The known fosterers are as follows:

Mohoua albicilla	Whitehead
Gerygone igata	Gray warbler
Gerygone albofrontata	Chatham Island warbler
Petroica melanocephala	Yellow-breasted tomtit
Miro australis	Toutouwai
Rhipidura flabellifera	Piwakawaka
Zosterops lateralis	Gray-breasted silvereye
Turdus merula	Blackbird
Anthornis melanura	Bellbird
Passer domesticus	House sparrow
Fringilla coelebs	Chaffinch

C. lucidus layardi.

This race of the shining cuckoo is yet to be studied for its host choice. The only statement in the literature is the assumption that the chief host (!) is likely to be *Gerygone flavolateralis* (Makatsch, 1955, p. 188), which assumption is based on a mention by Mayr to the effect that the distribution of *C. l. layardi* is probably coordinated with that of this "favorite" host.

---

[2] For pertinent references to published records see: Buller 1888, p. 132; Cayley 1950, p. 70; Fulton 1910, pp. 392–408; Makatsch 1955, p. 188; Michie 1948, p. 196; North 1912, p. 28; Oliver 1955, pp. 533–536; Parkin 1954, p. 207; Schönwetter 1964, p. 570; Stildolph 1939, pp. 84–93; White 1915, p. 152.

C. lucidus plagosus.

The south Australian and Tasmanian race of the glossy cuckoo has such a long list of recorded hosts, in contrast with much shorter list for the New Zealand race and the absence of such lists for some of the other subspecies of *C. lucidus*, that it seems advisable to discuss it apart from its conspecific relatives. Thanks to the kind assistance of numerous Australian observers I have been able to add to the published data many additional cases of the parasitism of this cuckoo, and now have a corpus of some 167 records involving 75 species.[3] No attempt has been made to "break down" these records to subspecies because there exists no agreed-upon reference list of valid races of Australian birds.

Of the 75 species included in the list 51 are known as fosterers of this cuckoo on the basis of single records only; 12 others have been reported twice as victims of the glossy cuckoo, 5 have been so noted three times, 2 four times, and only 5 have been noted as fosterers five or more times. In descending order of frequency the most important hosts are the following: yellow-tailed thornbill, *Acanthiza chrysorrhoa*, 40 times; brown thornbill, *Acanthiza pusilla*, 13 times; straited thornbill, *Acanthiza lineata*, and buff-tailed thornbill, *Acanthiza reguloides*, 7 times each; white-throated warbler, *Gerygone olivacea*, 6 times; brown warbler, *Gerygone richmondi*, and little thornbill, *Acanthiza nana*, 4 times each; large-billed warbler, *Gerygone magnirostris*, brown weebill, *Smicrornis brevirostris*, blue wren, *Malurus cyaneus*, yellow-tipped diamond bird, *Pardalotus striatus*, and yellow-winged honeyeater, *Meliornis novaehollandiae*, 3 times each.

Of the 75 species (89 species and subspecies) of birds parasitized by this cuckoo, one-third (25 species or 38 species and subspecies) are not known to be used by *C. basalis;* all the others serve to unequal degrees as hosts to both parasites.

Thornbills are thus the favorite hosts of this cuckoo, with the *Gerygone* warblers next. Thornbills, with 8 species and 71 records of parasitism, account for a little over 10 percent of all the hosts and over 30 percent of all instances of parasitism. This figure is un-

---

[3] For pertinent published references see: Barnard and Barnard 1925, p. 261; Barrett 1905, p. 22; Campbell 1898a, pp. 144–146; 1901, pp. 582–583; Carter 1924, p. 228; Cayley 1950, p. 71; Chandler 1910, p. 245; Cornwall 1907, p. 192; Dove 1916, p. 96; Fletcher 1915, p. 166; Hall 1898, p. 75; 1901, p. 128; Hanscombe 1915, p. 160; Hobbs 1961, p. 42; Howe 1905, p. 35; Jackson 1908, p. 202; Linton 1930, pp. 304–307; Littlejohns 1943, pp. 250–251; Makatsch 1955, p. 188; Mathews 1918, p. 359; Mattingley 1906, p. 66; McGilp 1929, p. 298; North 1893, p. 373; 1897, p. 26; 1912, pp. 20–23; Orton and Sandland 1913 p. 78; Ross 1913, p. 280; Rowley 1965, pp. 274–275; Sandland and Orton 1922, p. 137; Serventy and Whitell 1962, pp. 269–270; Smith 1926, p. 296; White 1908a, p. 31; 1910, p. 49; 1915, pp. 152–153.

doubtedly lower than it should be as the regular hosts are less invariably reported than are the seldom-used ones. In the Barrington area of New South Wales, Lindsay Hyem (*in. litt.*) found that about 50 percent of all *plagosus* eggs were laid in nests of *Acanthiza chrysorrhoa* alone. The *Gerygone* warblers, with 6 species and 16 records, account for 8 percent of all the hosts and 10.9 percent of all instances of parasitism compiled.

Hirundo neoxena	Welcome swallow
Hylochelidon nigricans	Tree martin
Rhipidura fuliginosa	Gray fantail
Rhipidura leucophrys	Willie wagtail
Myiagra rubecula	Leaden flycatcher
Myiagra cyanoleuca	Satin flycatcher
Monarcha trivirgata	Spectacled flycatcher
Microeca leucophaea	Brown flycatcher
Petroica multicolor	Scarlet robin
Petroica goodenovii	Red-capped robin
Petroica phoenicea	Flame robin
Petroica rhodinogaster	Pink robin
Melanodryas cucullata	Hooded robin
Amaurodryas vittata	Dusky robin
Heteromyias cinereifrons	Gray-headed robin
Poecilodryas cerviniventris	Buff-sided robin
Eopsaltria australis	Southern yellow robin
Colluricina harmonica	Gray shrike thrush
Lalage sueurii	White-winged triller
Epthianura albifrons	White-fronted chat
Epthianura tricolor	Crimson chat
Epthianura aurifrons	Orange chat
Gerygone olivacea	White-throated warbler
Gerygone richmondi	Brown warbler
Gerygone flavida	Fairy warbler
Gerygone magnirostris	Large-billed warbler
Gerygone mouki	Northern warbler
Gerygone fusca	White-tailed (Western) warbler
Smicrornis brevirostris	Brown weebill
Acanthiza lineata	Striated thornbill
Acanthiza nana	Little thornbill
Acanthiza inornata	Western thornbill
Acanthiza ewingii	Tasmanian thornbill
Acanthiza pusilla	Brown thornbill
Acanthiza uropygialis	Chestnut-tailed thornbill
Acanthiza reguloides	Buff-tailed thornbill

Acanthiza chrysorrhoa	Yellow-tailed thornbill
Acanthornis magnus	Scrub-tit
Sericornis maculatus	Spotted scrub-wren
Sericornis lathami	Yellow-throated scrub-wren
Sericornis magnirostris	Large-billed scrub-wren
Calamanthus campestris	Rufous field-wren
Chthonicola sagittata	Speckled warbler
Megalurus gramineus	Little grassbird
Acrocephalus australis	Australian reed warbler
Cisticola exilis	Golden-headed fantail warbler
Stipiturus malachurus	Emu wren
Malurus cyaneus	Blue wren
Malurus callainus	Turquoise wren
Malurus splendens	Banded wren
Malurus leuconotus	Black-and-white wren
Malurus melanocephalus	Red-backed wren
Artamus personatus	Masked wood-swallow
Artamus cinereus	Black-faced wood-swallow
Neositta chrysoptera	Orange-winged sittella
Ctimacteris picumnus	Brown tree-creeper
Pardalotus punctatus	Spotted diamond bird
Pardalotus striatus	Yellow-tipped diamond bird
Cyrtostomus frenatus	Yellow-breasted sunbird
Zosterops gouldi	Western Silvereye
Zosterops lateralis	Gray-breasted silvereye
Melithreptus brevirostris	Brown-headed honeyeater
Myzomela nigra	Black honeyeater
Acanthornis tenuirostris	Eastern spinebill
Acanthornis superciliosus	Western spinebill
Gliciphila melanops	Tawny-crowned honeyeater
Meliphaga chrysops	Yellow-faced honeyeater
Meliphaga leucotis	White-eared honeyeater
Meliphaga cassidix	Helmeted honeyeater
Meliphaga ornata	Yellow-plumed honeyeater
Meliphaga penicillata	White-plumed honeyeater
Meliornis novaehollandiae	Yellow-winged honeyeater
Passer domesticus	House sparrow
Aegintha temporalis	Red-browed finch
Neochmia phaeton	Crimson finch

C. basalis.

This species has the longest list of fosterers of any of the glossy cuckoos, comprising 100 species of birds. This figure makes no attempt to enumerate the subspecies involved, as the members of the Australian checklist committee are still undecided about many of them. In the following list the known hosts are merely listed by species in the order of the 1926 Australian checklist, but with their nomenclature brought up to date.[4]

If one considers the large amount of raw data summarized in this mere list, it is unfortunate to have to say that it does not convey a very realistic picture in some important respects. Thus, while I have had much kind cooperation from numerous Australian correspondents, the records here amassed are frequently without detailed information, and, as might be expected, it is often difficult to assess the frequency with which certain species are parasitized. Unusual host records are more apt to be reported than are repetitive ones of the frequent hosts, and it is the latter that are really important in the biology of the cuckoo. All in all, I have been able to compile some 386 records for these 100 hosts, and of these 100 fosterers 26 are included on the basis of only a single record apiece, 31 on the basis of two instances each, 16 on the basis of three records, 7 on the basis of four, and 20 are species for which there are five or more known instances of parasitism.

The fairy wrens of the genus *Malurus*, the thornbills, *Acanthiza*, and the robins, *Petroica*, are the most frequently used victims. Ten species of *Malurus* account for 109 records, or 28 percent of the total, and of these the blue wren, *M. cyaneus*, leads with 62 records, or 16 percent of the total, with the black-and-white wren, *M. leuconotus* second with 15 records. These figures are probably far too low, as only a smaller percentage of records of commonly used hosts are published, as compared to the fact that almost all unusual ones do find their way into print eventually. Thus, in a recent letter Lindsay Hyem wrote that in his area, near Barrington, New South Wales, *basalis* is very selective, probably 90 percent of their eggs being laid in nests of the blue wren. His statement is by no means unique, but he thought that

---

[4] For pertinent published references see: Barnard 1915, p. 43; Barnard and Barnard 1925, p. 260; Campbell 1898b, pp. 151–154; 1902, p. 12; 1906, p. 197; 1913, p. 71; 1927, pp. 300–301; Carter 1903, p. 89; Cayley 1950, p. 70; Chenery 1924, p. 224; Chisholm 1920, pp. 315–316; Cleland 1924, p. 181; Cohn 1924, p. 76; de Warren 1926, p. 78; Dickison 1928, p. 151; Dove 1924, p. 156; 1928, p. 224; Gilbert 1935, p. 22; Givens 1925, p. 28; Hill 1907, p. 21; Hill 1903, p. 165; Hobbs 1961, p. 42; Howe 1910, p. 163; 1913, p. 190; 1928a, p. 216; Kikkawa and Dwyer 1962, p. 169; Leach 1928, p. 91; 1929, pp. 180–181; Littlejohns 1943, pp. 250–251; Littler 1910, p. 85; Macgillivray 1914, p. 163; 1924, p. 15; Mc Gilp 1921, p. 240; 1923, p. 279; 1925, p. 5; 1926, p. 278; 1935, p. 12; Mellor 1917, p. 18; North 1893, p. 373; 1894, p. 327; 1895, p. 39; 1897, p. 26; 1912, p. 26; Orton and Sandland 1913, p. 78; Parsons 1918, p. 145; Ross 1913, pp. 280–281; 1919, p. 303; 1926, p. 137; Rowley 1965, pp. 274–275; Sandland 1909, p. 150; Schnöwetter 1964, p. 569; Serventy 1929, p. 192; Serventy and Whitell 1948, p. 237; 1962, p. 268; Smith 1926, p. 296; White 1910, p. 49; 1915, pp. 150–152; Whitlock 1910, p. 193; Wilson 1914, p. 170; 1918, p. 235.

possibly the fact that *basalis* is not numerous in his area may help to maintain their host electivity to so high a degree. Several authors have written of *M. cyaneus* that it is the most frequent host for *basalis*, some even calling it the "invariable" one. The thornbills, *Acanthiza*, also with 10 species, account for 58 records, or 15 percent of the total. The most frequently imposed upon of these birds is the yellow-tailed thornbill, *A. chrysorrhoa*, with 18 records, followed by three other species, *A. pusilla* with 11 records, *A. uropygialis* with 9, and *A. reguloides* with 8. The robins of the genus *Petroica*, involving 5 species, have been found to be parasitized 29 times, with the scarlet robin, *P. multicolor*, leading with 11 records, the red-capped robin, *P. goodenovii* with 10, the hooded robin, *P. cucullata*, with 4, the rose robin, *P. rosea*, with 3, while the flame robin, *P. phoenicea*, is known by me as a host on the basis of a single report.

Honeyeaters, family Meliphagidae, with 21 species involved, figure on the list with a total of 39 records, with 5 reported instances for one of the species, the tawny-crowned honeyeater, *Gliciphila melanops*, 4 cases for the yellow-winged honeyeater, *Meliornis novaehollandiae*, and 3 or fewer for the rest.

As might have been expected, small passerine birds are the regular hosts of this cuckoo, the one record for the diamond dove being an obvious "freak" occurrence.

Geopelia cuneata	Diamond dove
Hirundo neoxena	Welcome swallow
Microeca leucophaea	Brown flycatcher
Rhipidura fuliginosa	Gray fantail
Rhipidura rufifrons	Rufous fantail
Rhipidura setosa	Northern fantail
Rhipidura leucophrys	Willie wagtail
Myiagra cyanoleuca	Satin flycatcher
Seisura inquieta	Restless flycatcher
Petroica multicolor	Scarlet robin
Petroica goodenovii	Red-capped robin
Petroica phoenicea	Flame robin
Petroica rosea	Rose robin
Petroica cucullata	Hooded robin
Heteromyias cinereifrons	Gray-headed robin
Eopsaltria australis	Southern yellow robin
Epthianura albifrons	White-fronted chat
Epthianura tricolor	Crimson chat
Epthianura aurifrons	Orange chat
Gerygone olivacea	White-throated warbler
Gerygone richmondi	Brown warbler
Gerygone magnirostris	Large-billed warbler

Gerygone levigaster	Buff-breasted warbler
Gerygone fusca	White-tailed (Western) warbler
Gerygone mouki	Northern warbler
Gerygone palpebrosa	Black-throated warbler
Smicrornis brevirostris	Brown weebill
Aphelocephala leucopsis	Eastern whiteface
Aphelocephala castaneiventris	Western whiteface
Aphelocephala nigrocincta	Banded whiteface
Acanthiza lineata	Striated thornbill
Acanthiza ewingii	Tasmanian thornbill
Acanthiza pusilla	Brown thornbill
Acanthiza nana	Little thornbill
Acanthiza hamiltoni	Red-tailed thornbill
Acanthiza robustirostris	Robust thornbill
Acanthiza uropygialis	Chestnut-tailed thornbill
Acanthiza reguloides	Buff-tailed thornbill
Acanthiza chrysorrhoa	Yellow-tailed thornbill
Acanthiza iredalei	Sapphire (dark) thornbill
Sericornis lathami	Yellow-throated scrub-wren
Sericornis magnirostris	Large-billed scrub-wren
Sericornis maculatus	Spotted scrub-wren
Sericornis frontalis	White-browed scrub-wren
Hylacola pyrrhopygia	Chestnut-tailed heath-wren
Hylacola cauta	Mallee heath-wren
Calamanthus fuliginosus	Striated field-wren
Calamanthus campestris	Rufous field-wren
Chthonicola sagittata	Speckled warbler
Amytornis striatus	Striated grass-wren
Megalurus gramineus	Little grassbird
Acrocephalus australis	Australian reed warbler
Cisticola exilis	Golden-headed fantail-warbler
Stipiturus malachurus	Emu wren
Malurus cyaneus	Blue wren
Malurus melanotus	Black-backed wren
Malurus callainus	Turquoise wren
Malurus splendens	Banded wren
Malurus leucopterus	Blue-and-white wren
Malurus leuconotus	Black-and white wren
Malurus lamberti	Variegated wren
Malurus assimilis	Purple-backed wren
Malurus amabilis	Lovely wren
Malurus melanocephalus	Red-backed wren
Neositta chrysoptera	Orange-winged sittella
Neositta pileata	Black-capped sittella

Dicaeum hirundinaceum	Mistletoe bird
Pardalotus punctatus	Spotted diamond bird
Cyrtostomus frenatus	Yellow-breasted sunbird
Zosterops gouldi	Western silvereye
Zosterops lateralis	Gray-backed silvereye
Melithreptus atricapillus	White-naped honeyeater
Melithreptus affinis	Black-headed honeyeater
Melithreptus brevirostris	Brown-headed honeyeater
Myzomela sanguinolenta	Scarlet honeyeater
Myzomela nigra	Black honeyeater
Acanthornis tenuirostris	Eastern spinebill
Acanthornis superciliosus	Western spinebill
Gliciphila melanops	Tawny-crowned honeyeater
Gliciphila albifrons	White-fronted honeyeater
Gliciphila indistincta	Brown honeyeater
Gliciphila fasciata	White-breasted honeyeater
Meliphaga lewinii	Lewin honeyeater
Meliphaga leucotis	White-eared honeyeater
Meliphaga chrysops	Yellow-faced honeyeater
Meliphaga fasciogularis	Mangrove honeyeater
Meliphaga ornata	Yellow-plumed honeyeater
Meliphaga penicillata	White-plumed honeyeater
Meliphaga flava	Yellow honeyeater
Phylidonyris pyrrhoptera	Crescent honeyeater
Meliornis novaehollandiae	Yellow-winged honeyeater
Meliornis niger	White-cheeked honeyeater
Passer domesticus	House sparrow
Steganopleura bichenovii	Double-barred finch
Taeniopygia castanotis	Zebra finch
Aegintha temporalis	Red-browed finch
Zonaeginthus guttatus	Spotted-sided finch
Poephila cincta	Black-throated finch
Carduelis carduelis	Goldfinch
Chloris chloris	Greenfinch

C. osculans.

The black-eared cuckoo has been found to parasitize 11 species of birds, as follows.[5]

Aphelocephala leucopsis	Eastern whiteface

---

[5] For pertinent references see: Alexander, 1925, p. 237; Cayley 1950, p. 74; Chisholm 1935, p. 69; Gilbert and Keane 1913, pp. 80–82; Hill 1907, p. 21; Howe 1928b, p. 259; Makatsch 1955, pp. 182–183; McGilp 1923, p. 279; 1956, p. 12; North 1912, pp. 15–18; Orton and Sandland 1913, p. 78; Rowley 1965, pp. 274–275; Sandland 1909, pp. 150–151; Schönwetter 1964, p. 567; Serventy and Whitell 1962, p. 268; White 1908b, p. 158; 1915, p. 150.

Acanthiza chrysorrhoa	Yellow-tailed thornbill
Sericornis lathami	Yellow-throated scrub-wren
Sericornis maculatus	Spotted scrub-wren
Pyrrholaemus brunneus	Redthroat
Hylacola pyrrhopygia	Chestnut-tailed heath-wren
Hylacola cauta	Mallee heath-wren
Calamanthus isabellinus	Rusty field-wren
Chthonicola sagittata	Speckled warbler
Malurus cyaneus	Blue wren
Malurus assimilis	Purple-backed wren

The chief host, almost the exclusive one in some areas, is the speckled warbler, *Chthonicola sagittata,* while the next most frequently victimized fosterer is the redthroat, *Pyrrholaemus brunneus.* The dark, chocolate-brown eggs of *Chrysococcyx osculans* match those of *Chthonicola* very closely and those of *Pyrrholaemus* fairly well.

Of 53 instances of parasitism amassed from published as well as from unpublished sources, 34 involved *Chthonicola sagittata,* 9 *Pyrrholaemus brunneus,* 3 *Acanthiza chrysorrhoa,* 2 *Malurus assimilis,* and 1 each for the other host species. In other words, 80 percent of the total is of the two chief hosts, and a little over 60 percent refers to a single one, the speckled warbler.

While there is no reason to question the suitability of the regular hosts as fosterers of the young parasite, there is still little in the published record to document the fact that they can and do rear them successfully. As far as I have been able to learn, two of the less frequent hosts, *Malurus assimilis* and *Hylacola pyrrhopygia,* have been recorded explicitly as having been seen rearing and feeding nestlings or recent fledglings of the black-eared cuckoo. From one published source and two unpublished ones I have found documentation of similarly successful rearings by the speckled warbler, *Chthonicola sagittata.*

C. maculatus.

The Asiatic emerald cuckoo is known to parasitize babblers, warblers, and sunbirds, chiefly members of the latter two families.[6] The hosts listed below are taken from the literature, and I have been obliged to accept some of them as published. It should be kept in mind, however, that the eggs of this cuckoo and of the violet cuckoo, *C. xanthorhynchus,* are practically indistinguishable, and the original identifications were based on little more than the mere fact that the observerer noted only one of the two cuckoos in the area. As far as the biological implications of host choice are concerned, this makes

---

[6] For pertinent references to published records see: Ali 1962, p. 56; Baker 1907, pp. 682, 684; 1908, p. 278; 1927, pp. 162–163; 1942, p. 195; Dewar 1925, p. 154; Makatsch 1955, p. 186; Schönwetter 1964, pp. 568–569; Smythies 1953, p. 325.

little difference as these two cuckoos appear to use the same or a very similar range of fosterers.

The recorded hosts of the little emerald cuckoo are:

Stachyris nigriceps	Black-throated babbler
Stachyris ruficeps	Red-headed babbler
Tesia cyaniventer	Dull slate-bellied ground warbler
Bradypterus luteoventris	Brown bush warbler
Cisticola juncidis	Fantail warbler
Cettia fortipes	Strong-footed bush warbler
Orthotomus sutorius	Tailor-bird
Phylloscopus reguloides	Blyth's leaf warbler
Seicercus castaneiceps	Chestnut-headed flycatcher-warbler
Aethopyga siparaja	Yellow backed sunbird
Aethopyga gouldiae	Mrs. Gould's sunbird
Arachnothera longirostris	Little spider-hunter

C. xanthorhynchus.

The violet cuckoo is still imperfectly known and will probably continue to be so because of its preference for the higher branches of trees where it is observed with difficulty. Eggs or young attributed to it have been recorded with nine species of fosterers, chiefly warblers and sunbirds, but also babblers and one flower-pecker.[7] Because of the close similarity of the eggs of this cuckoo and those of its close relative *C. maculatus* and the overlapping of the ranges of the two, the identifications of some of the egg records may be less than completely certain, but they are given here as identified by their collector-observers.

All of the known hosts are involved with the nominate, mainland subspecies of the violet cuckoo. So far no one has reported any eggs or young of the Philippine race, *amethystinus*, or the Banguey Island race, *bangueyensis*.

The hosts reported to date are:

Trichastoma abbotti	Abbott's babbler
Napothera epilepidota	Small wren-babbler
Alcippe nipalensis	Nepal babbler
Cisticola juncidis	Fantail warbler
Orthotomus sutorius	Tailor bird
Seicercus xanthoschistus	Gray-headed flycatcher-warbler

---

[7] For pertinent references to published records see: Baker 1907, p. 682; 1927, p. 163; 1942, p. 195; Dewar 1925, p. 154; Hoogerwerf 1949, p. 91; Inglis 1908, p. 681; Makatsch 1955, pp. 186–187; Schönwetter 1964, pp. 569–570; Smythies, 1953, p. 325.

Dicaeum agile	Thick-billed flower-pecker
Aethopyga siparaja	Yellow-backed sunbird
Arachnothera longirostris	Little spider-hunter

It may be mentioned that Baker (1927, p. 163) considered *Cisticola* as probably an "abnormal" fosterer, but he accepted the record as an actual occurrence. Its nesting site is certainly different from the arboreal situations used by the other hosts chosen by the violet cuckoo.

C. klaas.

Klaas's cuckoo is now fairly well known, insofar as many, but casual, observations may be said to constitute an acquaintance with a species. It resembles the didric, *C. caprius*, in many ways, and the two are often ecologically sympatric. Like the didric, the Klaas's cuckoo evinces a wide range of choice of passerine hosts.[8]

Klaas's cuckoo has been found to parasitize 59 species (80 species and subspecies), 21 of which are also known to be victims of the didric. However, aside from species recorded as hosts but a single time for each of these two cuckoos, few of these fosterers are affected equally often by both species of glossy cuckoos. In fact the tawny-flanked longtail, *Prinia subflava*, recorded as a host of *C. caprius* 16 times and of *C. klaas* 20 times, and the Cabanis weaver, *Ploceus intermedius*, with 7 records as a host of the didric and 5 as a victim of Klaas's cuckoo, are the only two hosts that appear to be equally parasitized by both cuckoos. The more usual picture seems to be that a bird known to be a frequent victim of one of these parasites may be affected by the other one occasionally. Thus, the masked weaver, *Ploceus velatus*, has 105 records of parasitism by *C. caprius*, but only a single record by *C. klaas*. Similarly the red bishop, *Euplectes orix*, has been noted as a victim of the didric 77 times, of Klaas's cuckoo only twice. The only other hosts with more than a single record as host for each of the two

---

[8] For pertinent references to published records see: Bannerman 1933, pp. 117–119; Belcher 1930, p. 299; 1949, p. 19; Benson 1940, p. 402; 1946, p. 297; 1953, p. 35; Benson, Brooke, and Vernon 1964, p. 56; Braun 1931, pp. 148–149; 1934, p. 555; Chapin 1953, p. 725; 1954, p. 339; Chubb 1914, p. 63; Erlanger 1905, p. 485; Friedmann 1949a, pp. 139–146; 1949b, p. 517; 1956, pp. 396–399; Grote 1924, p. 34; Haagner and Ivy 1906, p. 35; Holman 1947, p. 641; Jackson 1938, pp. 503–504; Jerome 1943, pp. 100, 102; Joubert 1943, p. 5; Mackworth-Praed and Grant 1957, p. 779; Mackatsch 1955, pp. 184–185; Masterson 1953, p. 51; MacLeod, MacLeod, and Murray 1952, pp. 17, 22; Meneghetti 1944, p. 96; Pitman 1957, pp. 3–6; Pringle 1946, pp. 368–369; Pringle 1948, pp. 155–156; Roberts 1939, pp. 18–20; 1940, p. 143; Schmidt 1963, p. 176; Schönwetter 1964, p. 567; Sclater and Moreau 1932, pp. 512–513; 1933, p. 403; Sheppard 1958, pp. 6–8; Skead 1952, p. 12; 1954a, p. 87; Skinner 1929, p. 111; Sparrow 1936, p. 6; Stoneham 1952, p. 7; van Someren 1916, pp. 234, 384, 454; 1922, pp. 53; 1932, p. 277; 1939 p. 37; 1956, pp. 160, 358, 440–447; pp. 763–764; Vincent 1946, p. 59; Vincent 1934, Williams 1946, p. 138.

glossy cuckoos are the paradise flycatcher, *Terpsiphone viridis*, with 5 records for *C. caprius* and 10 for *C. klaas*, and the red-breasted sunbird, *Nectarinia erythroceria*, with 5 records for *C. caprius* and 22 for *C. klaas*.

The list of hosts common to the two cuckoos includes 2 species of *Motacilla*, 1 of *Turdiodes* and *Parisoma*, 2 of *Cisticola*, 1 of *Prinia*, 2 of *Nectarinia*, 1 of *Cyanomitra*, 1 of *Plocepasser*, 3 of *Passer* and of *Ploceus*, 1 of *Malimbus* and 2 of *Euplectes*. The possibility of error in the identification of the cuckoo eggs in some of these instances cannot be ruled out, although I have been at some pains to eliminate records that for one reason or another seemed uncertain. The eggs of *caprius* and *klaas* are not always distinguishable with certainty.

The data on Klaas's cuckoo comprise some 210 records of parasitism on 59 species of birds. The three most important groups of fosterers are as follows. Sunbirds (Nectariniidae) 85 records, or 40 percent of the total number, involving 16 species, or 27 percent of all reported hosts; warblers, flycatchers, and thrushes (Muscicapidae) 89 records, or 42.3 percent of total number, involving 25 species, or 42.3 percent of all reported hosts; weaverbirds (Ploceidae), 27 records, or 12.8 percent of the total number, involving 12 species, or 20.3 percent of all reported hosts. These figures are in sharp contrast to those for the didric, where 81 percent of all instances of host choice was of weaverbirds; where only 9 percent of the cases was of warblers, flycatchers, or thrushes, and only 4 percent was of sunbirds.

In descending order of frequency, the main hosts of Klaas's cuckoo are as follows: *Chalcomitra senegalensis*, 25 records; *Nectarinia erythroceria*, 22; *Prinia subflava*, 20; *Terpsiphone viridis*, 10; *Cinnyris afer*, 9; *Chalcomitra amethystina*, 9; *Apalis thoracica*, 8; *Batis capensis*, 8; *Alseonax minimus*, 8; *Ploceus reichenowi*, 6; *Ploceus intermedius*, 5; *Cinnyris venustus*, 5; and *Apalis flavida*, 5. The mere number of records, however, does not give a true picture of the relative frequency of parasitism of each host species, since these numbers are readily increased as further study is given to any one particular host. At Kampala, Uganda, *Alseonax minimus* was considered the commonest fosterer by Pitman (*in litt.*), outranking the sunbirds for which I have compiled larger numbers of such records.

Klaas's cuckoo agrees with the didric in that it has not been found to lay its eggs in nests of terrestrial nesters (larks, typical pipits, etc.) in treeless savannahs and also in that it usually avoids the nests of bulbuls and babblers. There is a single record for a single species of each of these families.

List of all known host species:

Motacilla aguimp	Pied wagtail
Motacilla capensis	Cape wagtail

Turdoides jardinei	Arrow-marked babbler
Pycnonotus barbatus	Yellow-vented bulbul
Batis capensis	Cape puffback flycatcher
Batis molitor	Chin-spot flycatcher
Alseonax adustus	Dusky flycatcher
Alseonax minimus	Pygmy dusky flycatcher
Terpsiphone viridis	Paradise flycatcher
Terpsiphone perspicillata	Cape paradise flycatcher
Terpsiphone nigriceps	Black-headed paradise flycatcher
Myioparus plumbeus	Gray tit-babbler
Parisoma subcaeruleum	Tit babbler
Diaphorophyia castanea	Chestnut wattle-eye
Apalis thoracica	Bar-throated warbler
Apalis flavida	Black-breasted bush-warbler
Eremomela icteropygialis	Yellow-rumped eremomela
Sylvietta rufescens	Long-billed crombec
Camaroptera brevicaudata	Gray-backed glasseye
Cisticola woosnami	Trilling grass warbler
Cisticola erythrops	Red-faced grass warbler
Cisticola cantans	Singing grass warbler
Cisticola natalensis	Striped grass warbler
Cisticola robusta	Stout grass warbler
Cisticola fulvicapilla	Tawny-cap grass warbler
Cisticola anonyma	Chattering grass warbler
Prinia subflava	Tawny-flanked longtail
Calamocichla rufescens	Rufous swamp warbler
Saxicola torquata	South African stone-chat
Lamprotornis caudatus	Long-tailed glossy starling
Zosterops senegalensis	Senegal white-eye
Nectarinia erythroceria	Red-breasted sunbird
Nectarinia famosa	Malachite sunbird
Nectarinia kilimensis	Bronzy sunbird
Nectarinia tacazze	Tacazze sunbird
Nectarinia pulchellus	Beautiful sunbird
Cinnyris cupreus	Coppery sunbird
Cinnyris venustus	Buff-breasted sunbird
Cinnyris afer	Greater double-collared sunbird
Cinnyris chalybeus	Lesser double-collared sunbird
Cyanomitra verticalis	Green-headed sunbird
Chalcomitra amethystina	Amethyst sunbird
Chalcomitra olivacea	Olive sunbird
Chalcomitra rubescens	Ruby sunbird
Chalcomitra senegalensis	Scarlet-chested sunbird

Chalcomitra veroxii	Mouse-colored sunbird
Anthreptes collaris	Collared sunbird
Passer domesticus	House sparrow
Passer melanurus	Cape sparrow
Passer iagoensis	Rufous sparrow
Plocepasser mahali	White-browed sparrow-weaver
Ploceus velatus	Masked weaver
Ploceus reichenowi	Reichenow's weaver
Ploceus cucullatus	V-marked weaver
Ploceus intermedius	Cabanis's masked weaver
Malimbus rubriceps	Yellow-winged redheaded weaver
Euplectes orix	Red bishop
Euplectes nigroventris	Zanzibar red bishop
Emberiza cabanisi	Cabanis bunting

Of the 59 hosts tabulated above, 30 figure in the list on the basis of single records; 11 others are birds for which I have been able to learn of two instances each; two have been reported as fosterers of Klaas's cuckoo 3 times and two others 4 times each.

C. cupreus.

The emerald cuckoo of Africa has been found to parasitize a good number and a wide variety of small passerine birds. Data are available on 60 instances of its parasitism, involving 34 species of hosts (42 species and subspecies).[9]

Unlike *C. caprius,* which is primarily parasitic on weavers, and *C. klaas,* which affects sunbirds and warblers more than any other birds, the present species cannot be said to favor one particular family of hosts. The most frequently reported fosterer is a bulbul, *Pycnonotus barbatus,* for which there are nine records; then, with four records apiece, are a weaver, *Ploceus cucullatus,* a sunbird, *Nectarinia erythroceria,* and a flycatcher, *Terpsiphone viridis;* following these, with three records each, are a shrike, *Dryoscopus cubla,* two sunbirds,

---

[9] For pertinent references to published records see: Bannerman 1933, p. 114; Benson 1952, pp. 443–445; 1953, pp. 35, 113; Benson and Benson 1947, pp. 4–5; Benson, Brooke and Vernon 1964, p. 56; Benson and White 1957, p. 44; Chapin 1939, p. 203; Cole 1957, p. 190; Connell 1959, p. 140; Friedmann 1949a, pp. 124–128; 1949b, pp. 516–517; 1956, pp. 393–395; Fry 1961, p. 271; Guichard 1950, p. 168; Haagner and Ivy 1906, p. 35; Jackson 1938, pp. 499–500, 1412; Keulemans 1907, pp. 245–247; Mackworth-Praed and Grant 1952, p. 509; Makatsch 1955, p. 184; Miles 1951, p. 4; Pitman 1929a, pp. 98–99; Priest 1936, 1948; Pringle, 1946, p. 368; Pringle, 1948, pp. 155–156; Roberts 1939, pp. 18–20; 1940, p. 143; 1963, p. 185; Ryves 1959, p. 175; Schönwetter, 1964, p. 568; Skead 1951, p. 197; Sparrow 1936, pp. 5–7; van Someren 1958, pp. 23–24; van Someren 1932, p. 277; 1939, p. 37; 1956, pp. 159, 251, 272, 287; van Someren and van Someren 1949, p. 95; Vincent 1965, pp. 81–86; Vincent 1934, p. 761; Winterbottom 1951, p. 27; Woodward and Woodward 1899, p. 117.

Chalcomitra olivacea and *Chalcomitra senegalensis*, and a weaver, *Ploceus reichenowi;* 3 species are known from two records each, while the other 21 have been noted as victims of this cuckoo but once.

The present list of fosterers is weighted, probably unduly, on the side of species occurring in the open woodlands and brush country rather than in the dense forests, but the emerald cuckoo is much more of a forest dweller than is either the didric, *C. caprius*, or Klaas' cuckoo, *C. klaas*. Observation is generally more difficult in heavy forests than in more open country, and, consequently, fewer nests are found in the former areas. It may be expected, however, that in time an increasing number of purely sylvan birds will be added to the host catalog of the emerald cuckoo. Thus, not a single species of forest bulbul has yet been found to be victimized, but, if we consider the frequency with which *Pycnonotus barbatus* is affected in the more open areas, it would seem probable that some of its sylvan relatives also are imposed upon.

In light of the above there is only little to be gained by estimating the proportional role of the various passerine families in the economy of the emerald cuckoo. It is true that our present data suggest that the weaverbirds (Ploceidae), with 12 species of hosts out of the total 34 and 20 instances out of the 60, rank first; the sunbirds (Nectariniidae), with 6 species of hosts and 14 instances come second; the warbler, flycatcher, and thrush assemblage (Muscicapidae), with 6 species and 9 records, and the bulbuls, also with 9 records but only a single host species, come next, followed by the white-eyes (Zosteropidae), with 4 species and 4 records. However, when more complete data on forest-dwelling birds become available, it will undoubtedly be necessary to alter this arrangement.

The currently known hosts are as follows:

Motacilla capensis	Cape wagtail
Pycnonotus barbatus	Yellow-vented bulbul
Parisoma subcaeruleum	Tit-babbler
Dioptrornis fischeri	White-eyed slaty flycatcher
Platysteira peltata	Black-throated wattle-eye
Horizorhinus dohrni	Dohrn's thrush babbler
Terpsiphone rufiventer	Red-bellied paradise flycatcher
Terpsiphone viridis	Paradise flycatcher
Prinia subflava	Tawny-flanked longtail
Oriolus larvatus	Black-headed oriole
Dryoscopus gambensis	Gambian puff-backed shrike
Dryoscopus cubla	Puff-backed shrike
Zosterops virens	Green white-eye
Zosterops ficedulinus	Principé white-eye
Zosterops griseovirescens	Annobon white-eye
Speirops leucophaea	Principé speirops

Nectarinia erythroceria	Red-breasted sunbird
Nectarinia kilimensis	Bronzy sunbird
Cinnyris chloropygius	Olive-bellied sunbird
Cinnyris reichenowi	Reichenow's sunbird
Chalcomitra olivacea	Olive sunbird
Chalcomitra senegalensis	Scarlet-chested sunbird
Passer melanurus	Cape sparrow
Ploceus xanthops	Jameson's golden weaver
Ploceus reichenowi	Reichenow's weaver
Ploceus cucullatus	V-marked weaver
Ploceus ocularis	Spectacled weaver
Ploceus subaureus	Golden weaver
Ploceus velatus	Masked weaver
Malimbus malimbicus	Crested malimbe
Amblyospiza albifrons	Grosbeak weaver
Euplectes orix	Red-bishop
Euplectes hordeaceus	Fire-crowned bishop
Pholidornis rushiae	Tit-weaver

C. caprius.

The didric cuckoo is the best known of the African species of the group. Over many years I have been able to amass some 426 records of its parasitism on a total of 67 species (84 species and subspecies) of hosts.[10]

---

[10] For pertinent references to published records see: Bannerman 1933, p. 114; Bates 1905, p. 96; Belcher 1924, p. 3; 1930, pp. 109–110; Benson 1952, p. 443; 1953, p. 35; Benson and Benson 1949, p. 165; Benson, Brooke, and Vernon 1964, p. 56; Benson and Pitman 1961, p. 161; Benson and White 1957, p. 44; Bergh 1943, p. 121; Chapin 1939, p. 199; Chubb 1914, p. 63; Distant 1897, p. 143; Farkas 1962, p. 28; Fischer 1880, p. 190; Friedmann 1949a, pp. 163–178; 1949b, p. 517; 1956, pp. 400–403; Fry 1961, p. 275; Grote, 1912, p. 522; Haagner and Ivy 1906, p. 37; Haydock 1950, p. 150; 1951, p. 3; Hoesch and Niethammer 1940, pp. 169–170; Holman 1947, p. 641; Hunter 1961, pp. 55–63; Ivy 1901, pp. 26–27; Jackson 1938, pp. 500, 803, 1317, 1352; James 1921, p. 185; Joubert 1943, p. 5; Layard 1875–84, p. 155; Makatsch 1955, pp. 185–186; Markus 1961, p. 33; 1964, p. 123; McLachlan and Spence 1957, p. 126; Miles 1951, p. 4; Moltoni and Ruscone 1940, pp. 17–18; Mouritz 1910, p. 68; Nicholson 1897, pp. 142–143; Ottow and Duve 1965, p. 435; Packenham 1948, p. 100; Paterson 1945, p. 226; Petit 1899, pp. 66–67; Pitman 1929b, p. 99; 1934, pp. 210–211; 1957, pp. 3–6; Plowes 1945, pp. 113–114; 1946b, p. 271; Priest 1929, p. 33; 1936, p. 275; Pringle 1948, p. 155; Reed 1953, pp. 138–140; Reichenow 1881, p. 16; 1894, p. 111; Roberts 1913, pp. 32–33; 1926, pp. 233–234; 1939, pp. 17–18; 1940, p. 143; Rowan and Broekhuysen 1962, p. 28; Serle 1954, p. 55; Skead 1947, pp. 1–42; 1951, p. 197; 1952, pp. 4–5; 1954b, p. 102; Sparrow 1936, pp. 6–7; Stoneham 1926, p. 65; 1929, p. 269; Swynnerton 1916, p. 284; van Someren 1916, pp. 233, 384, 454; 1918, p. 268; 1956, pp. 236, 464; van Someren and van Someren 1945, p. 44; Vaughn 1930, p. 11; Verheyen 1953, p. 315; Vincent 1947, p. 201; Winterbottom 1951, p. 15.

The didric is generally absent from treeless grasslands, and it is by this fact that we may explain the absence of terrestrial open grassland nesting birds, such as larks and most pipits, from the list of hosts. Hole-nesting birds, such as starlings, are also left alone by this cuckoo, and so too are the estrildine waxbills and their relatives.

Approximately 81 percent of all parasitized nest records or records of hosts feeding recently fledged didric cuckoos have to do with weaverbirds, Ploceidae, with a total of 346 instances divided among 36 species (or 50 species and subspecies). Of these records 198 are of species of the single genus *Ploceus*, involving 19 species (31 species and subspecies), while a single species of the genus, *P. velatus*, accounts for 105 records by itself, about a quarter of all the known instances of didric parasitism. Two other species, *P. capensis* and *P. cucullatus*, have 21 and 23 records, respectively. However, the bird with the second largest number of observed instances of parasitism is, not a species of *Ploceus*, but the red bishop, *Euplectes orix*, for which some 77 records have come to my notice. Next in frequency of choice as a fosterer is the Cape sparrow, *Passer melanurus*, with 43 records, or almost 10 percent of all the known instances of didric parasitism.

Flycatchers, warblers, and thrushes, forming the large family Muscicapidae, account for 38 records, or about 9 percent of the total, distributed among 16 species, or 23 percent of all recorded hosts. Of this assemblage the warblers of the genus *Prinia*, with 3 species, have been reported as hosts 18 times, 16 of these instances being of the one species, *Prinia subflava*.

Sunbirds provide about 9 percent of the known hosts (six species) with 17 records, or about 4 percent of the total known instances. It may be noted that Klaas's cuckoo, *C. klaas*, is much more partial to sunbirds as hosts and correspondingly less so to weaverbirds than is the didric.

Wagtails and pipits (Motacillidae) play a somewhat lesser role in the parasitism of the didric. There are in my files 12 reports of three species of this family serving as hosts to the cuckoo. A single one of these refers to a typical pipit (*Anthus*), the others concern two species of wagtails (*Motacilla*), birds less apt to be denizens of the open grasslands. Two species of Fringillidae account for seven records of parasitism or about 1.7 percent of all the cases. Other families of birds are less frequently used by the parasite, and all but one of them are passerine birds, the one exception being the mousebird, *Colius colius*, for which a single record (Ottow and Duve, 1965, p. 435) is known to date.

Of the 68 species of hosts, more than half (39 to be exact), are known in this relationship on the basis of single reported instances; 6 have been so recorded only twice; 3 each, three and four times;

and 17 have been found to be hosts on five or more occasions. These last are to be looked upon as the regular hosts of the didric cuckoo, and they may be listed here in order of the frequency with which they have been so recorded: *Ploceus velatus*, 105 times; *Euplectes orix*, 77; *Passer melanurus*, 43; *Ploceus cucullatus*, 23; *Ploceus capensis*, 21; *Prinia subflava*, 16; *Ploceus nigerrimus*, 8; *Motacilla capensis*, 7; *Chalcomitra senegulensis*, 7; *Ploceus intermedius*, 7; *Malimbus rubriceps*, 6; *Euplectes hordeaceus*, 6; *Emberiza flaviventris*, 6; *Motacilla aguimp*, 5; *Nectarinia erythroceria*, 5; *Ploceus pelzelni*, 5; *Ploceus ocularis*, 5.

List of all known host species:

Colius colius	White-backed mousebird
Motacilla aguimp	Pied wagtail
Motacilla capensis	Cape wagtail
Anthus novaeseelandiae	Richard pipit
Turdoides jardinei	Arrow-marked babbler
Parisoma subcaeruleum	Tit-babbler
Bradornis pallidus	Pale flycatcher
Bradornis microrhynchus	Small-billed flycatcher
Terpsiphone viridis	Paradise flycatcher
Turdus olivaceus	Olive thrush
Cercomela familiaris	Familiar chat
Cossypha caffra	Cape robin-chat
Dessonornis humeralis	White-throated robin-chat
Calamocichla leptorhyncha	Tana swamp warbler
Camaroptera brachyura	Glass-eye
Cisticola erythrops	Red-faced grass-warbler
Cisticola robusta	Stout grass-warbler
Cisticola ruficeps	Redpate grass-warbler
Prinia flavicans	Black-chested longtail
Prinia subflava	Tawny-flanked longtail
Prinia maculosa	Spotted longtail
Lanius collaris	Fiscal
Oriolus larvatus	Black-headed oriole
Nectarinia kilimensis	Bronzy sunbird
Nectarinia erythroceria	Red-breasted sunbird
Cinnyris chloropygius	Olive-bellied sunbird
Chalcomitra amethystina	Amethyst sunbird
Chalcomitra olivacea	Olive sunbird
Chalcomitra senegalensis	Scarlet-chested sunbird
Plocepasser mahali	White-browed sparrow-weaver
Passer domesticus	House sparrow
Passer melanurus	Cape sparrow
Passer iagoensis	Rufous sparrow

Passer griseus	Grey-headed sparrow
Passer eminibey	Chestnut sparrow
Petronia superciliaris	South African rock sparrow
Amblyospiza albifrons	Grosbeak weaver
Ploceus baglafecht	Baglafecht weaver
Ploceus pelzelni	Slender-billed weaver
Ploceus ocularis	Spectacled weaver
Ploceus capensis	Cape golden weaver
Ploceus subaureus	Smith's golden weaver
Ploceus xanthops	Jameson's golden weaver
Ploceus heuglini	Heuglin's weaver
Ploceus bojeri	Mombasa golden weaver
Ploceus xanthopterus	Zambesi brown-throated weaver
Ploceus castanops	Nile brown-throated weaver
Ploceus taeniopterus	Nile masked weaver
Ploceus intermedius	Cabanis' masked weaver
Ploceus velatus	Masked weaver
Ploceus cucullatus	V-marked weaver
Ploceus nigerrimus	Vieillot's black weaver
Ploceus melanocephalus	Black-headed weaver
Ploceus jacksoni	Golden-backed weaver
Ploceus rubiginosus	Chestnut weaver
Ploceus tricolor	Yellow-mantled weaver
Malimbus rubriceps	Yellow-winged redheaded weaver
Quelea cardinalis	Cardinal dioch
Euplectes gierowii	Gierow's bishop
Euplectes nigroventris	Zanzibar red bishop
Euplectes hordeaceus	Fire-crowned bishop
Euplectes orix	Red bishop
Euplectes capensis	Yellow bishop
Euplectes albonotatus	White-winged whydah
Euplectes ardens	Red-collared whydah
Emberiza flaviventris	Golden-breasted bunting
Fringillaria capensis	Cape rock bunting

In addition to the 67 species of hosts listed above, the following brief statement must suffice to place on record the races affected, where more than one subspecies of a given host is known to be parasitized:

Motacilla capensis: races *capensis* and *wellsi*
Prinia subflava: races *graueri*, *immutabilis* and *affinis*
Passer melanurus: races *melanurus* and *vicinus*
Ploceus ocularis: races *ocularis*, *crocatus*, and *suahelicus*
Ploceus subaureus: races *subaureus* and *aureoflavus*

Ploceus velatus: races *velatus* and *nigrifrons*
Ploceus cucullatus: races *cucullatus, collaris, bohndorffi, graueri, nigriceps,* and *spilonotus*
Ploceus nigerrimus: races *nigerrimus* and *castaneofuscus*
Ploceus melanocephalus: races *capitalis, duboisi,* and *dimidiatus*
Euplectes hordeaceus: races *hordeaceus* and *craspedopterus.*

Host Specificity

Avian brood parasites fall into three categories as far as host specificity is concerned: those that exhibit no such specificity, those that are specific in their parasitism as individuals only, and those in which the entire species is specific on one host species or a small group of related hosts. Members of the first category deposit their eggs in any available and generally suitable nest, regardless of the particular species of victim involved; this is true not only of the brood parasite as a species but also of each of its included individuals. These may be said to be nonhost specific.

Parasites whose individual members tend to lay all their eggs in nests of a single species of host, although the hosts may differ for many of these conspecific parasites, may be described as exhibiting individual host specificity. In some such cases there may be adaptive development of egg morphs with resemblance to the eggs of frequent fosterers. In the case of the European cuckoo, the best known example of individual host specificity, the individually host-specific producers of these ovomorphs have been termed "gentes," groups intermediate between morphs and geographical subspecies. Southern (1954, p. 220) considered that about half the species of parasitic cuckoos sufficiently studied have been found to have, or are suspected to have, such subdivisions. This conclusion seems to be an exaggeration and possibly was derived by counting as species some of the Asiatic races of *Cuculus canorus,* such as *telephonus* and *bakeri,* and putting them together with other species that lay but a single egg type that matches the eggs of its regular hosts (e.g., *Cuculus optatus*), It seems better to consider the ovomorphic gentes of *Cuculus canorus* and of *Cuculus micropterus* as the extreme of adaptive evolution rather than as a widespread condition in the cuckoos. The condition in *Chrysococcyx,* outlined below and in our discussion of egg morphism, helps to put this in proper perspective.

The third group, characterized by specific-host specificity, comprises species in which the individual host preferences of all the included members are similar, with the result that the species of parasite is restricted in its parasitism to a single species or to a small group of similar species of hosts. It would seem (but cannot be proved) that in some of the cuckoos' specific-host specificity is an evolutionary outgrowth from an earlier individual host specificity.

All three stages of host specificity are to be found in the glossy cuckoos. It must be said, however, that in such cases the "evidence" for nonhost specificity is an inference based only on the fact that in many places egg collectors and other nest observers have recorded a variety of parasitized nests without significant percentages of duplication of hosts within a limited area or over a limited time of observation. Careful, intensive field studies may reveal more actual or incipient individual host-specific trends than these present records suggest. Actually, we know that many brood parasites with a wide range of host species tend to utilize only a fraction of them with marked regularity. Thus, in the case of nonhost specific cuckoos, the lack of observable individual host preferences seems due, not necessarily to their definite absence, but to the fact that, while such preferences or specificities may be present as a "background" situation, they are rather easily ignored when a suitable nest of a different potential host becomes available, particularly when nests of favorite hosts are scarce. It may well be that some of these hen cuckoos have potential individual host preferences, but that these have not become fixed or ritualized to a degree where they impose an obligatory direction, and hence they are not apparent to the observer—and this is all that is implied when such cuckoos are described as nonspecific in their host selection.

In two sympatric Australian glossy cuckoos, *basalis* and *lucidus*, we find a difference in manner of host choice that may reflect one factor under the influence of which individual host specificity may have developed. *C. lucidus* very frequently (but not always) uses spherical, or at least dome-shaped, nests while *basalis* appears to be free from any such restriction, selecting both domed and open nests equally. This means that *lucidus* is thereby rendered more limited in its choice of hosts than is *basalis*. However, the number of available fosterers as nest-builders in either category is still considerable, but even within the domed-nesting species a difference exists in the list of fosterers frequently imposed upon by the two cuckoos. Thus, Serventy and Whitell (1962) write that *basalis* parasitizes the banded whiteface, *Aphelocephala nigrocincta*, western warbler, *Gerygone fusca*, blue wren, *Malurus cyaneus*, white winged wren, *Malurus cyanotus*, blue and white wren, *Malurus leucopterus*, variegated wren, *Malurus lamberti*, striated field wren, *Calamanthus fuliginosus*, Mallee heath wren, *Hylacola cauta*, brown thornbill, *Acanthiza pusilla*, and yellow-tailed thornbill, *Acanthiza chrysorrhoa*. Of these the two thornbills (especially the yellow-tailed one) and the blue wren are also listed as common hosts of *C. lucidus plagosus*, but not the others, while the spotted scrub wren, *Sericornis maculatus*, is recorded as victimized by *plagosus* but not by *basalis*. On rare occasions both species of cuckoos have been found to parasitize the same nest.

We may now turn to each of the nine species of *Chrysococcyx* of whose breeding habits we have some knowledge to determine the extent to which each exhibits host-specific trends.

1. *C. malayanus:* no information at all on the breeding habits for 6 of its races (*aheneus*, *jungei*, *salvadorii*, *misoriensis*, *rufomerus*, and *crassirostris*); in 3 others (*malayanus*, *albifrons*, and *poecilurus*) the only host records are for warblers of the genus *Gerygone* (*G. sulphurea* for *malayanus* and *albifrons*, *G. magnirostris* for *poecilurus*), but the total evidence is so slight that it cannot be said that other hosts will or will not be found to be used; in two races (*russatus* and *minutillus*) the *Gerygone* warblers are the most usual, but by no means the exclusive, hosts, with some 13 kinds of warblers, honey-eaters, etc. (*Gerygone*, *Heteromyias*, *Cyrtostomus*, *Meliphaga*, *Ptilotis*, and others) recorded as victims of *russatus* and 4 as victims of *minutillus*.

2. *C. lucidus:* this species, in its various races, shows the whole range of host selection from nonspecificity to individual host specificity to specific host specificity. The importance of this variability merits discussion here.

That specific, as well as individual, host specificity may both occur in different geographic segments of the same species of parasite is shown by the Pacific-island races of *C. lucidus*, which appear to be so restricted in their host choice to *Gerygone* that their distribution is correlated with, if not governed by, the presence of these little gray warblers as breeders. Thus, in his description and discussion of *C. lucidus layardi*, Mayr (1932, p. 7) was led to write that its distribution "is apparently closely linked up with that of its foster parent, *Gerygone flavolateralis* . . . . *G. fl. correiae* was found by the Whitney Expedition on Mai, Epi, Lopeui, Ambrym, Malekula, Aoba, Gaua and Vanua Lava. The collecting of one specimen of this cuckoo on Utupua Island was a surprise. It is not known what species serves there as foster-parent . . . ." Similarly, in his account of *C. l. harterti*, Mayr (1932, p. 8) wrote that the "occurrence of a Bronze Cuckoo on Rennell Island is obviously due to the presence of *Gerygone* on the same island . . . ." Certainly this marked and exclusive degree of host specificity is not true of the *lucidus* population that breeds in New Zealand (typical *lucidus*), where two species of *Gerygone* (*igata* and *albofrontata*) are the chief, but not the only, hosts, which are known to include forms of *Rhipidura*, *Petroica*, and *Zosterops* as well. Even less is this true of the populous segment of the species breeding in much of Australia (*C. l. plagosus*), for which no fewer than 75 kinds of local hosts are now recorded. It causes one to ask if there are no suitable fosterers other than *Gerygone* on Bellona, Rennell, Loyalty, and other islands, and it also makes one wonder why no breeding populations of either *lucidus* or *malayanus* have become established in the Solomon Islands or in the Bismarks, where the elsewhere-favorite hosts are to be found.

3. *C. basalis:* the number of mere egg records in collections and those mentioned in field observations give the impression that this cuckoo is generally nonspecific in its host selection, with a long list of 100 fosterers reported. However, intensive field studies may reveal trends toward individual host specificities, as the following facts suggest. One egg collector in Australia informed me that he had in his personal collection some 15 sets of eggs, each with a single egg of *C. basalis*, no less than 9 of which were of the blue wren, *Malurus cyaneus*, and 7 of which came from one locality, indicating that in that immediate area the *basalis* hens were more inclined to use the nests of the blue wren than those of any other potential host species. Furthermore, the large number of instances of blue wren parasitism reported by Barrett (1905, p. 22), Campbell (1901), Cleland (1924, p. 181), de Warren (1926, pp. 78–79), Dickison (1928, p. 151), Dove (1928, p. 224), Givens (1925, p. 28), McGilp (1921, p. 240; 1926, p. 278), North (1912), Parsons (1918, p. 145), White (1915, pp. 150–152), and many others have clearly demonstrated that of all the known fosterers *Malurus cyaneus* is the favorite host of *C. basalis*. In the Barrington area of New South Wales, Hyem (*in litt.*) thought that as many as 90 percent of all *basalis* eggs were laid in nests of the blue wren. Another observation suggestive of individual host specificity in this cuckoo was reported by Cohn (1924, p. 76), who found six nests of the red-capped robin, *Petroica goodenovii*, each of which had an egg of *C. basalis*. "From the similarity of the eggs and the fact that I saw only one Cuckoo near these nests, I feel reasonably certain that the same Cuckoo laid all the eggs . . . ." Until further data become available it is unprofitable to attempt any probing interpretations, but the suggestion of specialized host trends is obvious.

4. *C. osculans:* no definite observational data on individual hens, but the large number of instances of parasitism on *Chthonicola sagittata* and the close correspondence between the eggs of this host and those of the cuckoo argue for the existence of frequent individual host specificity on the speckled warbler. The fact that the species *C. osculans* also parasitizes a number of other birds, even if less frequently, indicates a degree of divergence from a one-host trend that amounts to an absence of host specificity in some individuals of this cuckoo.

5. *C. maculatus:* no reliable or even inferential information. The similarity of its eggs to those of its *Arachnothera* host may suggest a trend toward specificity, but there are no critical data.

6. *C. xanthorhynchus:* as in *C. maculatus*.

7. *C. klaas:* meager data and the fact that no egg resemblance has been developed with reference to the majority of its numerous species of hosts make it difficult to argue for marked host specificity in this cuckoo. However, Pitman (1957) examined 100 nests of *Prinia subflava* at Broken Hill, Zambia, and found 7 of them to contain one *klaas* egg each, all of one coloration type, suggesting that one, or a very few, hens there were more or less specific on this longtail, or at least favored it as a host.

8. *C. cupreus:* no data other than the vague suggestion of possible individual host specificity underlying the observable egg adaptation toward two of its numerous hosts.

9. *C. caprius:* as indicated in our discussion of the egg morphism of the didric cuckoo, the development of host-egg resemblance for two of its commonly used fosterers, *Euplectes orix* and *Passer melanurus*, and the large number of instances of parasitism on each of these, suggests a considerable frequency of individual host specificity in this cuckoo. The absence of such adaptive coloration in those eggs laid in the nests of a great number of its other hosts does not necessarily indicate, however, an absence of host-specific trends in many other didric hens. This is particularly true in the case of didrics parasitic on masked weavers, as discussed below. Because intensive field studies of African birds are still few in number, observations directly suggestive of host specificity in didric parasites are relatively scarce, but the following instances are pertinent.

R. A. Reed (*in litt.*) kindly sent me a transcript of his observations made at "Tonqani," near Johannesburg, Transvaal. Over a period of years he studied a number of colonies of red bishops, *Euplectes orix*. In the 1955 season he regularly inspected every nest in five colonies of these birds, recording incubation and fledging periods. Not once during the summer did he find a didric cuckoo egg or chick in any of them, although adult didrics were commonly seen about there. These same colonies had been heavily parasitized by the didrics the previous year, but in 1955 the cuckoos concentrated on Cape sparrows, *Passer melanurus*. This indicates that within one season several didric hens were markedly specific on red bishops (1954), and that the next year the same or, more probably, other didric hens were equally inclined to use the nests of the Cape sparrow. In both seasons it seems some hens were markedly host specific. A comparable case is that of G. Duve (*in litt.*), also near Johannesburg, who found that some didrics, laying plain blue eggs, were parasitic on red bishops almost exclusively.

Ottow and Duve (1965) presented a summary and interpretation of Duve's observations, pointing out that, although the red bishops were parasitized very heavily (52 instances in the one small area), other species of birds nesting nearby and known to be parasitized by didrics in other localities (*Prinia*, two species of *Ploceus*, etc.) were never bothered by the cuckoos. This suggests that the local didric hens were rigidly fixed, or specific, on *Euplectes orix*. It was concluded (p. 432) that each female *caprius* was restricted to a single host species. That such host specificity is purely an individual matter is supported by the fact that in other areas where both the didric cuckoos and the red bishops are breeding the latter are not parasitized. Thus, in the eastern Cape Province, Skead (1956, p. 125) reported that his colony of red bishops was never parasitized, although adult didrics were seen from time to time in the vicinity. Skead noted Reed's 16 records of parasitism on this bird from near Johannesburg and emphasized the fact that his local cuckoos were not *Euplectes* parasites.

Many years earlier I reported (Friedman, 1928, p. 37) that in the northern Transvaal I had found in several instances didric cuckoos appeared to have established "territories" around trees containing colonies of masked weavers, *Ploceus velatus*, and that in four cases their territories seemed restricted to single trees in an area where the trees inhabited by the weavers were fairly widely separated—about a quarter of a mile apart. These colonies contained but a single species of weaver, from which it would follow that the parasite by restricting its attentions to the colony in effect would be host specific. In two of these colonies where a didric cuckoo was seen day after day and at different times of the day I cut down and examined every nest. "In the first case there were 37 nests; of these 20 were in use and of these 4 contained a single egg apiece of the didric cuckoo. The eggs were so similar as to indicate that all were the product of the same female. In the second case there were 28 nests; of these 18 were in use and of these 3 contained an egg of the didric apiece, again apparently the product of one individual" (Friedmann, 1949a, p. 172).

Near Bloemhof, Transvaal, Plowes (1946a, p. 142) found three white eggs of the didric in as many nests of the masked weaver. That he considered them all the product of one hen is indicated in his conclusion that this cuckoo lays at least three eggs, "as I found that number of white eggs in one Masked Weaver colony. . . ." One further instance of host specificity is that reported by Serle (1950, p. 356) from British Cameroons. In a colony of black weavers, *Ploceus nigerrimus*, four nests were parasitized by the didric cuckoo. The four didric eggs involved were very similar, suggesting that they had probably all been laid by one bird which, by inference, was prone to use this one species of fosterer.

To sum up, we have either no data at all (*ruficollis, meyerii, flavigularis*) or no usable data (*maculatus, xanthorhynchus, cupreus*) for half of the species of glossy cuckoos. For the other six species for which some (still uneven and at best meager), information is available, the only currently permissible interpretation informs us that in all species there seem to be some individuals that are not host specific and others that are host specific, and that in some areas all of the individuals have the same host choice, making for a local situation of specific-host specificity. This last statement is true for geographic segments of *malayanus* and *lucidus*, and almost so, in some areas, for *osculans*. As far as the current observational records permit of interpretation, individual host specificity is found together with individual nonhost specificity, in parts of the populations of *malayanus, lucidus, osculans, klaas,* and *caprius*.

This is a rather surprising state of affairs. From the standpoint of the reproductive biology of avian brood parasites, the matter of host specificity would seem to be an important, almost a basic, characteristic, explainable as a result of a prolonged adaptive process under the influence of natural selection. To find that it is subject to geographic, subspecific, and even individual variation shows otherwise. In some parasites, such as the European cuckoo, practically all the individual hens are host specific; in others, such as the brown-headed cowbird the great majority are nonspecific, but in the glossy cuckoos we find all stages within each of several species! Lest the novelty of this situation seem unique, however, one may recall that a similar diversity in another aspect of their total behavior exists in many birds, including some of the glossy cuckoos, namely in their migratory habits, where the same species may have highly migratory as well as completely sedentary races and, as in the case of the song sparrow, migratory and sedentary sympatric individuals.

Egg morphism

Inasmuch as adaptive resemblance between the egg shells of brood parasites and those of their regular hosts is very marked in some instances and inasmuch as this is one of the more obvious areas in which evolutionary adaptation to a parasitic mode of reproduction may be expressed, it is essential that we review the situation—and the evidence behind it—in the various species of glossy cuckoos. Fortunately, the coloration and dimensions of the egg shells are known for 9 of the 12 species, even though our knowledge of some of them is less ample than we might like.

The characteristics of the egg shells, coloration, size, gloss, and porosity, etc., are not necessarily simple to explain in an adaptive-evolutionary sense, since they may have come about in more ways than one. Furthermore, egg shells of brood parasites seem to be unusually subject to natural selection and consequently are relatively unreliable indications of past events or of interspecific relations. Thus, one species of parasite may have begun with an originally broad range of egg variability and later may have developed specialized egg morphs, uniform for each individual hen and each specific on a single species of fosterer, while another may have begun with a constant, or only narrowly variable, egg pattern. In the latter case, the parasite may have remained with a single egg type and may have come to select hosts with fairly similar eggs, or it may have developed a broader range of coloration than it had originally. Unfortunately, in no case can we claim to know with any finality which course was followed. All that we can do is to describe the present situation in each of the nine species and see if there are any clues or suggestions as to trends, past conditions, or appreciable, inferential, evolutionary changes in them, and, in addition, to see if together they yield any hints of their history as a group.

In our attempted reconstruction of the phylogeny of the species of the genus *Chrysococcyx* we have already seen that the African members of the group are markedly different from the Asian and Australian ones. The gap, both in morphological characters and in geographic distribution, that separates them from their eastern relatives is the largest void in the phylogenetic picture. It is pertinent at this time to point out that there is a correspondingly great difference in their eggshell characters as well. The eggs of three of the four African species (*caprius*, *cupreus*, and *klaas*, the eggs of *flavigularis* being unknown as yet) are far more variable within each species—actually polymorphic—than are the known eggs of the southern Asiatic and the Australasian species (*basalis*, *lucidus*, *maculatus*, *malayanus*, *osculans*, and *xanthorhynchus*). Some of the latter, of whose eggs sufficient numbers are known to give a trustworthy picture, are remarkably uniform, as, for example, *basalis*, *lucidus*, and *osculans*. This seems to be the case, although with less supporting evidence (smaller yet sufficient numbers of eggs) in *malayanus*, but not in *maculatus* and *xanthorhynchus*.

The degree of variability of the eggs, chiefly in their coloration, ranging from a monomorphic to a polymorphic condition, is not obviously related to, or correlated with, the diversity and the number of kinds of hosts used regularly. Thus, the species of glossy cuckoos with very extensive lists of hosts include *basalis* and *lucidus*—each with practically monomorphic eggs—and *caprius*, *cupreus*, and *klaas*—each with polymorphic eggs. On the other hand, *osculans*, with a single egg type, uses only a few species of fosterers, and its eggs agree quite closely with those of its most favored host, *Chthonicola sagittata*. It is to be remembered that even those species of cuckoos with extensive lists of known hosts tend to parasitize only a fraction of them with any great regularity.

The basic fact of polymorphism, regardless of whether it applies to eggshell characters or to any other phenotypic aspect of a species, would appear to be adaptive or at least would make adaptive evolution more readily possible. In the case of brood parasites, eggshell adaptation is of particular importance, but even here the resulting situation is not necessarily simple to interpret. Thus, it is obvious that a species of cuckoo with a single egg type, but using a wide variety of fosterers, would inevitably come up against some whose eggs its own approximated fairly closely and others whose eggs were widely dissimilar. In some cases, where enough data are available to establish the correlation between acceptance or rejection of parasitic eggs by fosterers and the degree of egg similarity, it is clear that such resemblance does confer a significant biological advantage on the parasite. Examples of this are the "gentes" of the European cuckoo, *Cuculus canorus*, and the Indian breeding population of the jacobin crested cuckoo, *Clamator jacobinus*. Strangely enough, however, in other cases lack of egg resemblance does not always appear to mitigate critically against the parasites, as in the case of the jacobin cuckoos breeding in southern Africa (Friedmann, 1964, pp. 20, 21).

It follows from the above that, before we may go more deeply into the problems related to egg adaptation and egg morphism, it is necessary to present the data for each of the nine species of glossy cuckoos with all pertinent details.

1. *C. malayanus:* eggs are known of five of the subspecies of this glossy cuckoo; in all cases they can best be described as monomorphic with fairly narrow variational limits. In typical *malayanus* the egg is dark olive-green with some small brown specks forming a wreath of darkish brown. Schönwetter (1964, p. 570) noted that such coloration is the forerunner of the development of the surprising bronze tone found only in the eggs of some glossy cuckoos and of some species of the related genus *Cacomantis*. In *C. m. malayanus* the egg color is not adapted to that of its hosts' eggs as far as the still meager data permit a generalization. In *C. m. albifrons*, Bartels (1925) found the egg to be bronze colored (*ex* nest of *Gerygone sulphurea*). In *C. m. poecilurus*, Schönwetter described the eggs as uniform yellowish olive-brown or greenish olive-brown, somewhat darker, more bronze than in *C. lucidus plagosus*. In *C. m. russatus* the egg varies from pale to

dark olive-brown, slightly freckled with dark brown; in some the dark color may be accentuated at the two ends of the egg, forming indistinct bands. North (1912) merely described the eggs as dark bronze with an olive or chocolate tone, with a few flecks at the obtuse end. In *C. m. minutillus* the eggs are uniformly greenish olive or dark bronze, like those of *C. m. poecilurus*.

Measurements (in mm.) are given as follows by Schönwetter (1964, p. 587): *C. m. malayanus:* length 18; width 12.8; weight of full egg 1.5 grams. *C. m. poecilurus:* length 19.6 (19.0–20.2); width 13.7 (13.3–14.7); weight of empty shell 0.12 grams; thickness of shell 0.08; weight of full egg 2.0 grams; relative weight of shell to that of full egg 6 percent. *C. m. russatus:* length 20.3 (19.8–21.0); width 1.36 (13.4–14.0); weight of full egg 2.02 grams. *C. m. minutillus:* length 18.9 (18.5–19.3); width 13.7 (13.2–14.2); weight of full egg 1.85 grams.

2. *C. lucidus:* eggs monomorphic with some variation in the overall tone, especially in the nominate race. Because the eggs of two races (*lucidus* and *plagosus*) present slight differences, this general statement needs to be amplified. In typical *lucidus* the eggs seen by most observers or authors (North, 1912) are uniformly olive-brown with a somewhat bronze tone. However, years earlier Buller (1888) described them as usually greenish-white to pale olive washed with brownish gray. This is probably the reason why Oliver (1955, pp. 533–536) wrote that the eggs of *lucidus* are greenish or bluish white to olive-brown or dark greenish-brown. In the Australian race, *plagosus*, the eggs are also uniform, varying from yellowish olive-brown to greenish olive-brown (like bronze) but sometimes with a more grayish tone. Serventy and Whitell (1962, p. 269) wrote that the bronze-olive pigment is soluble in water, leaving the washed egg light bluish. This explains Oliver's description, and also recalls the similarly removable part of the reddish-brown pigment in the eggs of *C. osculans*.

In the case of *plagosus* there is little or no egg resemblance to the eggs of the numerous hosts, but since many (though not all) of the hosts build domed or globular nests, the lower level of the internal illumination there may help to compensate for the lack of similarity.

Schönwetter (1964, p. 587) gives the following measurements (in mm.) for the eggs of the two races of *C. lucidus:* length 18.3 (17.2–19.4) in *plagosus*, 18.9 (18.0–20.3) in *lucidus;* width 12.9 (12.0–14.2) in *plagosus*, 13.1 (12.5–15.2) in *lucidus;* weight of empty shell 0.095 grams in *plagosus*, 0.10 grams in *lucidus;* thickness of shell 0.065 in *plagosus*, 0.06 in *lucidus;* weight of the full egg 1.66 grams in *plagosus*, 1.73 grams in *lucidus;* percentage of weight of empty shell to that of full egg 5.7 percent in *plagosus*, 5.8 percent in *lucidus*.

3. *C. basalis:* egg apparently monomorphic, white, minutely

speckled and blotched with pinkish red; in some cases, described by Schönwetter (1964, p. 569), the spots are less pinkish and more olive-brown. The texture of the egg is smooth, the pores indistinct. In Schönwetter's table we find the following dimensions (in mm.): length 18.1 (16.9–19.0); width 12.7 (11.9–13.3); weight of empty shell 0.09 grams (0.08–0.11); thickness of shell 0.06; weight of full egg 1.55 grams; relative weight of shell to that of full egg 5.8 percent.

The eggs of this cuckoo show some resemblance to those of some of its hosts, especially of the genera *Malurus*, *Ephthianura*, *Neositta*, *Stipiturus*, *Gerygone*, and *Petroica*, and little or no resemblance to others, such as *Rhipidura*, *Sericornis*, *Smicrornis*, *Cisticola*, *Chthonicola*, *Calamanthus*, *Meliornis*, *Zosterops*, *Aegintha*, and *Taeniopygia*.

4. *C. osculans:* monomorphic; elliptical or compressed-oval in shape, uniformly dark reddish-brown or chocolate-brown, very similar both in coloration and in size to the eggs of the most favored host, the speckled warbler, *Chthonicola sagittata*, also agreeing fairly closely with those of one of its few other fosterers, the red throat, *Pyrrholaemus brunneus*, but not similar in color to those of other irregularly used hosts, the yellow-tailed thornbill, *Acanthiza chrysorrhoa*, and the Mallee heath wren, *Hylacola cauta*. That these latter species all make domed or globular nests with dim internal visibility may help to offset the lack of similarity between their eggs and those of the parasite. According to Chisholm (1935, p. 70) the pigment on the shells of *osculans* eggs is, at least partly, very superficial, as some of the reddish-brown color rubs off on moist fingers. The eggs of *osculans* are very different from those of any of the other glossy cuckoos in their rich, dark color. The nearest to them are the eggs of *lucidus* and *malayanus*, which are unmarked, bronze or olive; those of the others are very different, light-colored, and show varying degrees of freckling and spotting. For its body size, *osculans* lays a smaller egg than any of its congeners, 19–22 × 14–15 mm. (*ex* Serventy and Whitell, 1962, p. 268), possibly an adaptation to its highly restricted parasitism on a very few host species. Schönwetter (1964, p. 586) gives the following measurements (in mm.) for *osculans* eggs: length 21.1; width 15.5; weight of full egg 2.75 grams.

5. *C. maculatus:* present data, chiefly *ex* Baker (1942, p. 80) and Schönwetter (1964, p. 568) hardly more than suggests that the eggs of this cuckoo are polymorphic. It is difficult from the descriptions, which are all I have to rely on, to state whether there are two or more fairly distinct types or one variable, but not readily divisible, one; eggs are whitish, usually with a yellowish tinge and sometimes a slight pinkish one, and with numerous pale brown-red flecks which are most frequent at the obtuse end of the egg, generally similar to the eggs of some of the sunbird hosts, such as *Aethopyga siparaja seheriae*. Eggs

taken from nests of *Arachnothera longirostris* show a wreath of small spots of brown, less reddish than those of the host. Another egg, also attributed to this cuckoo, is so densely marked with brown and gray as to be unusually dark in color. The eggs of this cuckoo are short, broad, and oval to elliptical in shape, the pores fairly coarse for so small an egg. The eggs are very thin shelled for a cuckoo (the weight of the shell only 5.1 percent of that of the full egg, as compared with 7.4 percent in *C. caprius*), only slightly thicker than the eggs of the sunbirds. Baker (1942, p. 203) gives the dimensions of the eggs of this cuckoo as averaging 16.9 × 12.3 mm., the maximal ones being 18.0 × 12.6 and 16.3 × 12.8 mm., the minimal ones 15.1 × 12.0 and 15.9 × 11.2 mm. Schönwetter's figures give a range of 15.4–18.5 × 12.0–12.9 mm., but in his table (p. 587) gives the following measurements (in mm.): length 16.9; width 12.3; weight of empty shell 0.07 grams; thickness of shell 0.05; weight of full egg 1.37 grams; relative weight of egg shell to that of full egg 5.1 percent.

It should be mentioned that there is still some uncertainty about the variational limits of the eggs of *C. maculatus* and *C. xanthorhynchus*. Baker (1942, p. 80), who had seen more of each than anyone else, admitted that the eggs of the two "are not individually distinguishable . . . ," yet he described an egg type of *C. xanthorhynchus* which seems quite different from any he mentioned of *C. maculatus* (see our description of *C. xanthorhynchus* for further data).

6. *C. xanthorhynchus:* said by Baker (1942) and by Schönwetter (1964, p. 569) to be similar in their size and color variations to those of *C. maculatus;* white, tinged with yellow, or pinkish, and flecked in various tones of brown and reddish, achieving a fair resemblance to the eggs of the hosts *Arachnothera longirostris* and *Aethopyga siparaja seheriae* and only moderately similar to those of other hosts of the genera *Dicaeum*, *Cisticola*, *Orthotomus*, *Trichastoma*, *Alcippe*, and *Napothera*. In the case of eggs laid in nests of the little spider hunter, *Arachnothera*, Baker (1942, p. 80) wrote that "an egg has been evolved which agrees wonderfully well with those of the Spider-Hunter, some indeed of the eggs of the Violet Cuckoo have to be weighed before identification can be accepted. These eggs are pinkish, nearly always pale, with a ring of reddish spots around the larger end, well defined in both the Cuckoos' and the Spider-Hunters' eggs . . . Eggs intermediate between the two types simulating Sunbirds and Spider-Hunters are also to be found and are in most cases accepted . . . ." It should be clarified that Baker was writing about eggs of both *xanthorhynchus* and *maculatus* in this sentence, the eggs simulating those of the sunbirds being *maculatus*. In Burma, Smythies (1953) found *xanthorhynchus* eggs to vary from pure white to pink in their ground color, with a wreath of reddish flecks at the larger end.

Baker gives the dimensions of nine eggs of the violet cuckoo as averaging 17.31 × 12.25 mm., the largest eggs measuring 17.9 × 12.0, and 16.1 × 13.3, the smallest ones 15.8 × 12.6, and 16.2 × 11.2 mm. Schönwetter's figures are as follows: length 17.2 mm.; width 12.5 mm., weight of full egg 1.40 grams.

All known eggs of the violet cuckoo are of the nominate race.

7. *C. klaas:* eggs polymorphic, seven main types, plus variations that do not agree closely with any of them. The main types are: 1. white with numerous flecks of Indian red (oviduct egg, taken by Lynes, 1934, p. 56). 2. cream-colored flecked over all with grayish and brownish (*"Passer"* type of Schönwetter, 1964, p. 567). 3. pale blue with round speckles of reddish-brown and violet (found in nests of *Chalcomitra, Prinia,* and *Cisticola*); also one oviduct egg reported by Chapin (1939, p. 201). 4. pale green, with a loosely formed ring of dusky, narrow markings found in a nest of a sunbird, *Chalcomitra senegalensis.* 5. light, buffy chestnut or creamy chestnut with markings of pale, but bright, chestnut, found in nests of *Prinia subflava* (Pitman, 1957, pp. 3–6). In this instance it is worth noting that at Broken Hill, Zambia, Pitman examined 100 nests of the *Prinia* and found 7 of them to contain eggs of *klaas.* The cuckoos' eggs were all of one type: "bluntly ovate and a handsome light buffy chestnut on a creamy chestnut with pale markings of bright chestnut . . . . In no instance does the cuckoo's egg mimic the wavy markings, scrawls and straggling hair lines of this *Prinia;* otherwise they can be considered an excellent imitation of many of the rufous buff and buffy chestnut eggs of *Prinia.* This suggests a possible preponderance of rufous buffy eggs of *Prinia,* or rather that this variety of egg is predominant, which, however, is not the case . . . ." The *Prinia* eggs are very variable, and Pitman found no apparent preference by klaas's cuckoo for any one type, "though it is interesting that the blue type appears to be avoided . . . ." 6. pinkish white, heavily spotted with darker pink, all in nests of *Batis capensis.* (MacLeod and Hallack [1956, pp. 2–5]). 7. uniform, dark chocolate-brown, recorded so far as I know only by Pitman (1957, pp. 3–6) from a nest of *Anthreptes collaris,* at Malindi on the Kenya coast. This egg phenotype is of particular interest in that it reflects (or appears to reflect) the condition found in *osculans* and, to a lesser extent, in *lucidus* and in *malayanus.*

Variants, apparently fairly close to type 4, taken in Uganda, have been described as greenish-white speckled with brown and slate; others nearer to our type 3 have been reported as verditer blue spotted with red-brown.

Pitman's observations on the lack of precise, adaptive host-egg similarity in *klaas* eggs laid in *Prinia* nests are further corroborated by those of others dealing with still different hosts. Thus, a record by Bell-Marley (in Friedmann, 1949a, p. 136) involving the amethyst sunbird and another by Roberts (1940, p. 143) concerning a parasitized nest of the paradise flycatcher showed similar discrepancy in appearance of the eggs of the parasite and of its hosts. On the other hand, Pitman himself (1957, pp. 3–6) wrote that at Entebbe, Uganda, the sunbirds, *Nectarinia erythroceria* and *Chalcomitra senegalensis,* were common hosts. "The eggs of both . . . species are generally dark brownish in appearance, and the eggs of *C. klaas* are likewise. . . ." Again, Pitman (*in litt.*) summarized much of his experience with eggs of *klaas* in Uganda by describing them as resembling to a fair degree the eggs of some of the commonly used hosts, particularly in their densely speckled pattern.

The eggs of *klaas* are much like those of *caprius* in their variable color patterns but are smaller in size and, in general, somewhat more slender. According to Pitman, the eggs of *klaas* are "tougher" than those of either *caprius* or *cupreus.* Eggs of *klaas* vary in size from 15.2 to 19.5 mm. in length and from 11.4 to 12.6 mm. in width. The larger measurements in my earlier account (1949a, p. 137) now appear to have been of *caprius* eggs misidentified as *klaas* in the literature.

Egg measurements (in mm.) given by Schönwetter (1964, p. 586) are as follows: length 18.9 (16.9–20.0); width 12.8 (12.1–13.5); weight of empty shell 0.10 (0.08–0.11) grams; thickness of the shell 0.07; weight of full egg 1.65 grams; relative weight of shell to weight of full egg 6.1 percent.

The known eggs of *klaas* are all of the nominate race.

8. *C. cupreus:* apparently polymorphic, but only a small number of eggs are known; these may be divided into four types: 1. white, either immaculate or with a few purplish flecks forming a loose wreath at the obtuse pole. 2. white or cream, very thickly speckled with olive-brown, found in nests of olive sunbird by Benson & Benson (1947, p. 4) in Nyasaland and by Moreau in Tanzania; this egg type agrees fairly well with those of the host. 3. pale pinkish to pinkish white, spotted with brown and gray, "similar to those of *Pycnonotus,* but smaller . . ." (van Someren, 1956, p. 159); found in nests of the bulbul, *Pycnonotus barbatus,* in Kenya. 4. pale blue (in collections, faded afterward to white), described by Schönwetter (1964, p. 568).

In spite of the meager quantity of evidence, there is reason for interpreting as "probable" some adaptation in egg coloration to at least two hosts, the yellow-vented bulbul, *Pycnopotus barbatus,* and the olive sunbird, *Chalcomitra olivacea.* The eggs of the parasite are smaller than those of the bulbul, but larger than those of the sunbird. The bulbul is the most frequently recorded host of the emerald cuckoo (9 instances out of a total of 62 cases of parasitism involving, in all, some 41 species and subspecies of hosts).

The measurements given in my earlier account (1949a, p. 121) were based on two doubtful examples (*ex* nests of *Colius* and *Amblyospiza*) and are too large. One egg, subsequently measured, was 20.5 × 13 mm. Schönwetter (1964, p. 587) gives the following size data (in mm.): length 17.8; width 12.2; weight of the empty shell 0.06 grams; thickness of shell 0.04 mm.; weight of the full egg 1.43 grams; relative weight of shell to that of full egg 4.2 percent.

There appear to be no differences between the eggs of the subspecies of *C. cupreus* (eggs of *intermedius* and of *sharpei* known).

9. *C. caprius:* eggs polymorphic, five main types plus some variations that do not agree very closely with any of these. The main morphs are: 1. unmarked white, stated by Schönwetter (ed. Meise, 1964, p. 567) to be rare, but also reported by Priest (1948, pp. 47–48) and by Moreau (1949, p. 535); recorded from nests of *Parisoma subcaeruleum* and *Ploceus velatus, Ploceus intermedius, Ploceus ocularis,* and *Euplectes orix* (Ottow and Duve, 1965, p. 435). 2. uniformly greenish-blue, a common type frequently found in nests of *Euplectes orix,* the eggs of which host are similar in color but usually smaller in size. In the Transvaal R. A. Reed (*in litt.*) informed me that all *caprius* eggs he found in nests of the red bishop (*E. orix*) were "quite indistinguishable from those of the host, being a plain deep blue and of the same size and shape as those of the host. . . ." Again, G. Duve (*in litt.*), also in the Transvaal, found only blue eggs of *caprius* with *Euplectes orix,* no blue eggs of the parasite in the nests of the other common local host, *Ploceus velatus,* with which only speckled cuckoo eggs were found. A plain, blue *caprius* egg is known from a nest of the black-chested *Prinia, P. flavicans,* found close to a nesting colony of *Euplectes orix.* It is possible that this egg was deposited by a didric otherwise parasitic on the red bishops nearby. Ottow and Duve (1965) distinguish two types of unmarked blue eggs, a pale type which Duve found in 3 nests of *Ploceus capensis* and in 7 of *Euplectes orix* near Johannesburg, and a darker type found by Duve in 13 nests of *Euplectex orix* in the same area. 3. Pale green or cloudy white, sparsely splashed with grayish and with grayish brown (referred to by Schönwetter as the *Ploceus velatus* type), found with similarly colored eggs of *Ploceus velatus* but also with whitish eggs of *Ploceus intermedius cabanisi,* and with greenish-blue eggs of *Ploceus capensis olivaceus.* This is a frequent egg morph of the didric cuckoo. Chapin (1939, p. 179) obtained an oviduct egg of this type. 4. Background color varying from dull white to fairly bright pale-green, blotched and speckled with coarse, heavy, and, in some instances, dark-brown and grayish markings. This type has been reported from nests of *Passer melanurus,* whose eggs

generally are fairly similar, but also from nests of *Euplectes orix* and of *Ploceus capensis olivaceus*, both of whose eggs are uniformly bluish, and from nests of *Ploceus velatus* and *Ploceus xanthops jamesoni*, both of which species lay speckled eggs. According to Schönwetter this is the most frequent type of *caprius* egg (10 out of 24 that he examined). Near Johannesburg, R. A. Reed (*in litt.*) found that all *caprius* eggs found in nests of *Passer melanurus* were lighter in color than those of the host, with some tinge of blue in the whitish ground color and with freckling, in every egg examined, finer and more evenly spread, although the freckling was heaviest around the obtuse pole of the eggs.

Roberts (1926, pp. 232–234) described a number of didric eggs of this morph, comparing them with those of the hosts in whose nests they were found, reported a fair approximation between them in four clutches of *Passer melanurus*. In other cases, however, there was little or no egg similarity, as was further shown by Plowes (1945, p. 113), who noted no less than four different didric egg morphs in nests of *Ploceus velatus* alone, none of them agreeing with the eggs of the host.

5. Pinkish background color, with speckles and larger markings of pinkish brown, and brownish gray (not listed by Schönwetter, but recorded from a nest of *Ploceus velatus* by R. A. Reed [*in litt.*]; apparently a relatively uncommon egg morph). The egg described by Markus (1961, p. 33) was merely described as light pink speckled with pinkish brown; the one reported by Reed had a pinkish ground color, with dark frecklings of browns and grays sparsely scattered, except on the obtuse end where these markings coalesced to form a ring.

Other, somewhat variant, egg morphs have been described, as follows: cream color, finely blotched with light reddish brown and underlying pale mauve; very pale green with reddish-brown blotches, especially near the larger pole; blue with greenish spots (Markus, Priest, and others).

Judging from the data presented above, together with further notes by Hunter (1961, p. 55), Markus (1963, p. 47; 1964, p. 123), Moreau (1949, pp. 535–536), Reed (1953, p. 138), and others, and from the conclusions of Schönwetter (1964) it may be said that the didric cuckoo shows adaptive egg resemblance in coloration to two of its common hosts, *Euplectes orix*, and *Passer melanurus*, but that this is by no means constant. The degree of adaptation or, perhaps more accurately, the incidence of approximate resemblance is greater in those individual didrics parasitic on red bishops than in those laying eggs in the nests of Cape sparrows. In the case of those didrics parasitizing masked weavers there is less evidence for constant egg adaptation. Markus (1961, p. 33) found three types of didric eggs in nests of this host. Hunter (1961) studied about 120 nests of the masked weaver and distinguished 10 egg morphs of this species. He found that in the parasitized nests (12, or 10 percent of the total) the didric eggs more often resembled one of these color morphs, less often those of two other types.

Since the egg pattern of the masked weaver is so variable as to permit the designation of 10 recognizable types, it is obvious that it would be very difficult, if not quite improbable, for a parasite's egg to have evolved any great degree of resemblance. Yet, it seems that some adaptive evolution has transpired and is going on, but in so unclear and complicated a situation that it is not possible to measure or to define it. The colored illustrations given by Ottow and Duve (1965, pl. 1, figs. a and b) of two very different sets of eggs of *Ploceus velatus*, each with an egg of *caprius*, show a marked resemblance between parasite and host. These are extreme instances of positive egg similarity with this favorite, but ovopolymorphic host. In other cases the eggs of the two show no such close agreement. Duve's own records reveal that four of the egg morphs of *caprius* were found in nests of *Euplectes orix*, a host that lays unmarked bluish eggs only, with which only two of the parasitic egg types correspond. Yet, so experienced an oologist as Pitman (MS., 1965) considered that the didric cuckoo's eggs have become adapted to at least half a dozen species of hosts. The evidence for this conclusion is unknown to me; when Pitman's work is published this point will be of much interest.

Of the large number of species of hosts (67) recorded in this report for the didric, with a total of 426 instances of parasitism, the three most frequent fosterers are the red bishop, *Euplectes orix*, with 77 cases, the masked weaver, *Ploceus velatus*, with 105 instances, and the Cape sparrow, *Passer melanurus*, with 43 records. It is, perhaps, due to the polymorphic nature of the masked weaver's eggs that only individual, but not invariable, egg resemblance is to be found with them, while with the other two fosterers the egg adaptation of the didric is quite readily discernible, even if not highly perfected with regard to the Cape sparrow.

There is also some evidence for adaptive resemblance of egg size in the didric. Pitman (MS., 1965) reported that seven didric eggs taken from nests of *Ploceus cucullatus* and *Ploceus nigerrimus* measured 22.2 × 15 (20.4–23.3 × 14–16 mm.), while nine others from nests of smaller species of *Ploceus* with correspondingly smaller eggs, *Ploceus intermedius* and *Ploceus pelzelni*, measured 19.9 × 13.7 (18–21.4 × 13–14.7 mm.). For ready comparison the egg sizes of the hosts involved may be stated:

Ploceus cucullatus: 21.7–25.7 × 14.9–16.5 mm.
Ploceus nigerrimus: 22–26.2 × 15.4–17 mm.
Ploceus intermedius: 20–23.6 × 13.8–15.4 mm.
Ploceus pelzelni: 18–19.5 × 13–19 mm. (all, *ex* Chapin 1954, pp. 316, 338, 358–363, 367).

There is a close agreement in size between didric eggs (average 21.7 × 14.9) and those of the red bishop (average 20.5 × 14) and of Cape sparrow (average 19 × 14 mm.). However, not infrequently the cuckoo eggs are larger than even these host eggs in the same nest. Thus, Markus (1964, p. 123) found a large didric egg, 25 × 14.5 mm., in a red bishop's nest and another measuring 23.7 × 14.3 mm. in another nest of the same species.

The eggs of the didric cuckoo vary in length from 21 to 25 mm. and in width from 13.8 to 17 mm.; the largest ones seen by me or recorded in the literature were 24.8 × 16.5; 24.3 × 17; 25 × 15.5 mm.; the smallest ones were 20.8 × 14.2; 21.1 × 14.5; 21.2 × 14.3 mm. Didric cuckoo egg measurements tabulated by Schönwetter (1964, pp. 536, 586) are as follows: length 21.5 mm.; width 14.8 mm.; weight of the empty shell .19 grams; thickness of the shell 0.095 mm.; weight of the full egg 2.55 grams; relative weight of the shell to that of the full egg 7.4 percent; body weight of the bird 40 grams; relative weight of full egg to body weight of the hen 6.4 percent.

To sum up the foregoing data, we may note that egg monomorphism is characteristic of those species of *Chrysococcyx* found in the Australasian portion of the range of the group, which are also, at least in the present reconstruction of their history, nearer to the older stock of the genus—*malayanus*, *lucidus*, *basalis*, and *osculans*. In the two Asiatic species, *maculatus* and *xanthorhynchus*, the still meager evidence suggests polymorphism, while in the three African "climax" species, *caprius*, *cupreus*, and *klaas*, the eggs are definitely polymorphic.

In the monomorphic egg-laying species the following specific differences should be noted. In the case of *malayanus* there appears to be some slight geographic, subspecific variation in egg coloration, but not much within each racial entity, merely the range of color implied in such descriptions as "yellowish olive-brown to greenish olive brown," or "sometimes slightly freckled." In *lucidus* and in *osculans* there is an easily rubbed off, superficial pigment, but the adaptive value of this color is not dependent on its durability or removability; in fact in *lucidus* there is no evidence that it is host-egg adapted before or after alteration, while in *osculans* it is highly adapted to its main host prior to any color loss and such loss occurs, if at all, after the critical period of acceptance or rejection by the host is past. Such discoloration probably occurs, although seldom in nests undisturbed by man, as the eggs must be rubbed to produce it. In *basalis* some degree of resemblance exists to the eggs of some of its hosts but not to those of others.

In the polymorphic egg producers of India, *maculatus* and *xanthorhynchus*, we find a range of host-egg similarity from very close to only fair or moderate. Coming to the African species, *klaas* shows no egg resemblance to those of many of its hosts and not more than a "fair" degree to others; *cupreus*, with a systematically very diverse group of hosts, gives evidence of probable egg adaptation toward two hosts, a bulbul, *Pycnonotus barbatus*, and an olive sunbird, *Chalcomitra olivacea*, the very disparity of which makes one wonder if the present "probability" is not merely a matter of coincidence in fairly small samples and not really a statistically significant adaptation. Finally in *caprius* there is some evidence for host-egg similarity for two of its frequent fosterers, the red bishop *Euplectes orix* and the Cape sparrow, *Passer melanurus*, some, but not constant, for its other most frequent fosterer, the masked weaver, *Ploceus velatus*, and no convincing adaptation toward its numerous other, less-used hosts. Interestingly, the *caprius* eggs seemingly adapted to the Cape sparrow, *Passer melanurus*, have been reported so far only from southern Africa, in the range of that host species. This makes it appear like a real adaptation; if it occurred as well in more equatorial regions where this particular host is absent, it might seem that it was a widespread phenotype that happened to be suitable in southern Africa to the Cape sparrow.

Egg adaptation occurs to a well-developed degree in the Australian species, *osculans*, to a lesser degree in *basalis*, in the two Indian species, *maculatus* and *xanthorhynchus*—but only with some of their host species, and to a variable degree in three African species, *caprius* (well-developed with two hosts, not with others), *capreus* (again only for two of its hosts and not others), and to only a "fair" degree in *klaas* with a few of its frequent hosts. The most perfect adaptations are between *C. osculans* and its chief host *Chthonicola sagittata*, between *C. maculatus* and *Arachnothera longirostris*, and between *C. caprius* and *Euplectes orix* and *Passer melanurus*.

There is, then, no well-defined, progressive path of adaptation; it is more of a sporadic type of development in different sections of the genus *Chrysococcyx*. In some instances it is possible to "explain" the lack of adaptive evolution, as in many instances of the parasitism of *C. caprius* on *Ploceus velatus*, which host lays such a wide range of egg phenotypes that it would be difficult for the parasite to come under any steady, selective influence. Another instance is the frequency with which *C. lucidus plagosus* parasitizes birds that build domed or covered nests in which the poor illumination tends to minimize the effect of visual differences between the eggs of the parasite and those of the host.

In the case of the European cuckoo, *Cuculus canorus*, it is well known that the egg is extremely small for the size of the bird, a little over 3 percent of the body weight, while the egg of most self-breeding birds is usually about 10 percent of the body weight. Whether the small egg of *C. canorus* is the result of a progressive, adaptive reduction in egg size, permitting the bird to use hosts much smaller than itself, is only conjectural, but the fact remains that the bird does use chiefly small passerine species as fosterers. While the glossy cuckoos do not exhibit such striking egg reduction, they do lay eggs that are fairly small in relation to their body size, which may be of adaptive value in approximating the size of the eggs of some of their frequent hosts. For example, the body size of *C. basalis* is much greater than that of the species of *Malurus* that it parasitizes, but the eggs of the two are very similar in dimensions. Again, the egg of the African yellow-bellied emerald cuckoo, *C. cupreus*, is surprisingly light in weight, almost as light as eggs of the two much smaller Asiatic species, *C. maculatus* and *C. xanthorhynchus;* the full egg weight is 1.43 grams in *cupreus*, 1.37 grams in *maculatus*, and 1.40 grams in *xanthorhynchus*, whereas the dimensions of the eggs are 17.8–20.5×12.2–13 mm. in *cupreus* and only 15.1–18×11.2–13.3 mm. in the two Indian species. The body size and weight of *cupreus* exceed the figures for *maculatus* and *xanthorhynchus* by approximately 40 percent. The eggs of these two very small species of *Chrysococcyx* were compared by Burton (1935, p. 276) with those of two Indian species of *Cuculus*, *poliocephalus* and *saturatus*. His results emphasize the difference in extreme egg reduction in these species of *Cuculus* and in *Chrysococcyx*, as he was led to write of the little Asiatic emerald cuckoo, *C. maculatus*, that its "eggs are very large for cuckoo's eggs, in proportion to the size of the bird, the bulk being as much as it is in the eggs of *poliocephalus* . . . and *saturatus* . . . birds of, perhaps, between three and four times the cubic contents of the tiny Emerald Cuckoo."

The largest and heaviest eggs of all the glossy cuckoos are those of *osculans* and *caprius*. This is in agreement with their larger body size, but if Schönwetter's figures are correct, the egg weight in *C. caprius* is 6.2 percent of the body weight, while in *C. lucidus plagosus*, a much smaller egg and bird, the egg weight is 7.9 percent of the body weight.

Although in some cases there may be selective value in approximate size agreement in the eggs of the parasite and of the host, this does not always operate on a critical level. Thus, in New Zealand, the little gray warbler, *Gerygone igata*, a bird that lays an egg about 18 × 12.5 mm., is parasitized by two very dissimilar cuckoos, the nominate race of the bronze cuckoo, *Chrysococcyx lucidus*, which produces an egg of very similar size, and the larger, very different, long-tailed cuckoo, *Urodynamis taitensis*, that lays an egg about twice as long and twice as broad (32 × 27 mm.).

The recent experimental work of Tinbergen (1951, p. 45; 1954, pp. 246–247) has shown that discrepancy in size does not deter an egg's acceptance by many birds. In fact, he found that the unusually great size of some of the egg models used had the effect of increasing the observable, released incubatory response of the birds. In his experiments the largest models used were too big for the bird to cover with its body, but even this did not act as a deterrant. Within much more reasonable dimensional discrepancies, the same effect seems to apply to many hosts of brood parasites. In general, the eggs of brood parasites are usually larger than those of their hosts, but this is not always the case, as has already been mentioned in *Chrysococcyx basalis* and its *Malurus* hosts.

In proportion to the body size of their producers, the eggs of parasitic cuckoos are relatively small compared with the same ratio of egg to body size in the host species. Heinroth (1922) found this ratio in self-breeding passerine birds to vary from 8 to 14 percent with an average of 11 percent. In seven species of parasitic cuckoos Schönwetter (1964, p. 535) found the ratio to range from a minimum of 3.2 percent in *Cuculus canorus* to a maximum of 7.9 percent in *Chrysococcyx lucidus plagosus*, with an average of 5.4 percent.

The genus *Chrysococcyx* represents one extreme development of the family Cuculidae. Its included species are the smallest of all the cuckoos and are parasitic wholly on fairly small species of hosts. The glossy cuckoos do not have this "area" of hosts to themselves, however, as some of the larger cuckoos (*Cuculus*, *Urodynamis*, *Cacomantis*, and others) also make use of these small fosterers. The need for reduction in egg size in the species of *Chrysococcyx* has been less than in the larger forms that share with them the nests of small passerine victims.

The evolutionary significance of dissimilarities in different stages of the life cycle of organisms is well known and is a matter of particular importance in brood parasites. As was pointed out in my study of the crested cuckoos of the genus *Clamator* (1964, p. 29), brood parasites are subject to the impact of natural selection on two levels. "Whereas in the case of self-breeding birds the entire biology of the species is a closely coordinated unit . . . on which selection may operate, in the case of brood parasites there is cleavage resulting in two fairly separate parts. The evolutionary climate ambient to the egg and nestling stages is that of the host species and has relatively minor connections with, and repercussions upon, the selective factors surrounding the life of the adult parasite." From this point of view it is of interest to note that the coloration of the eggs of the sympatric and partly homoxenic *plagosus* and *basalis* is markedly different, plain olive-bronze in the former and white spotted with pink in the latter. The two species reveal far greater differences in their egg shells than in their plumages.

Inasmuch as the available observational data fails to reveal any reliable, measurable difference in the adaptive success or failure of these very distinct egg types (in the relative frequency of their acceptance or rejection by the hosts), it is not possible to evaluate this, the most striking distinction achieved by these two closely related species. The degree to which both species use hosts that construct domed or covered nests, with the consequent low level of illumination surrounding the eggs, is one factor that obscures the evolutionary value of the two diverse egg patterns. In the case of open nests this factor would not be present, and since many eggs of both species are deposited in such nests, the problem is open to further study. It is hoped that it may be investigated by Australian ornithologists, and the results should be of much interest.

Mode of Egg-laying by Adult Cuckoos

Mode of deposition

While egg deposition is undoubtedly accomplished by direct laying into the host nests in the great majority of instances, no one has ever reported an eye-witness account of it. This is not evidence against it; it is merely the usual absence of direct observation that applies even to our knowledge of nonparasitic birds that are much easier to watch. At the same time, some writers have concluded that, when parasitizing certain types of nests, especially the small, semipendant ones of some of the sunbirds, the glossy cuckoos may have to place the eggs in them with their bills after having first laid them on the ground nearby. Baker (1942, esp. pp. 122–132) reviewed all the data known to him concerning European and Indian cuckoos and concluded that he could find no "evidence to prove or disprove the contention that one of the methods adopted by Cuckoos to place her egg in the nests is by carrying it in her beak to the place she has chosen for it. I think it *is* fully proved that she would not use this method if she could lay in the nest direct or could project it into it through the entrance, while supporting herself on the nest, or a twig, or something else. It does happen, however, that Cuckoos' eggs are found in a great number of nests in which it would seem impossible to have placed them by any other means than by the beak.

"Personally, I think it is highly probable that this method is very frequently adopted. . . ."

This kind of assumption has been made in the literature for some of the glossy cuckoos in Africa, Australia, and Asia, but in almost all instances it is unsupported by actual observations. However, in the case of two of the Australian species, *C. malayanus russatus* and *C. basalis*, there are on record some pertinent observations for each. Because of the great interest attached to them they may be repeated here.

In the case of *C. malayanus russatus* there are two records. Barnard (1926, pp. 6–7) saw one of these cuckoos clinging to the side of a "nest of *Gerygone magnirostris*. I was quite close to the bird at the time and could not mistake its identity. I waited till it flew off, then examined the nest and found two eggs of the *Gerygone* and a freshly laid egg of the Cuckoo . . . ." The commentator (A. J. Campbell) added to this that in answer to a question, Barnard replied, "The bird (*L.* [=*C.*] *russatus*) when seen at the *Gerygone*'s nest was clinging to the material with the head at the entrance, but not inside, the bird's tail pointing to the ground; therefore it was impossible for the cuckoo to have been leaving the nest (*i.e.*, laying in it). The assumption is therefore that the egg was *placed* in the nest and not *laid* in it; also from the size of the bird the nest would be considerably disturbed, if the bird had entered to lay. The nest in question was not disarranged in any way."

A second case was reported by Seaton (1962, p. 176), who saw one of these cuckoos fly to the nest of a yellow-breasted sunbird, *Cyrtostomus frenatus*, "carrying an egg in its bill; it clung to the side of the nest and, placing its head in the aperture, deposited the egg in the nest chamber. I rushed to the nest and on examination found the egg, which was still warm, coloured and freckled like the egg previously deposited [in another earlier nest by this cuckoo]." The sunbirds returned to the nest, chattered a little, and then deserted it, starting a new nest nearby shortly afterwards.

Many years ago Bennett (1879, p. 245) made an observation on the narrow-billed bronze cuckoo, *C. basalis*, indicative of mandibular egg placement. He had once shot a female *basalis* and found it had an egg of its own species in its throat. This led him to suspect that the bird was on its way to a host's nest in which it would have deposited the egg held in its mouth. Some time later he found a nest of *Malurus lamberti* containing two eggs of its own. Wishing to get a complete clutch, he left it untouched and returned a few days later. As he came near he saw a female *basalis* clinging to the side of the nest with its head thrust down into the entrance. His approach caused the cuckoo to fly off, and he examined the nest and found it to contain three eggs of the fairy wren and one of the cuckoo. He concluded "that the cuckoo must have carried the egg in her mouth and then deposited it in the nest, for it did not appear possible for the bird to get the whole of its body into the nest; indeed so small was the aperture that I had to tear the nest open to obtain the eggs . . . ."

Another instance of mandibular deposition by the same species of bronze cuckoo was reported by Selby (1946, p. 186), who found a nest with two eggs of the red-capped robin, *Petroica goodenovii*, on the ground. The robins were excitedly worrying a cuckoo "which was sitting on the sand. Very shortly the Cuckoo rose, picked up its egg in its bill, and placed it in the Robins' nest—leaving the two Robin eggs as they were. The Robins worried the Cuckoo the whole time, until it disappeared, after which the hen returned to the nest as if nothing untoward had happened . . . ." In this case the nest was on the ground and able to withstand the weight of the parasite had it entered to lay an egg.

Another less conclusive instance of mandibular oviposition by *C. basalis* may also be recalled. A. C. Allen (reported by Ross 1946, pp. 246–247) saw one of these cuckoos on the ground with an egg in its mouth. Two blue wrens, *Malurus cyaneus*, nesting nearby were much excited by the presence of the parasite, "which soon flew to a small scrub and perched on the side of a nest. It stayed there for about a minute making convulsive movements with its body and flapping its wings. It then flew to an adjacent sapling, but the egg had disappeared and the bill was closed. Mr. Allen then examined the nest and it contained two eggs of a Wren and a white egg liberally speckled with small red spots showing that the intruder was a Horsfield Bronze-Cuckoo (*Chalcites basalis*) . . . ." In this instance the actual insertion of the egg was not really observed, although the implication of the account strongly suggested it.

Still another case, called to my attention by K. A. Hindwood, may be mentioned. Len Harvey (1961, p. 3) saw a female *basalis* carry her own egg in her bill to a blue fairy wren's nest, and a few seconds later the cuckoo flew off with one of the wren's eggs in her bill. This was at Invermay, near Ballarat, Victoria.

In Kenya and Uganda, Pitman (*in litt.*) concluded that *C. klaas* probably also resorted to mandibular egg insertion into nests of some of its sunbird hosts, although he did not have the good fortune to observe such behavior. Others have made similar suggestions for *C. cupreus*, although also without direct observations.

By now we have seen that there is sufficient evidence to establish the conclusion that mandibular egg placement does occur. By virtue of the behavioral pliability behind this fact, nests that would otherwise be unavailable to the cuckoos are made accessible for their parasitism. It does appear, however, that this is an occasional rather than a regular mode of egg laying. By and large, there is little reason to assume that natural selection would ordinarily favor the evolution of such a habit as a regular pattern, as it would seem to be connected with a poor host choice. A bird nest too small to accommodate the body of the parasitic hen would usually prove inadequate to hold the young cuckoo after the first week or 10 days of its nestling growth. Even Baker (1942, pp. 122–132), who was inclined to believe in mandibular oviposition in a nest too small or too insecurely suspended to bear the weight of an adult hen Cuckoo, attempted to use as "proof" of this method of egg deposition the argument that such a nest cannot even "bear the weight of the young Cuckoo when half grown and often breaks down before it is half fledged. . . . It is equally certain that the Cuckoo cannot enter so small a nest. It is a very strange sight when a young Cuckoo gets too large for its abode. At first the nest itself expands and the young bird sits with its head out of the entrance encased in a trellis-work of grass, etc., which gradually gets thinner and thinner until it bursts and the cuckoo is thrown headlong to the ground . . . ." Even if, as Baker suggests, the catapulted young parasite is then fed on the ground by its foster-parents, it would seem that in many instances the destruction of the nest would be fatal to the nestling in it or that an altricial young prior to the fledging stage would not survive long either out of, or deprived of the protection of, the nest.

While mandibular egg deposition may thus seem to have slight evolutionary value, nevertheless, that occasionally brood parasites do resort to this behavior pattern is of interest since it evidences a degree of psychobiological adaptiveness that is in itself quite remarkable. This, in turn, makes one wonder if the habit may have started early in cuculine history with more ordinary, less flimsy or insecure, or less uncomfortably small types of host nests. It is conceivable that it might have had a value, both immediate and in the long range of natural selection, of being a more rapid method of egg deposition than direct laying into the nest; it certainly could have been advantageous to the parasite, especially in nests well guarded by their owners. Once such a habit, or such an extension of it, had become part of the scope of the innate behavior of the cuckoos, it could reappear from time to time.

The glossy cuckoos usually lay but one egg in any one nest. While there are records of two and even of three eggs of some of these cuckoos in a single host nest, they are definitely exceptional. As is well documented, multiple eggs deposited in the same nest are extremely rare in the European cuckoo, *Cuculus canorus*, but are quite frequent, in fact usual, in some of the crested cuckoos of the genus *Clamator*. The species of *Chrysococcyx* agree much more with *Cuculus* than with *Clamator* in this aspect of their parasitism. The rarity of multiple versus single eggs in individual nests is true of all the glossy cuckoos of whose eggs enough is known. While the following figures relate particularly to some of the African species on which I have more extensive data, the picture is similar in the Australasian members of the genus. In *C. caprius* my records show 231 host nests with a single didric cuckoo egg in each, 12 nests with two each, and only 2 nests holding three of the parasitic eggs apiece. In other words, out of a total of 261 didric cuckoo eggs, 245 were "singles" when laid, and 16 were "multiples" or "extra" eggs. That there may be some slight local or individual variation in this matter of multiple-egg laying is suggested by the fact that of 12 nests with two didric eggs each, 4 were found in central Natal (but over a period of seven years)—all in nests of the Cape weaver, *Ploceus capensis olivaceus*.

In the case of *C. klaas* the number of nest egg records is much smaller, but it reveals that in each of 29 nests there was a single *klaas* egg, and in 3 nests there were two such eggs apiece. Years ago H. L. White (1915, p. 145) summarized his large number of records for three Australian glossy cuckoos, *basalis*, *lucidus* (*plagosus*), and *osculans*, and found that there was usually but one cuckoo egg in a nest. Occasionally he found two *lucidus* or *basalis* eggs together and once even three *basalis* eggs, but in these cases it is unknown if the multiple eggs were laid by the same or by different hens. In the two Malaysian species *maculatus* and *xanthorhynchus*, Baker's data included only single eggs per nest, 11 in the case of *maculatus*, 9 for *xanthorhynchus*.

In the instance White described where three *basalis* eggs were in the same nest, they were actually buried at different levels in the nest lining, so that this case was in effect, more comparable to three separate nests than to one with multiple parasitism. Another instance of three *basalis* eggs in a nest of *Malurus cyaneus*, reported by Parsons (1918, p. 145), also involved eggs buried under later nest lining, but in this instance it was not specified if they were buried together or at different times.

Interval between eggs

The interval between eggs is still a matter of some uncertainty. There is in the literature a tendency to assume that the small cuckoos, such as *Chrysococcyx*, lay at daily intervals in contrast to the larger *Cuculus* which lays at intervals of 48 hours. For example, in discussing the two Asiatic species *maculatus* and *xanthorhynchus*, Baker (1942, p. 168) wrote that two of his correspondents, C. M. Inglis and A. M. Primrose, believed that these cuckoos laid at intervals of 24 hours, but added that, inasmuch as he had never taken any but single eggs of these birds, he could neither prove nor disprove the suggestion. Unfortunately, neither Inglis nor Primrose have recorded their observational data.

In the case of the African *caprius* we have better, although conflicting information. In my earlier account (1949a, pp. 161–162) I stated that the interval between eggs seems to be one day, not two as in *Cuculus*, and pointed out that the pertinent evidence was of two kinds. "In the ovaries of breeding females that I examined there was less difference in the degree of collapse and disintegration of the discharged follicles than in comparable material of *Cuculus*. This implies a shorter interval between successive discharge follicles, which leads me to think the eggs may be laid at intervals of one day. More direct, observational data are supplied by Pringle (Ostrich, 1946, pp. 368–369) who noted a female didric (ostensibly, but not absolutely certainly, the same individual) returning to a Cape sparrow's nest on three successive days, and each day depositing an egg in the nest."

Recently Ottow and Duve (1965, p. 433) have interpreted Duve's very intensive and important field observations to imply a much longer interval between eggs—at least four days. This surprising conclusion was based on Duve's conviction from his observations that he was reasonably certain that only three or four female didrics were in attendance as parasites on a colony of red bishops, *Euplectes orix*, and that he had practically every nest under observation. From this he assumed that, if, as he thought, these didrics parasitized only the bishops (and they would have had to fly "considerable distances" to lay in other nests of other colonies of the same host) and if they laid at daily intervals, he would have expected at least three or four times as many didric eggs as he found in his daily inspection of each nest in the colony.

The weak points in Duve's data are that his cuckoos were not marked for easy individual sight identification, that he may have failed to find some of the bishops' nests, and that the cuckoos might have made "considerable flights" to other host colonies or might have laid some of their eggs in nearby nests of other species of birds. In other words, the four day interval postulated is an interpretation and not an established fact. At the same time, it should be stressed that while Duve's conclusions are at variance with Pringle's observations and with the results of an examination of the ovarian follicles, the intensity and meticulousness of Duve's field work make his work worthy of serious consideration. It is to be hoped that further studies along the same line may be made for the additional light they may shed on this problem. In our present state of knowledge, I do not think it likely that a four-day interval exists, but at the same time I would not rule out, or ignore, Ottow and Duve's interpretation. Further substantiation in greater detail is needed to make it acceptable because of the exceptional and unexpected length of this longer interval.

Duve (both *in litt.* and in his joint paper with Ottow [1965]) has attempted to coordinate a longer egg interval with the fledgling-feeding tendency of the adult didric. This I think is unnecessary, since the feeding of newly fledged didrics by adults of their own species is apparently an occasional rather than a "routine" behavior and as far as published observations indicate, is done mainly by the males and not by the egg-producing females.

Number of eggs

The number of eggs laid by one glossy cuckoo in one breeding season is another aspect of their breeding biology on which we still need further information. There are no data, either direct or inferential, on any of the Australasian species of these birds. In the case of the African species, *klaas,* I noted (1949a, p. 137) that one dissected hen had one nearly ripe egg in the oviduct and three much enlarged yolks in the ovary, suggesting that at least four eggs would have been laid by this bird. In the case of *caprius,* Plowes (1946b, p. 271) found three white eggs of this cuckoo in a small colony of masked weaver nests (*Ploceus velatus*) near Bloemhof, Transvaal, and concluded that, since this is an uncommon egg morph of *caprius,* all were probably the product of the same hen, which would thus have laid at least three eggs. In another colony of masked weavers containing 37 nests, I reported (1949a, pp. 158–159) that examination showed that 20 were in use and that of these, 4 each contained one *caprius* egg. The eggs were all alike in size, color, and markings and were probably all the product of the same hen. In another case, a colony of 28 nests of the same weaver, 3 contained one egg each of the didric, again all alike in color, markings and size. In this case I collected the female didric and "although the bird was badly spoiled by the shot, I could make out with the aid of a hand lens that there were three discharged egg follicles in the ovary. There might, however, have been more but I could not make out any others definitely. . . ." Ottow and Duve (1965, pp. 433–434) concluded from their data that each female didric lays not more than four or five eggs during a breeding period. It is not clear from their paper if by a breeding "period" they mean an annual breeding season or a section of such a season, comparable to a single clutch or to one nesting of a two- or three-brooded bird. Also, as we have seen above in our discussion of egg intervals, there is some reason to ask if this number accurately represents the total.

Removal of Host Eggs by Adult Cuckoos

The habit of removing one or more of the hosts' eggs from a nest has been known for a long time in many quite unrelated avian brood parasites, cuckoos of several genera (*Cuculus, Clamator, Chrysococcyx, Cacomantis,* etc.), cowbirds (*Molothrus*) and widowbirds (*Vidua*), and possibly honey-guides (*Indicator*). While the correlation of this habit with a parasitic mode of reproduction seems obvious, the origin of the behavior is still completely unknown. As yet, no one has been able to suggest an antecedent behavioral trait that might have been altered into one of removal of eggs from the host's nest by the parasitic bird. While egg removal by the adult parasite operates to its own advantage by reducing the clutch size in the parasitized nest, thereby ostensibly aiding the potential success of the young cuckoo, it is inconceivable, that the laying adult can have any anticipatory purpose. Actually, in many egg-removing parasites the evicting habit of their newly hatched young takes care of possible nest-mate competitors, rendering the earlier removal of one or more eggs less important than it might appear to be. It would seem (but at this state of our knowledge "seem" is the strongest word that may be used) that the function of egg removal by the adult parasite is to keep the total clutch in the nest from exceeding the limits acceptable to the incubating host.

The glossy cuckoos shed no new light on the early stages of this particular behavioral trait, an evolutionary problem of great interest, but one that remains blanketed in obscurity. In fact, we still do not know if all the species even have the egg-removing habit, although it is highly probable that all do. The habit has been reported on good evidence for only four of the species: *lucidus* (unpublished data from two observers), *basalis* (Atkins 1922, p. 314; Ingle 1912, p. 254; Ross 1919, p. 303); *klaas* (Pitman, *in litt.*), and *caprius* (Pringle 1946, p. 368; Skead, *in litt.*). To this may be added that it has been said to occur in *maculatus* and in *xanthorhynchus*, although without direct evidence. In the case of *cupreus* it has been suggested by Chapin (1939, p. 203) that the male may remove an egg from a nest occasionally, but it is not clear that this is necessarily connected with the deposition of a substitute egg by his mate.

In connection with *C. lucidus plagosus* it may be noted that Braddy (1949, p. 238) and Chalk (1950, pp. 219–220) both recorded seeing an adult glossy cuckoo that flew to a thornbill's nest (*Acanthiza chrysorrhoa*) and "clung by its feet to the lower part of the nest and rapidly searched for and found the entrance, into which it thrust itself, leaving only the end of the tail exposed. In a split second it withdrew itself backward from the nest with the egg of the thornbill in its bill. This it cast to the ground. A second time it plunged into the nest and repeated the act, except that the second egg thrown out proved, on our investigating it, to be that of its own species . . . ." This observation is given here because it shows the instinctive nature of the act, with no recognition of the difference between the eggs of the host and of the parasite, which is what is tacitly assumed to hold as well for the host in its usual acceptance of the alien egg. In this particular instance both eggs were in an advanced state of incubation, which indicates that a considerable number of days had elapsed since the act of parasitism. It is, of course, impossible to tell if the egg-removing cuckoo had also laid the egg in the nest. Even if it was the same bird, the time between the two acts would make it uncertain that there was any real connection between them.

In the case of *C. klaas* in Uganda, Pitman (*in litt.*) considered egg removal the usual, normal procedure in all nests parasitized, and he wrote me that such removal was performed only by the male cuckoos. Unfortunately it is not clear on what observational evidence he based this statement, and one can only await the publication of his work to see what actual data he may have had. In my earlier account (1949a, p. 137) I attempted to summarize what was then known by saying that: Klaas' cuckoo often removes an egg from the nest when depositing its own, but whether it does so regularly or not remains to be established. Several observers have seen one of these cuckoos with an egg in its bill and have seen it break the shell and swallow the contents. Captain Pitman also wrote me that he considered the removal of one or more eggs from the nest by the adult male was also characteristic of the didric, *C. caprius*.

In some species there is inferential evidence pointing to egg removal by adult cuckoos, based on the fact that in parasitized nests the number of the host's eggs is often reduced from the normal clutch size by the number of cuckoo eggs laid in it. This is true for instances of parasitism recorded for the species *osculans*, *malayanus*, *lucidus*, *basalis*, *maculatus*, *xanthorhynchus*, *klaas*, *cupreus*, and *caprius*. As an example, dealing in this instance with *caprius*, we may cite the work of Hunter (1961, pp. 55–63), who studied the masked weaver, *Ploceus velatus*, 12 of whose nests he found to be parasitized. In none of these were there more than two eggs of the host in addition to that of the cuckoo (in nonparasitized nests three eggs comprised the usual clutch), an indication that the cuckoo parasite regularly removed at least one of the host eggs from nests into which it deposited its own.

That host-egg removal is not invariably the case even in a species as well known (relatively) as *caprius* is indicated by an observation sent me by Neuby-Varty from Southern Rhodesia. He found a nest of a tawny-flanked longtail, *Prinia subflava affinis*, with four eggs of the *Prinia* and one of the didric cuckoo. Since in hundreds of nests of this warbler Neuby-Varty had never found more than four eggs, he concluded that the cuckoo had not removed any warbler eggs in this instance.

As a further instance of lack of egg removal by the adult parasite, we may cite Reed's observations (1953, pp. 138–140). He studied the didric's parasitism on the red bishop, *Euplectes orix*, and reported that the cuckoo does not usually remove an egg of the host, "the normal Red Bishop clutch [being] three eggs, and nearly all nests containing cuckoo eggs [carrying] a total of four eggs . . . ."

However, the bulk of the observations on *caprius* suggest that egg removal is frequent, probably more often present than absent, from the picture. We may mention the case reported by Pringle (1946, pp. 368–369), who saw a didric cuckoo leave the nest of a Cape sparrow, *Passer melanurus*, with one of the sparrow's eggs in its bill. It flew to a nearby tree where it broke the egg shell, ate some of the contents, and dropped the shell fragments to the ground. Pringle kept the nest under daily observation and found that the cuckoo (presumably the same bird) returned the following morning and again the next day, each time removing one sparrow egg and laying one of its own (all three cuckoo eggs so similar as to make it highly probable that they were all from the same hen). Pringle's description suggests that the egg removing was done by the female didric, not by her mate as Pitman's statement (*supra*) might lead one to assume. However, Pringle did not specifically state that he observed the second and third egg removal, but only that the first was done by a female cuckoo.

Ottow and Duve (1965, p. 434) concluded, from Duve's extensive data on didrics parasitic on a colony of red bishops near Johannesburg, that the adult cuckoo removed eggs of the host only from nests in which there were more than two eggs. Occasionally two host eggs were missing from a nest, which these authors interpreted as implying that a second didric hen was involved in the particular instances. In six nests, each with two didric eggs, four no longer contained any of the bishop eggs. Eggs of the didric were found with one host egg in 17 nests, with two host eggs in 26, with three host eggs in 4, and with four host eggs in only a single nest. Duve assumed, but showed no real proof, that the female didric did the actual removal of the eggs.

In our present study we are looking primarily for evidences of evolutionary change within the genus *Chrysococcyx*, and must admit that present data fail to show any progressive, or regressive, alteration in this particular segment of the parasitic behavioral program. It may be that fuller knowledge of all the species will indicate a trend toward greater utilization of egg removal in the behavioral nexus associated with brood parasitism in certain species and less in others. The glossy cuckoos arose from an earlier parasitic stock which already had the habit of removing eggs from the nests of their hosts, and, so far as we may see, they have not altered the expression of this trait. In the European cuckoo, *Cuculus canorus*, which, in the present state of our knowledge, must serve as a "standard of comparison," the male has not been found to be involved in the removal of eggs from host nests. If Pitman's statement should be found to have general validity, this involvement of the male may shed some light on the particular development this portion of parasitical behavior has undergone in the glossy cuckoos.

Host-parasite nestling relations

Aside from the evicting habit by which the young cuckoo eliminates its nest-mates (discussed in the next section), a few other aspects of the nest-inhabiting period of the parasite's life call for comment. Although the available data are still incomplete, they are here given more as a basis for future additions than as a statement of any finality. The topics of biological interest are: the length of the incubation period of the cuckoo's eggs, the duration of the nestling stage, and the duration of attentive behavior on the part of the host after the young parasite is fledged, i.e., after it leaves the nest.

The incubation period has not been reported for any of the glossy cuckoos except *C. caprius*, and in that species the few published statements are not at all harmonious. Skead (1947, pp. 23–24) wrote that the incubation period was 10½ days (in a nest of the Cape weaver, *Ploceus capensis olivaceus*). From piece-meal data on several nests containing *caprius* eggs, I estimated (1949a, p. 163) it to be a day longer. More recently, Hunter (1961, pp. 55–63) studied the parasitism of *caprius* on the masked weaver, *Ploceus velatus*, and concluded that the eggs of the cuckoo took about 12 days to hatch. In the case of *C. osculans*, Chisholm (1935, p. 70) wrote of a nest of a speckled warbler, *Chthonicola,* with an egg of *osculans* and stated that "two weeks later the egg had hatched. . . ." This is the nearest to a statement of the incubation period I have found for this species, and it was not written as an accurate, precise measurement. Inasmuch as any shortening of the incubation period would seem to be a selectively critical factor in a group of brood parasites, it would be very interesting to know if the glossy cuckoos reveal any adaptive differences, even slight, in the duration of their prenatal development. It is not clear from present fragmentary data if we can assume that the incubation period is shorter in *caprius* than in *osculans;* more data on these two and on the other species of the group are needed.

The duration of the nestling stage (from hatching to fledging) has not been recorded for any of the Australian and Asian species of *Chrysococcyx;* in the case of *klaas* the nestling period was at least 12 days in a nest of the amethyst sunbird, *Chalcomitra amethystina* and it was suggested (Friedmann 1949a, p. 146) that the exact length of the period might vary somewhat with different species of fosterers. In *caprius*, Skead (1947, pp. 23–24) found the nestling period, with the Cape weaver as a host, to be 10 to 15 days; Pitman (*in* Friedmann 1949a, pp. 180–181) found a young *caprius*, about a fortnight old, in a nest of a sunbird, *Nectarinia erythroceria,* while Hunter (1961) found that a young *caprius* remained in the nest of a masked weaver for 20 days. R. A. Reed (*in litt.*) found a young didric, *C. caprius,* hatched in a red bishop's, *Euplectes orix*, nest, had a nestling period of between 19 days, 18 hours, and 22 days. The reason for this uncertainty may be seen from the following details. On March 4 at 7:15 a.m. the nest contained four identical, plain blue eggs, and at 12:15 p.m. on March 5, it contained one hatched didric cuckoo and three eggs. At 6:30 a.m. on March 25 the didric cuckoo chick was still present in the nest, but when this nest was examined again at 6:30 a.m. on March 26 it was empty and deserted.

In nests in which the cuckoo eggs hatch several days later than those of the host (i.e., probably nests parasitized after incubation has begun in the host's own eggs), the young parasite is unable to evict the larger, heavier young of its foster-parent. On this point R.A. Reed sent me the following notes, which may be given in toto.

> It is by no means always the didric chick which hatches first when a nest is parasitized by this species. Out of a total of 40 nests which I found parasitized by this cuckoo and a total of 37 which I have found containing the young of this cuckoo, three contained cuckoo chicks considerably younger than their nest mates (the offspring of the host). On February 22, 1955 I found a newly hatched didric chick in the nest of a red bishop together with two red bishop chicks approximately seven days old. When I revisited this nest on March 2 I found the didric chick dead in the bottom of the nest apparently trampled to death by its nest mates. On March 2, 1955 I found in the nest of a Cape sparrow not more than 100 yards from the above red bishop nest, a newly hatched didric cuckoo chick together with one addled Cape sparrow egg and a Cape sparrow chick approximately six to seven days old. When I revisited this nest on March 4 the Cape sparrow chick and egg were still present with the cuckoo which was calling fairly loudly for food. Unfortunately, on my next visit this nest had been robbed of all its contents. The third case was that of a didric cuckoo chick which I judged to be approximately seven days old (it was quite naked) in a Cape sparrow nest which it shared with three nearly fully-fledged Cape sparrow chicks . . . . This didric chick was calling so lustily for food that it could be heard from 15 to 20 yards away.
>
> From these records it would appear that when the didric chick is hatched several days later than its nest mates it is incapable of evicting them and is sometimes reared with them. Yet it appears that if all the eggs in the nest are hatched at about the same time the didric chick evicts the young of the host. As an example I cite a red bishop's nest in which I found one didric cuckoo chick and one red bishop chick both approximately two days old on January 15, 1955. On January 17 when I again visited this nest it contained only a didric cuckoo chick. On another occasion I found a red bishop's nest

> containing 5 similar eggs and when I visited it on February 5, 1956 it contained two red bishop chicks, one approximately 24 hours old and the other freshly hatched together with one didric chick approximately one to two days old. When this nest was again visited on February 11 it contained only a didric cuckoo chick. . . .

In the case of the European cuckoo, *Cuculus canorus*, the habit of the very young nestling of evicting its nest-mates from the nest is always described as facilitated by the hollow, somewhat concave shape of its back, affording a place on which to balance the egg or young to be evicted. No such hollowing has been described for any of the glossy cuckoos, but the didric, *C. caprius*, does have a decidedly flattened back which is somewhat hollowed by the action of the bird, which in the process of evicting usually raises its featherless wings above the plane of its back to help balance the object it is about to evict. Otherwise it would be difficult to see how the young cuckoo could carry an egg almost its own size up a perpendicular nest wall several times it own length.

Mellor (1917, p. 18) noted of *C. basalis* that a newly hatched chick had an "abnormal spike" at the alula and that its claws were curved and exceedingly sharp. This has not been noted in other species of glossy cuckoos.

The length of time after fledging during which the fosterer continues to feed the young parasite is of interest insofar as it interferes with the host's renesting and rearing a brood of its own. The survival of the population of the host species is clearly of importance to the parasite if the latter is to continue to have an adequate supply of host nests. The data available on four species of glossy cuckoos suggest that each instance of parasitism may have a prolonged effect, sufficiently lengthy to affect adversely the possible recuperation of the host species. Thus, in the south Australian *basalis* Kikkawa and Dwyer (1962, p. 171) found that the fledgling still gapes for food from passing birds for as long as six weeks after leaving the nest, a much longer period than the usual postfledging feeding period of the host involved in this observation (*Acanthiza chrysorrhoa*). It was not stated, however, that the *Acanthiza* actually gave much attention to the young cuckoo for this long time.

In the African *klaas*, J. Paludan (*in litt.*) wrote me that at Leopoldville, Congo, he watched a pair of *Cyanomitra verticalis* that continued to feed a young Klaas's cuckoo which they had reared for at least 10 bays after fledging. A still-longer period was noted by Ryves (1959, p. 175) who watched a pair of *Nectarinia kilimensis* feeding a fledgling *cupreus* for 26 days after it left their nest.

The data on the didric, *C. caprius*, reared by a Cape weaver studied dy Skead (1947), who found it to be fed by its host for about a fortnight after leaving the nest, may be extended by the observations of R. A. Reed in the Transvaal, who kindly sent me the following (*in litt.*).

> At 5:45 p.m. on March 13 a fully fledged didric chick in a red bishop nest was about to leave the nest as I touched it. At 6:30 a.m. on March 15 when I revisited this nest the chick had left. On March 19 I found this bird lustily uttering its hunger call close to the nest, accompanied by a red bishop. This chick I kept under daily observation. By March 21 it had moved approximately 50 yards downstream from the nest and by March 22 it had established itself in some shrubbery approximately 80 yards from the nest, where it remained for the rest of the period during which I had it under observation. . . . The bird was seen on March 22 sitting quietly for 15 minutes at a time; occasionally preening; black sunbirds, Cape sparrows and streaky-headed seedeaters close at hand in same tree but the chick ignored them; immediately it heard a red bishop call it assumed the begging attitude—drooping wings a-shiver and high-pitched twittering—before the foster parent arrives beside it. A moment later the female red bishop alighted beside it and fed it with food apparently from its throat or crop; feeding the chick in a series of regurgitations before flying off. The chick continued to twitter weakly and to shiver its drooping wings for several seconds after the foster parent had left. . . . On March 25 it was still uttering its hunger call and was attended by the female red bishop. On this occasion it flew after its foster parent across the shrubbery.
>
> At 6:30 a.m. on March 25, 1955 a didric chick was still occupying another nest of a red bishop approximately 150 yards downstream from that described above. At 6:30 a.m. on March 26 it had flown from the nest, being fully fledged. I continued to record the presence of only one didric chick in the shrubbery until April 3 when two juveniles were calling quite close to one another. On April 4 both juveniles were present in the same tree. This was the last occasion on which I recorded two juvenile didrics together in this area. I continued, however, to record a single juvenile which, on April 6, after being fed by a female red bishop with 44 regurgitations from its crop or throat, flew in swift pursuit of its foster parent, twisting and weaving for approximately 100 yards to a mulberry tree. Watching this bird on April 9 I noted that it was still being fed by its foster parent, which it vigorously pursued after each feeding although still remaining in the close vicinity of the shrubbery patch. On April 11 I recorded that this chick now appeared very green—not coppery—on the back and was still begging vigorously from the female red bishop. April 12 was the last date on which I saw this bird, which never, during my observation of it, had strayed more than 200 yards from its original nest site. As will be noted, this bird could have originated from either of the two red bishop nests recorded in this area so that the maximum post-nestling

> period during which this bird could be said to have remained with its fosterer was 28 days and the minimum 18. . . .

The same observer found the period of postfledging feeding of *caprius* by masked weavers, *Ploceus velatus*, lasted from 22 to 26 days; and by Cape sparrows, *Passer melanurus*, from 17 to 37 days! Because of their unique richness in detail, further quotation from Reed's notes seem desirable.

> On December 23, 1954, a juvenile didric was uttering the hunger call and was attended by Cape sparrows. This bird I observed almost daily and, on December 31, it was joined by another juvenile didric also waited upon by Cape sparrows. Subsequent to that date I observed only one didric in company with Cape sparrows in this area and the last time I saw this bird was January 29, 1955. During this period, under close observation for nearly a month, I always found this didric within a radius of approximately 50 yards of the tree where it was first seen. Because there were two didrics together at one time I cannot say which of the two remained in the area to the last and I must therefore state that the maximum post nestling period was 37 days but the minimum was at least 29.
>
> I have one more postnestling record for a didric reared by Cape sparrows and that is of a chick which was fully fledged in a Cape sparrow nest at 6:30 a.m. on March 11, 1955 and which had left the nest by 6:30 p.m. on the same day. This chick remained in this vicinity—I always found it within a radius of approximately 30 yards of a central point—until March 28th, giving a period of 17 days . . . .

A parasitic bird, reared by any of a number of possible host species, is aided by a fairly broad tolerance of food items and even of feeding methods. Thus, the method of feeding the fledgling didric cuckoo by red bishops is quite different from that employed by either the Cape or masked weaver or by the Cape sparrow. The red bishop invariably feeds the young with regurgitations from its crop. Reed informed me that on several occasions he counted more than 40 of these short, jerky regurgitations in a single continuous feeding. On the other hand, the masked and the Cape weavers bring a sizable grub or other insect, and each feeding operation consists of a single offering. Whereas these birds feed their own young and their parasitic young on insects exclusively, the red bishop uses soft seeds extensively. The droppings of young didrics reared by red bishops often are full of small grass seeds.

While the cuckoo young in general may thus experience a more varied diet than do the young of any one of its fosterers, there are, of course, obvious limits to what it can take in its stride. That all the glossy cuckoos are parasitic on small passerine species in itself limits the range or variety of their nutriment.

Eviction of nest-mates by nestling cuckoos

Like the related genera *Cuculus* and *Cacomantis*, *Chrysococcyx* also evinces the behavior pattern of eviction of nest-mates by the newly hatched young. As in the other two genera, this habit is dispalyed only in the first days of the nestling's life and disappears by the time the young cuckoo's eyes begin to open. Eviction of nest-mates, either young or eggs, has been observed and recorded for five species of *Chrysococcyx*—*lucidus*, *basalis*, *osculans*, *klaas*, and *caprius*, and inferred, without actual direct observation, for *maculatus*, *xanthorhynchus*, and *cupreus*. In all probability the habit occurs in the other glossy cuckoos as well, but as yet no data are available on them.[11]

In the case of *C. lucidus*, Oliver (1955, p. 535) concluded that the parasitism of this species must have a considerable effect on the population of its chief host in New Zealand, the gray warbler, *Gerygone igata*, whose "first brood . . . unless delayed, escapes the attention of the cuckoo but [whose] later broods suffer heavy casualties in their nestling stage as the young cuckoo invariably throws out all eggs and young from the nest it occupies . . . ." In other species of *Chrysococcyx* it appears that eviction of nest-mates is frequent, but not invariable. Both Pitman and Chapin (*in* Friedmann 1949a, pp. 180–181) have sent me notes on nests containing young of the host and of the cuckoo (*caprius*), but we do not know if these were instances where the young parasite made no effort to oust its companions or if it tried to do so but failed.

In a previous discussion (1956, pp. 404–405) I pointed out that no one had yet made a direct observation of the actual evicting act by a young *caprius*, a statement that is still true a decade later. The precise age, in days, at which the newly hatched young cuckoo becomes an evictor and the age at which it ceases to be one has been reported with some variation. Thus, Skead (1952, pp. 7, 9) noted that a nestling *caprius* in a *Motacilla* nest made no effort to oust the two eggs of the host for its first two days, after which it proceeded to evict them both. In a *Ploceus capensis* nest, a young didric evicted an egg and a newly hatched young of the fosterer on its second day. In another *Ploceus* nest the young parasite was half way through its

---

[11] For pertinent published references on eviction of nest-mates see: *lucidus*—Campbell 1901, p. 581; Dickison 1928, p. 151; Oliver 1955, p. 535; *basalis*—Campbell, 1901, p. 579; de Warren 1926, p. 78; Dickison 1928, p. 151; Leach 1929, pp. 177–182; *osculans*—Chisholm 1935, p. 70; *maculatus* and *xanthorhynchus*—Baker 1942, p. 155; *klaas*—Friedmann 1956, pp. 399–400; MacLeod and Hallack 1956, pp. 2–5; *caprius*—Friedmann 1956, pp. 404–405; Hunter 1961, pp. 55–63; Reed 1953, pp. 138–140; Skead 1952, pp. 7, 9; Skead, *in* Rowan and Broekhuysen 1962, p. 28. In addition to these I have numbers of unpublished notes from Pitman, Chapin, and other observers in my files.

third day when it ousted its nest-mates. On the other hand, Reed (1953, pp. 138–140) reported that a nest of *Euplectes orix* contained one chick and two eggs of the bishop bird when a didric egg in the nest hatched; four days later the nest was found to contain three young bishops and the young didric cuckoo, indicating that no eviction had transpired. In another nest of a red bishop Reed found only a young *caprius* about four days old. He then put two *Euplectes* eggs in the nest, and 4½ hours later both were out of the nest. This suggests that the evicting habit persisted until the didric's fourth day at the least. Notwithstanding the apparent absence of eviction in the first case reported, Reed concluded that the nestling *caprius* "appears to eject the eggs or young of its host in all cases because in no single instance were large Didric Cuckoo chicks found with Red Bishop young in the same nest . . . ."

Hunter (1961, pp. 55–63) concluded that the young cuckoo was unable to eject chicks of the masked weaver, *Ploceus velatus*, if it hatched too long after they did. Unfortunately, no more explicit time was given, but it would seem to be a matter determined by the size and weight of the *Ploceus* chicks, plus their increased ability to withstand the actions of the would-be evictor.

The young of normal, self-breeding birds are often crowded in the nest and cannot help but push against each other, although they make no attempt to evict. Furthermore, the crowding usually comes later when the young are larger, and since the evicting habit of the young cuckoo is restricted to the first few days, before the nest is really crowded, it follows that it is not a result of crowding but is merely a contact reaction.

We know that the young of some parasitic cuckoos, such as the crested cuckoos, *Clamator*, and koels, *Eudynamis*, do not practice eviction and that in the nests on which they are reared crowding often is very great. We know also that parasitic widowbirds, *Vidua*, and cowbirds, *Molothrus*, do not have the evicting habit, although not infrequently the host young are starved out by the parasite and their dead bodies removed by their own parents.

The nest-mate evicting habit reveals no alteration in the glossy cuckoos; it is apparently a trait that was already present in the stock from which they evolved, and, as far as present observations go, they have neither added to, nor subtracted any features from, its mode of expression. In some Ploceine nests it is often difficult for the young didrics to evict their nest-mates, yet species of *Ploceus* with domed nests with tubular entrances are among the commonest victims of *caprius*. Similarly, the nests of many of the sunbirds used frequently by *klaas* present difficulties for the would-be evictor as they are often deep, frail, pouchlike structures. It might be said of the glossy cuckoos that they have retained the evicting habit in spite of their wide use of "difficult" nests—certainly many of them more difficult as eviction sites, with all the violent exertion and pushing involved, than those commonly parasitized by species of the genus *Cuculus*.

Fledgling feeding by adult cuckoos

The atavistic behavior pattern of feeding fledgling glossy cuckoos by adults of the same species has been observed and recorded for four of the members of the genus *Chrysococcyx* (*caprius*, *cupreus*, *klaas*, and *lucidus*) with a total of at least 33 independent observations, not counting such old, unsupported statements as that of Heuglin (1871, p. 777), who noted adult *caprius* feeding young ones on several occasions in October 1861, at Keren, or indefinite, dataless observations along the same lines by others. These 33 cases are divided as follows: *caprius* 15 (plus some incompletely described ones), *cupreus* 2, *klaas* 12, and *lucidus* 4 cases in print.

The number of these definite observations is sufficient to indicate [12] that fledgling feeding is neither uncommon nor unusual, while the assiduous and repetitive feedings in some of these cases make it impossible to assume that they were chance happenings which were based on the reactivation of a residual responsiveness by a passing adult cuckoo to the food-begging of the young.

In earlier discussions of this intriguing and theoretically significant tendency I was inclined to wonder if the actual observations might not have been of instances of courtship feeding, in which case either the observer assumed the fed bird to be a young one rather than a potential mate or that the food-bringing cuckoo itself might have mistaken a well-grown fledgling for an adult female. Some years later I found that Watson and Bull (1950) had raised a similar question about Hursthouse's (1944) record of fledgling feeding by the glossy cuckoo, *C. lucidus*, in New Zealand, even though in that instance the presence of the foster-parent, *Gerygone igata*, enhanced the likelihood that the fed bird was, not an adult, but a young cuckoo. My original question stemmed from the fact that the early records involved adult-male cuckoos only in instances where the sex of the feeding bird was specifically mentioned. Even now, with a greater number of such cases on record, there is still only meager evidence that adult females

---

[12] For pertinent references to these cases see: Baird 1945; Benson and Serventy 1957; Fell 1947, p. 513; Fulton 1910; Graham 1940, p. 4; Haydock 1950; Heuglin 1871; Holman, *in* Bannerman, 1933, Hursthouse 1944; Maclaren 1952, 1953; Millar 1926, 1943; Moreau 1944; Moreau and Moreau 1939; Oliver 1955; Olivier 1957; Ottow and Duve 1965, p. 432; Pike, *in* Friedmann, 1956; Robinson 1950, p. 107; Smith 1957, p. 309; Symons. *in* Friedmann 1949a; Thomas 1960; van Someren 1939; and Worman 1930.

of these cuckoos do feed fledglings of their own kind. Out of the 33 instances on which I have compiled data, the sex of the food-bearing bird was stated in only 13 cases, and in 12 of these it was male. In only a single instance, of which I was unfortunately unaware at the time (Millar 1926, p. 28) was the food-bearing bird stated to be a female, and this account was written in so loose and anecdotal a manner that it seemed too unfirm a basis for a unique unit of information. In all the other cases, either the sex of the food-bringing bird was not mentioned, or some element of uncertainty was expressed.

Maclaren (1952, pp. 684–685; 1953, p. 167) reported a case that may have involved a female as well as a male food-bringing didric cuckoo.

> Once a male and what I considered to be a female each caught caterpillars and returned to perches two feet apart four times running, at intervals of 40 to 45 secs., without taking apparent notice of one another.
>
> There were at least five birds concerned in this orgy—the definite male, the presumed female . . . and three others which may have been female or immature; these spent much time chasing one another. Twice in half-hour stretches one of these three fed another female or immature bird, to apparent repletion. Each time the catcher returned to the neighbourhood of the other stationary bird it displayed, with drooping wings, cocked tail and extended neck. As it hopped nearer it gave four or five bobs, and uttered three or four low calls of the type associated with the species. The caterpillar was taken without any display by the recipient . . . .

That the food bearers in this case always displayed when offering the caterpillar suggests (but does not prove) that they were adult males. Similarly, in a case concerning *C. klaas*, Baird (1945, pp. 565–566) reported seeing an adult male catching dysdercid bugs and feeding them to two young cuckoos. He also stated that a week or so earlier a friend had seen a "pair of Klaas's Cuckoo fly backwards and forwards . . . with Dysdercid bugs . . . . It can only now be presumed that the parent birds must at this time have been feeding the young while still nestlings . . . ." There is no proof, however, that the "pair" of klaas cuckoos actually were a pair or that both (or either) had been bringing the bugs to any young cuckoos, in or out of the nest. The fact that Baird saw the adult male feeding two fledglings may suggest that it was acting in a parental way, but it might also be that it was indulging in courtship feeding with two hens simultaneously.

Another fact that caused me to question the basic nature of fledgling-feeding behavior is that in the cases most completely reported—the relatively few with corroborative details—the feeding male presented each morsel of food, usually a caterpillar, with a definite courtshiplike ceremony, raising first the head and then the tail and going through somewhat stiff, jerky, bowing motions. Moreau (1944, pp. 98–100) noted that the male sometimes bowed once or twice after his food offering had been accepted by the bird he was feeding. Moreau observed that this was quite similar to the actions of a male *caprius* watched by Jackson as it fed a female in the presence of a fledged young bird, and concluded that, if his own observations involved the feeding, not of adult females, but of fledglings, as he thought they did, then it would appear that the males use the same presentation ceremony with fledged young as with adult hens.

Some idea of the repetitive extent of individual feedings, suggestive of the fact that the catering adult was not merely indulging in courtship feeding, may be gathered from the following cases: Maclaren (1952, pp. 684–685; 1953, p. 167) recorded one feeding "bout" that involved 6 caterpillars in 2 minutes 35 seconds; Moreau (1944) recorded one male didric bringing 21 caterpillars in 15 minutes to one presumed fledgling and also cited a case by Elliott of *C. klaas* "assiduously" feeding a fledgling of that species.

If, as outlined in our hypothecated phylogeny within the genus *Chrysococcyx*, the New Zealand-Australian species, *lucidus*, is more "primitive" than the African species, *klaas* and *caprius*, discussed above, or if it merely represents another, distinct portion of the genus, it is of interest to know that it too has been observed to feed fledglings of its own kind. In other words, this atavistic behavior appears, from present meager data, not to be restricted to just one portion of the genus.

Baird (1945) and Moreau & Moreau (1939, pp. 298–299) suggested that the relationship involving attentive behavior of an adult to a young of the same species of glossy cuckoo may become established when the young bird is "hardly out of the nest . . . ." K. D. Smith (1957, p. 309) also reported that in Eritrea in October he saw adult didric cuckoos (not identified as to sex) on several occasions feeding young "just able to fly." Actually, in *C. lucidus* Howe (1905, pp. 35–36)[13] reported seeing the adult cuckoo come to a nest of *Acanthiza chrysorrhoa* containing a nestling *lucidus* and feed it; "meanwhile the foster-parents were in a great state of excitement and repeatedly dashed at her until she left the vicinity." The sex of the cuckoo was, of course, merely assumed to be female. This observation has the merit of eliminating any possibility that the adult cuckoo may have mistaken a nestling for an adult, and it strengthens the conclusion that these cuckoos do feed young of their own kind. In this connection one may

---

[13] Howe's paper contains a mixture of observations on *Chrysococcyx lucidus* and *Cuculus pallidus*, but this note appears to refer to *C. lucidus*, although it was interpreted by Moreau (1949) as *Cuculus pallidus*.

recall that Layard long ago (1875–84, p. 155) quoted Mrs. Barber to the effect that *C. caprius* in South Africa remained near the nests it parasitized, "watching over" them. This, of course, is not evidence in itself, but it makes one wonder what actual observations Mrs. Barber may have had.

This leads us to a recently published statement. Ottow and Duve (1965, p. 432), based on the latter's extensive field studies in the Transvaal, concluded that the tendency of *C. caprius* to feed its own fledged young was sufficiently consistent and well developed to play a role in restricting the size of the breeding territory of each adult didric cuckoo, ethologically attached as it was to the nests from which would emerge its future charges. They thought that this caused a very real limitation on the freedom of movement of the didrics, especially if compared with the unhampered movements of a non-fledgling-feeder such as *Cuculus canorus gularis*. However, it is by no means established that the latter cuckoo is not also territorial, and the regularity of fledgling feeding by the didric needs further quantitative, observational proof.

Benson and Serventy (1957, pp. 347–349) suggested that feeding of young by the adult cuckoo may be due to the fact that those young were reared by seed-eating fosterers and, in their need for insect food, depended on their own species. This suggestion was answered by a more probable one by Marshall and Moreau to the effect that, as responsiveness to the food-begging calls and movements of the young is still present—even if relatively vestigial—in the adult cuckoos, it may have some survival value for those young reared on seeds and in need of the animal protein of insect food.

Even if the recrudescence of attentive parental behavior may occasionally have some such value for the recipients of it, this value cannot be looked upon as explaining its occurrence. It would seem more to the point to ask if species of fosterers that rear young parasites on seeds alone might be disadvantageous, or at least ill-adapted, for the cuckoo, and if in time they might be eliminated from its selection of hosts. This line of thought would raise the related question as to whether these particular victims are "normal," regularly used hosts at present or whether they are imposed upon only occasionally.

The basic, theoretical, biological interest attached to fledgling feeding is that it is a revealing atavism. That it occurs in those cuckoos that also exhibit a tendency toward courtship feeding serves to stress the similarity in the two behavior patterns. The persistence of food-offering in courtship may well expedite the response to the begging reactions of fledglings and may help to bring into expression what must have been an ancestral habit prior to the advent of parasitism in the cuckoos.

In his study of display behavior of birds, Armstrong (1942, pp. 29–35) considered courtship feeding a "recrudescence of an infantile mode of behaviour . . . ," and noted that it is usually accompanied by a considerable amount of psychobiological excitation and appears to be present mainly in species in which the pairing union is strong and prolonged. The fact that this situation is probably not true of the glossy cuckoos led me (1949a, p. 185) to suggest that when this ancient, vestigial courtship activity appears in these birds it may be lavished on fledglings as well as on prospective adult mates. It still seems possible that the catering cuckoos (males in most instances) may not always be aware of the maturity or immaturity of the individuals they feed. However, it does seem that they deliberately offer food to birds too young to be mistaken for adults, so that, in part at least, they are fledgling feeders as well as courtship feeders.

Moreau (1944) considered fledgling feeding an indication that the whole picture of brood-parasitism was not as "advanced" or "perfected" in the glossy cuckoos as in some other genera of the family. However, there are a good number of observations on the Australian pallid cuckoo, *Cuculus pallidus*, that show it to indulge in fledgling feeding at least as often, it not more frequently, than do the species of *Chrysococcyx*. That such a habit is found in a member of the genus *Cuculus* is more surprising, since this behavior has not been noted in the European *Cuculus canorus*, the best observed of all parasitic cuckoos. It shows that the extremely high development of specialization for brood parasitism in *C. canorus* is a specific and not a generic matter. In his summarizing book on all that he knew of Indian and European cuckoos, Baker (1942, p. 177) concluded that there was no evidence to support the thought that any of these parasites ever exhibit any interest in their eggs or young. While this suggests that the Asiatic forms of *Cuculus* (*canorus*, *optatus*, *micropterus*, etc.) and of *Hierococcyx*, *Cacomantis*, *Penthoceryx*, *Clamator*, *Surniculus*, and *Chrysococcyx* had not been found to feed fledglings, it certainly is not true for the koel, *Eudynamis scolopacea*, which has been reported as doing so not infrequently. The absence of Asiatic records of fledgling feeding by *Cacomantis* is offset by Australian observations of this behavior in the fan-tailed cuckoo, *Cacomantis flabelliformis*. Another Australian cuckoo known to exhibit this trait is the large channel-bill, *Scythrops novaehollandiae*.[14]

Fledgling, and even nestling, feeding occurs from time to time in a number of species of cuckoos belonging to at least five genera. The significant difference between *Chrysococcyx* and *Cuculus* in this regard

---

[14] For pertinent references on Australian instances, other than *Chrysococcyx*, see: Chisholm 1940, 1950; Friedmann 1949b; Hanscombe 1915; Howe 1905; Jackson 1949; Learmonth 1949; Robinson 1950; White 1950.

is that this atavism is more widespread in the former, where it has been noted in 4 out of 12 species, than in the latter genus, where only 1 out of 12 included species has been observed to exhibit this tendency. Inasmuch as *Eudynamis* and *Scythrops* are monotypic, comparisons with them are meaningless. *Cacomantis* is still too imperfectly known to yield significant comparisons here. If the present absence of fledgling feeding is to be interpreted as being due to its elimination during the past history of each species and, conversely, if its presence is taken to imply the opposite, the difference noted above for *Chrysococcyx* and *Cuculus* may be taken as an indication that the glossy cuckoos, as a group, are not as advanced as *Cuculus* in their development of brood-parasitism.

It may be mentioned that only a single instance of this type of behavior has been reported for a single species of cowbird (Friedmann 1963, p. 27, *ex* Walton 1903) and none for any of the other groups of parasitic birds, honey-guides, weavers, or ducks.

Summary and conclusions

The glossy cuckoos, forming the genus *Chrysococcyx,* are the smallest members of their family, and by virtue of their small size and their glossy, "metallic" plumage are a natural assemblage, closely related to, but distinct from, other genera of the Cuculinae, especially *Cacomantis* and *Cuculus.* They probably originated in the Australo-Malaysian area, possibly in Pliocene time, from the stock represented today by the other two genera mentioned above or at least from the common stock that also gave rise to them. All three of these genera are very similar in their structure, in their habits, and particularly in many details of their brood parasitism. While *Cuculus* has come to occupy a much more extensive part of the earth's land surface than the other two and, in one of its species, *Cuculus canorus,* has come to develop a degree of adaptive specialization unknown in the other two, *Chrysococcyx* also experienced a greater geographical and speciational expansion than has *Cacomantis* and it has come to occupy a niche in its parasitism on small passerine birds in some parts of the world—such as Africa, New Zealand, and some of the islands of the South Pacific, where it is largely alloxenic with respect to other cuckoos—as well as to flourish in other places—such as Australia and southern Asia, where it is partly homoxenic with members of both its related genera.

Two new terms, alloxenia and homoxenia are proposed to facilitate thinking and discussion of brood parasitism. Alloxenia, with alloxenic as its adjective, implies that different species of parasites use different hosts, while homoxenia, with homoxenic as its adjective, conveys the thought of two or more species of parasites sharing the same host species.

From its original locus *Chrysococcyx* expanded its range southeastward to include Australia, Tasmania, New Zealand, and the highlands of New Guinea. From this area it moved westward into northern Malaya, Burma, India, and southern China, and also to Borneo and the Philippine Islands; later, from its Asiatic area of occupancy, it progressed farther to the west and came to include in its domain all of Africa south of the Sahara, although not the islands of the Indian Ocean (Seychelles, Aldabras, Mauritius, Reunion, Madagascar, the Comoros, etc.). Inasmuch as Madagascar became separated from Africa in the Pliocene and inasmuch as no glossy cuckoo occurs in that great island, it becomes necessary to postulate a not earlier than Pliocene time for its westward spread, and, this, in turn, implies a correspondingly earlier date of origin in the ancestral homeland of the group.

The evolutionary implications of the current distribution of the species and subspecies of glossy cuckoos are discussed following their listing in the appendix (pp. 111–113).

Morphologically there are three groups of species within the genus. The connections between the species of each group are obvious, but those between the groups are conceivable only as inferences, since the intermediate steps have long since disappeared. What appears to be the earliest group comprises the obviously closely related species, *malayanus*, *lucidus*, *basalis*, *ruficollis*, and *osculans*, the last named one being a little more distinct from the others than any of them are from each other. Then, with a gap in a strict chronology of characters, comes a second group including *meyerii*, *maculatus*, and *xanthorhynchus*. Following this, with a still greater hiatus both geographically and morphologically, comes the African group which includes *flavigularis*, *klaas*, *cupreus*, and *caprius*.

Similarly, in the development of irridescent, glittering plumage the genus reveals a discordant, unchronological diversity, with great development in *meyerii* in New Guinea, in *maculatus* and *xanthorhynchus* in southern Asia, and in *cupreus* in Africa, with a total loss of this character in *osculans* of Australia and various degrees of intermediacy in *malayanus*, *lucidus*, *basalis*, *ruficollis*, *flavigularis*, *klaas*, and *caprius*. The genus differentiated into a dozen species, some with numbers of races, but within these dozen entities no one discernible progression of evolutionary trends can be found that parallels their hypothecated phylogeny. Close similarities, both in morphology and in ethology, exist between some of them, such as *malayanus*, *lucidus*, and *basalis* or between *maculatus* and *xanthorhynchus*, while other species, such as *osculans* and *caprius*, are unique extremes.

More of a sequential, phylogenetic display of change can be found through the genus in the matter of the ventral pattern of the first pennaceous plumage. The young of the first of the three groups of species mentioned above—*malayanus, lucidus, basalis,* and *osculans*—are uniformly unbarred grayish-white below from the chin to the under tail feathers; those of the other two groups have the underparts heavily barred in their young, except for *meyerii,* which agrees in this respect with the Australasian species, and, in so doing, acts as a perfect "step" or intermediate between the Australasian group and the Asiatic *maculatus* and *xanthorhynchus.* In its adult plumage *meyerii* is already in line with the south Asian species; in its juvenal stage it resembles *malayanus, lucidus, basalis,* and *osculans.*

The variety of expression of migratory behavior is likewise a matter of development within the several species rather than a traceable progression throughout the genus. The great range of migratoriness, from none at all to annual long-distance movements of as much as 2000 miles over open seas without landmarks, previous experience, or even communication and guidance between successive generations, is amazing in scope. However, it reveals no continuous pattern across the genus. For that matter, it shows no uniformity even within the same species. Thus, *C. lucidus* has four races, two of which are highly migratory and two are sedentary.

The main point of interest in this study has to do with the features of brood parasitism exhibited by the members of the genus *Chrysococcyx* and particularly with clues to the course of evolutionary changes in these features that a comparative survey might reveal. The genus could hardly be expected to reveal any evidence as to the origin and basic stages in the development of the parasitic mode of reproduction, since it obviously evolved from a primordial cuculine stock that was already entirely parasitic in its mode of reproduction and that already had developed the evicting behavior in the very young nestling and the egg-removing behavior in the adult. The glossy cuckoos retained, to a greater degree than *Cuculus* (except for one species, *C. pallidus*) and than most of the species of *Cacomantis,* the atavistic habit of feeding fledged young of their own kind and, not unrelated, the similar habit of courtship feeding of the adult hens by the cocks.

The present study shows that the glossy cuckoos have, in the course of their history, greatly enlarged their range of hosts, but that, while doing so, individual species of *Chrysococcyx* have come to concentrate on partly or largely different groups within that broader range of hosts. Thus, *C. malayanus* is restricted to a great extent to warblers of the genus *Gerygone,* although one of its races, *C. m. russatus,* has expanded its fosterer selection to include other hosts as well. *C. lucidus* has retained a fixation on *Gerygone* in one of its races (*C. l. layardi*), but has gone far afield in its use of many other birds in New Zealand (*C. l. lucidus*) and especially so in southern Australia (*C. l. plagosus*), where its hosts total some 75 species of many genera, although it shows very marked preference for species of *Acanthiza* and to a somewhat lesser extent for *Sericornis* and *Malurus*.

C. basalis has the most extensive host catalog of any of the glossy cuckoos, totaling some 100 species but showing a very strong inclination toward the use of wrens of the genus *Malurus* and, to a lesser degree, species of *Acanthiza*, *Rhipidura*, *Petroica*, *Hylacola*, and other warblers and honey-eaters. A great reduction in the number of species of victims is characteristic of *C. osculans*, which is very largely parasitic on *Chthonicola*, with the eggs of which its own have a remarkable similarity, and also on *Pyrrholaemus*. Of the host choice of *C. ruficollis* we know nothing, but it may be expected to be somewhat similar to that of *C. malayanus* and *C. lucidus*. Also, of the Papuan, *C. meyerii*, there are as yet no data as to what birds it depends on to raise its young.

The Asiatic *C. maculatus* and *C. xanthorhynchus* are parasitic on sunbirds and warblers and a few other hosts, but, insofar as present knowledge permits a generalization, the sunbirds, *Arachnothera* and *Aethopyga* are their mainstay.

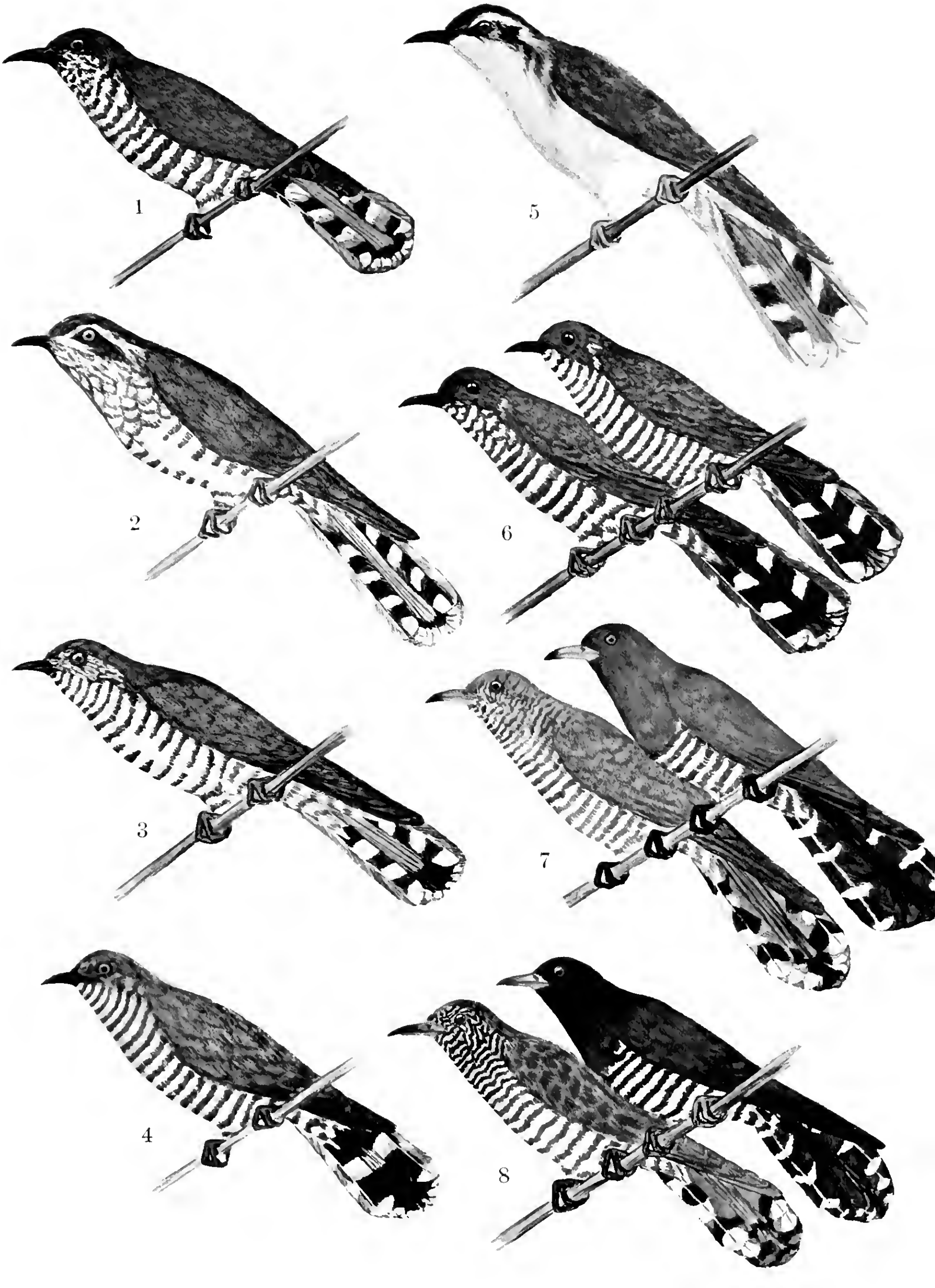
Of the African species, no hosts are yet known for *C. flavigularis:* for the others a large number are now recorded, and there is considerable overlapping, or what I have here termed homoxenia, among them. However, *caprius* is far more prone to use weavers, Ploceidae, while *klaas* tends to use warblers, Sylviidae, and sunbirds, Nectariniidae, to a great extent; *cupreus* is a less selective parasite, using a common bulbul, *Pycnonotus*, more often than any other host, but also using weavers, warblers, and sunbirds.

On the whole, *Chrysococcyx* presents an uneven performance, in an evolutionary sense, in the development of host-adaptive, individually divergent egg morphism, with the related development of individual, and even of specific, host specificity. The species which show these traits best developed are *osculans*, with a single egg type and one most regular, favorite host choice, and *caprius*, with several ovomorphs, three of which are more or less related each to a regular, frequent host species. Inasmuch as these two cuckoos are quite far apart in the phylogeny within the genus and inasmuch as none of the other species show any comparable degree of adaptive egg morphism, one can only conclude that the genus *Chrysococcyx* has not revealed a continuity of adaptive evolution in this important feature of brood parasitism. What has been achieved in this direction has transpired within individual species.

Egg coloration shows agreement between some closely related species and discordance between others. Thus, the eggs of the related *malayanus* and *lucidus* are plain olive-bronze, but in the also closely related *basalis* they are white, speckled finely with pinkish red; in *osculans* they are deep mahogany-reddish; while in *klaas* and *caprius* they are variable, the last named species having half a dozen ovomorphs, varying from unmarked white, pale greenish, pale or darker bluish to any of these colors or even pale, creamy grayish, variously spotted or even blotched with shades of brownish and grayish.

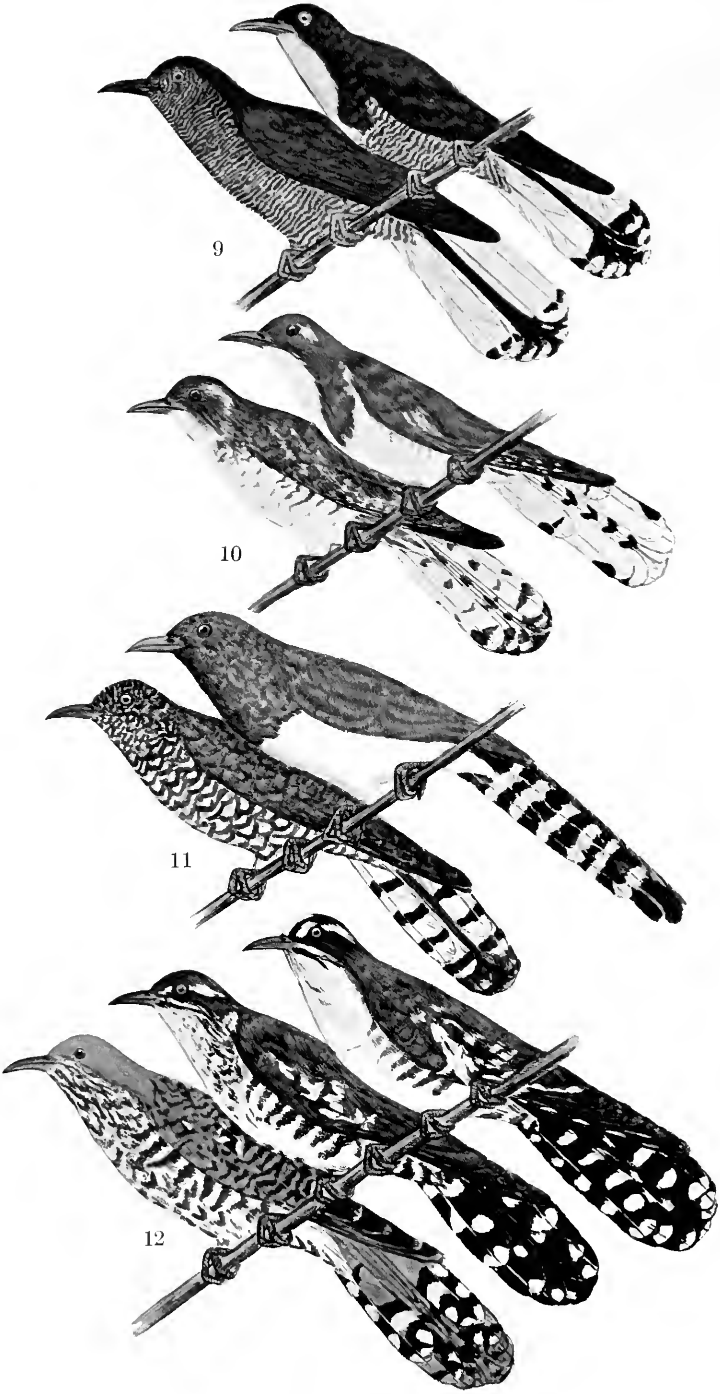
In size the eggs of the glossy cuckoos are relatively small for the body size of the birds, but they show none of the drastic reduction in size found in the European cuckoo, *Cuculus canorus*. In many parasitized nests the *Chrysococcyx* eggs are somewhat smaller than those of the host species, in others the reverse is the case. Apparently the need for reduction in egg size has been less than in the larger cuckoos that, like *Chrysococcyx*, use nests of small passerine victims.

As indicated in the present survey and discussion of host selection, host specificity, and egg morphism, the glossy cuckoos as a group have evolved diverse host preferences and have done this to varying degrees of rigidity or intensity, but they have not gone so far as to evolve gentes within any of their species, as has *Cuculus canorus*. All of the changes described in this paper, all the expansions of the range and variety of host nests utilized, and the contracting specializations within these enlarged choices of hosts, have made it possible for the glossy cuckoos to find relatively noncompetitive niches, as far as their congeners are concerned, and yet to take advantage of a vast passerine fauna in three continents and many oceanic islands. The degree to which sympatric species of *Chrysococcyx* have become mutually alloxenic is an indication of evolutionary change; the degree to which they are still homoxenic implies the distance they have still to travel toward a theoretically perfect intraspecific independence and noncompetitive coexistence.



Australian and Asiatic Glossy Cuckoos

1. *C. malayanus;* 2. *C. lucidus;* 3. *C. basalis;* 4. *C. ruficollis;* 5. *C. osculans;* 6. *C. meyerii* (male and female); 7. *C. maculatus* (male and female); 8. *C. xanthorhynchus* (male and female).



African Glossy Cuckoos

9. *C. flavigularis* (male and female); 10. *C. klaas* (male and female); 11. *C. cupreus* (male and female); 12. *C. caprius* (male, female, and hepatic young female).

Appendix

1. The existing species and their distribution

The forms of the genus *Chrysococcyx* and their ranges are as follows:

1. *C. malayanus* (Raffles): Malay Peninsula (from Patani southward), the Philippine Islands, the East Indies (Java, Sumatra, Borneo, Celebes), the Moluccas, the Lesser Sunda Islands, New Guinea, and adjacent islands, and northern Australia. In this vast range the species has become differentiated into 11 races, as follows:

C. malayanus malayanus (Raffles): Malay Peninsula from Patani southward, the Philippine Islands (Negros, Mindanao, Basilan, Tawi Tawi, Bongao), and Sumatra.

C. malayanus albifrons (Junge): Java.

C. malayanus aheneus (Junge): Borneo (including Maratua Island).[15]

C. malayanus jungei (Stresemann): central and southern Celebes.

C. malayanus rufomerus (Hartert): Lesser Sunda Islands (Roma, Damar, Leti, Moa, Sermatta, Timor, Sumba, Kisar[?]).

C. malayanus salvadorii (Hartert and Stresemann): Babar Island (known only from the type from Tepa).

C. malayanus misoriensis (Salvadori): Biak Island in Geelvink Bay.

C. malayanus poecilurus (G. R. Gray): Western Papuan Islands, Wagieu, Misol, Aru Islands, Vulcan Island, Dampier Island, Fergusson Island, all of New Guinea except part of the south coast.

C. malayanus russatus (Gould): Cape York Peninsula of northern Australia, and the Merauke area to the Mimika River, of southern New Guinea.

C. malayanus minutillus (Gould): northern Australia from the Kimberly district in the northwest, to Arnhem Land and to northern Queensland south of the range of *russatus;* also Melville Island (considered by some as a distinct species, although poorly differentiated from *malayanus*).

C. malayanus crassirostris (Salvadori): the Moluccas (Halmahera, Ternate, Buru, Ceram, Amboina, Goram, Tenimber Islands, Kei Islands, Soron (one dubious record), northwestern New Guinea; and also listed from Kisar Island, from which place the race *rufomerus* has also been reported (no Kisar specimens seen by the author).

2. *C. lucidus* (Gmelin): breeds in New Zealand, Chatham Islands, possibly Norfolk and Lord Howe Islands, Tasmania, southern Australia, the Santa Cruz Islands, Banks Island, the New Hebrides, the Loyalty Islands, New Caledonia, Rennell and Bellona Islands; in winter in the Lesser Sunda Islands, New Guinea, the Solomon Islands and the Bismarck Archipelago. The species is divided into four races, as follows:

C. lucidus lucidus (Gmelin): breeds in New Zealand and the Chatham Islands (possibly also in Norfolk and Lord Howe Islands); winters in the Solomon Islands,

---

[15] According to Smythies (1960, p. 255): "There is a possibility that a similar but distinct species occurs on Kinabalu . . . ," but I have seen no evidence, or specimen material of it.

Nissan and Feni Islands (east of New Ireland), and the Bismarck Archipelago; migrates through the Louisade Archipelago.

C. lucidus plagosus (Latham): breeds in Tasmania and southern Australia; winters in the Lesser Sunda Islands (Lombok, Sumbawa, Flores, and Wetar), New Guinea, and perhaps in the Bismarck Archipelago.

C. lucidus layardi (Mathews): resident in the Santa Cruz Islands, Banks Island, the New Hebrides, the Loyalty Islands, and New Caledonia.

C. lucidus harterti (Mayr): resident in Rennell and Bellona Islands.

3. *C. basalis* (Horsfield): breeds in southern Australia and Tasmania; winters chiefly in the Sunda Islands from Java to Sumbawa; recorded also from the Malay Peninsula, Sumatra, Borneo (once), North Natuna Islands (once), Kangean Islands, Christmas Island (in the Indian Ocean), and Celebes (once); on migration noted on the Aru Islands and the Cape York Peninsula.

4. *C. ruficollis* (Salvadori): resident in the highlands of New Guinea, chiefly at altitudes above 6000 feet, occasionally lower (4000 feet).

5. *C. osculans* (Gould): breeds in Australia, chiefly in drier areas than *basalis* and *lucidus,* but overlapping them and extending much farther north across the interior; relatively rare in the southern coastal areas; absent from Tasmania; the extent to which it is migratory is not yet clearly known, but it has been recorded from Cape York, the Aru and Kei Islands, and from Batjan.

6. *C. meyerii* (Salvadori): resident in the tropical forests, second growth, and clearings, of New Guinea at altitudes up to 4000 feet, commonest at 2500 feet.

7. *C. maculatus* (Gmelin): breeds from the central Himalayas west as far as Kuman, through Assam, southeastern Tibet and Szechwan, to Hupeh, south to Yunnan, Burma (in evergreen forest up to 8000 feet), and Annam. In winter or on migration, in India, Hainan, Cochinchina, Malay Peninsula, and Sumatra.

8. *C. xanthorhynchus* (Horsfield): resident (possibly partially migratory locally) from Assam, southwestern Yunnan, and Burma (where reported only in the evergreen-forest areas), and southern Annam, south to eastern Bengal, the Malay Peninsula, Siam, Cochinchina, the Andaman and Nicobar Islands, Sumatra, Simalur, Sipora, the Lingga Archipelago, Java, Borneo (where sparingly distributed in the lowlands, and found in gardens in Sarawak, on the edges of mangrove swamps, and on the seashore), the North Natuna Islands, and the Philippines (Luzon, Mindoro, Samar, Cebu, Leyte, Basilan, and Palawan). The species has been divided into three races, one of which may be doubtfully valid, as follows:

C. xanthorhynchus xanthorhynchus (Horsfield): range as above except for the Philippine Islands, other than Palawan.

C. xanthorhynchus amethystinus (Vigors): Philippine Islands, except Palawan, as given under the species range.

C. xanthorhynchus bangueyensis (Chasen and Kloss): only known from Banggi Island off the north coast of Borneo (doubtfully distinct from the nominate race, but its status requires additional material for clarification).

9. *C. flavigularis* (Shelley): resident in the forests from Sierra Leone to Togo from southern Cameroon eastward across the Congo to the Uelle and to the Semliki Valley, and to western Uganda (Bwamba) and southward to the vicinity of Luebo in the Kasai; mainly in the tall virgin forest, but ranging out into heavy gallery forests in the Uelle and Kasai districts of the Congo.

10. *C. klaas* (Stephens): breeds throughout much of Africa south of the Sahara, in both savanna and forested regions, from Senegal and Gambia, east to and across northern Nigeria and the southern Sudan to northwestern Ethiopia and to southwestern Arabia (Asir), and south to Damaraland and the Cape Province; also to the island of Fernando Poo in the Gulf of Guinea; migratory in the southern part of its range (roughly south of the Zambesi River), where it is present only from

late October to March or early April; partly or irregularly migratory in parts of equatorial eastern Africa. The species has been divided into three races, as follows:

C. klaas klaas (Stephens): range includes all of that given for the species, except southwestern Arabia, and the coastal belt of the Juba River area of southern Somalia.

C. klaas arabicus (Bates): southwestern Arabia (Asar, near Faifa, Asir); validity of this race is uncertain and will remain so until further material becomes available.

C. klaas somereni (Chapin): the Juba River area of southern Somalia, possibly the adjacent northeast corner of Kenya.

11. *C. cupreus* (Shaw): breeds throughout much of sub-Saharan Africa, chiefly in evergreen forest but also in dense scrub country, avoiding arid regions and areas over 8000 feet in altitude, from Senegal, east across upper Guinea to the southern Sudan to Ethiopia, south to the islands in the Gulf of Guinea (Fernando Poo, Principe, and São Tomé), to Gabon, and Angola, the Rhodesias, and to Transvaal, Natal, and the eastern part of Cape Province; migratory in the southern part of its range, where present only in the breeding season, late October to late March. The species has been divided into four races, the status of two of which have been matters of uncertainty, as follows:

C. cupreus cupreus (Shaw): from Senegal and Gambia to the Sudan and east to Ethiopia.

C. cupreus intermedius (Hartlaub): from Cameroon east across the Congo and Uganda to western Kenya and south to southern Angola and the Zambesi valley (Mozambique).

C. cupreus sharpei (van Someren): South Africa, especially the eastern part; winters to the north, but winter range uncertain.

C. cupreus insularum: the islands of the Gulf of Guinea (São Tomé and Principe).

12. *C. caprius* (Boddaert): breeds throughout most of Africa south of the Sahara in wooded country and in bushy areas, but not in treeless grasslands or desert areas, occurs from sea level to about 7000 feet, from Senegal, and the countries of upper Guinea east to Ethiopia, and south to Cape Province; also in the islands of Zanzibar, and Mafia on the east coast, and to Fernando Poo in the Gulf of Guinea; one record from southwestern Arabia (Aden); definitely migratory south of the Zambesi, where it occurs mainly during the breeding season, September to April.

From an evolutionary standpoint, the ranges of the present dozen species, with their 32 more or less distinct races, are of interest in that they reveal more numerous and more extensive areas of sympatry for two or more of the species than they do areas of intrageneric allopatry. Inasmuch as it is now well established that speciation and subspeciation are attended in their incipient stages by geographic isolation, it becomes necessary to postulate considerable subsequent movement of the various species to account for their present distribution. Thus, we find *malayanus* sympatric with *xanthorhynchus* in the Malay Peninsula (nominate races of both), in Borneo (*C. malayanus aheneus* and typical *C. xanthorhynchus*), and in the Philippines—at least in Basilan (typical *C. malayanus* and *C. xanthorhynchus amethystinus*). In southern Australia three species of the genus occur together to some extent, although partly separated ecologically (*C. lucidus plagosus*, *C. basalis*, and *C. osculans*); in Africa *klaas*, *cupreus*, and *caprius* are extensively sympatric, as are also *flavigularis*, *klaas*, and *cupreus* in a more restricted area.

The still meager data suggest altitudinal allopatry for the two Papuan species, *meyerii* and *ruficollis*, although there may be some overlapping. Allopatry is clearly indicated for typical *C. lucidus* in New Zealand and for two of its races *layardi* in New Caledonia, New Hebrides, and the Loyalty Islands and *harterti* on Rennell and Bellona Islands. The two Asiatic species, *maculatus* and *xanthorhynchus,* appear to be ecologically and altitudinally largely allopatric, but not rigidly so (*xanthorhynchus* has a range that extends far beyond that of *maculatus* to the east, encompassing areas as distant as Borneo and the Philippines, but this is something beyond the contiguous allopatry the two species show in southern Asia). The breeding range of *osculans* implies an extensive area of allopatry in spite of its southern sympatry with *basalis* and *lucidus plagosus.*

In view of the fact that the point of origin, geographically and phylogenetically, is only inferential in all the 12 species of the group, the only safe conclusion that may be drawn from their current dispersal is that the several species each went their own way with no discernible repetition of any generic pattern. The variety of their geographic dispersal is a telling, though commonplace, commentary on the opportunistic aspect of evolutionary history.

When one says that each species of *Chrysococcyx* has gone its own way, this does not imply any incipient, directive "way" peculiar to each. This becomes clear when the morphological characters of the geographic races of any of the polytypic species of the genus are examined. Thus, to take but one instance, the variations in the distribution of rufescent coloration in the rectrices of some of the subspecies of *malayanus* are not selectively "adaptive"; they are not characters that help to make their bearers more or less fitted for the particular places in which they live. If these characters were plotted on a map they would show no progressive, rectilinear, or orthogenetic correspondence with the geographic, spatial relations of the races. The emergence of these slight differences as constantly recurring phenotypes is merely the result of each population's having had to utilize the fragment of the total gene pool of the species available to it. The possibility exists that these external characters, while diagnostic in the museum sense, are not selectively important in themselves but that they may be the outward manifestations of genes that have some adaptive value. This is, admittedly, beyond the capability of present evidence to prove or to disprove, but the thought should be kept in mind. The "way" of each species is, not what it "set out to do or to be, but what has happened to it."

The high incidence of sympatry in the glossy cuckoos causes one to ask if these birds have not yet achieved their final, biologically "perfected" stage, especially since in many instances (*plagosus, basalis,* and *osculans*; *klaas* and *caprius*) they are partly homoxenic (sharing the same hosts), even if they show trends toward alloxenia (using different hosts). If their geographical and ecological sympatry were accompanied by highly developed and rigidly regulated alloxenia, these coexisting species of *Chrysococcyx* would be, as far as their breeding is concerned, distinctively separated, even though their hosts were sympatric. Such a condition does obtain in some avian arthropod ectoparasites, as was shown by Clay (1949), and such reproductive differentiation would in itself suffice to counteract the Gauseian principle that two or more kinds of related animals with identical or very similar ecological requirements are not able to coexist indefinitely because one of them will prove more efficient than the other and thus will displace the latter. The glossy cuckoos are possibly still on the way toward the eventual circumvention of this situation.

On the other side of the picture, it appears that in all these cases of sympatric species of glossy cuckoos the forms involved have complete specific independence. So far as I have been able to learn (and I have examined several thousands of specimens in all), no instances of hybridization have been found between any of them. Furthermore, I know of no observations of mixed courtship behavior, although there often is no ecological or other habitat isolation to prevent it.

This is especially significant in the case of *plagosus* and *basalis,* as these species are superficially fairly similar, and it points to the existence of very effective isolating mechanisms. In the absence of personal field experience with these two Australian cuckoos, I cannot evaluate accurately the potential ethological barriers from the published accounts of their vocalisms, posturings, and so forth, but it may be assumed that it is here that the restriction of random mating is controlled. Mayr (1963, pp. 95–107) has brought together from many groups of animals data which show that differences in behavior which may seem slight to human eyes may be all important in this respect. He concluded that, if one were to estimate the relative importance of the various isolating mechanisms, behavioral isolation would head the list.

Cuckoos as a family appear to be remarkably free from hybridization. In her 1958 compilation of known avian hybrids A. P. Gray listed none for any members of the family. Subsequently Parkes (1965, pp. 94–95) has reported only one instance of crossing between two species of terrestrial, sedentary coucals, *Centropus viridis* and *Centropus bengalensis,* in Luzon. The absence of any such records in the other, more arboreal and more active cuckoos, suggests that specific differences in appearance, vocalisms, and behavior are constantly effective in their role of isolating mechanisms.

2. The plumages of *Chrysococcyx flavigularis*

Although this report is not intended to include detailed plumage descriptions of the well-known species of glossy cuckoos, in this case it may be useful to have such an inclusion. The following description is based on that of Reichenow (1902, p. 100), with modifications due to other material seen and with the addition of Chapin's notes (1939, pp. 199–201).

Adult male: upper parts glossy bronze to copper-red, according to Reichenow and Shelley, but dark, glossy bronze-green in the material I have examined personally; the two median rectrices dark purplish coppery color, darkest on the middle portion and at the end, the next pair similar on the inner web but yellowish-white to white on the outer web, except for a coppery-bronze band near the tip and also on the basal portion of the feathers, with a white tip; the remaining rectrices white with interrupted dusky bronze subterminal bands and similar bases, the outermost rectrix almost entirely white; remiges dark brown, barred incompletely with whitish or pale buffy on the inner webs; chin and middle of throat and breast bright yellow, bordered with bright, dark glossy green (like the top and sides of the head); posterior underparts of body and the under wing coverts pale cinnamon-buff with narrow, somewhat wavy bars of dusky earth-brown, some of these bars with a faint bronze sheen, the interspaces between the bars a little more than one and a half times as broad as the bars; under tail coverts similar but the dusky bars more widely separated; iris dull chrome-yellow, edge of eyelids light yellowish-green; bill dull greenish-yellow, base of the maxilla blackish; feet dull yellowish-green, claws black; wing 91.5–100; tail 70–80; culmen from base 17–18; tarsus 14 mm.

Adult female: top of head dark bronze-green with fine, whitish transverse vermiculations on the forehead, sides of crown, and sides of occiput—occasionally these fine markings extend right across the crown and occiput and hind neck; nape, back, scapulars, upper wing coverts, rump, and upper tail coverts dark glossy bronze-green, sometimes with a slightly lighter, more golden, tinge; the lesser and median upper wing coverts with narrow cinnamon tips and widely spaced narrow bars of the same; remiges fuscous, with a faint bronze sheen, especially on the outer web, and, in some, probably younger, adults, with incomplete bars of pale cinnamon on the outer webs, and always with incomplete wedge-shaped bars of the same on the inner margins of the basal two-thirds of the inner webs; median rectrices dusky blackish-brown with a faint coppery sheen and narrowly tipped with pale brownish-white; the next pair similar on the inner web, but banded on the outer web with pale cinnamon; the next pair with the inner web blackish-brown banded with cinnamon and with the outer webs largely white with a blackish-brown subterminal band immediately before the white tip; the two outermost pairs wholly white with some incomplete dark-brown bars on the inner web; lores, sides of face, auriculars, sides of neck, and entire underparts from chin to vent pale buffy-white to white, finely marked with somewhat wavy, narrow bars of dusky-brown, some with a faint bronze sheen; iris gray to pale yellowish-brown; eyelids greenish; bill dark brownish-black above, dull yellow below; wing 92–97; tail 58–64; culmen from the base 15.5–17; tarsus 12.5–13.5 mm.

Juvenal (males only seen, but sexes probably alike): similar to adult female, but with the feathers of the forehead, crown, occiput, nape, scapulars, and upper wing coverts with cross bars; underparts as in females but slightly more brownish in ground color; iris grayish-white to brownish-white; bill dark brown on maxilla, yellow on mandible; feet yellow.

References*

ALEXANDER, W. B.
1925. Visit to Coomooboolaroo. Emu, vol. 24, pp. 236–237.
ALI, SÁLIM A.
1962. The birds of Sikkim. Pp. 414.
ARMSTRONG, EDWARD A.
1942. Bird display. Pp. 381, pls. 22.
ATKINS, W. A. N.
1922. Cuckoo carrying egg. Emu, vol. 21, p. 314.
AYRES, THOMAS
1884. Additional notes on the ornithology of Transvaal. Ibis, ser. 5, vol. 2, pp. 217–233.
BAIRD, D. A.
1945. A note on *Lampromorpha klaasi* (Stephens) and the care of its young. Ibis, vol. 87, pp. 565–566.
BAKER, E. C. STUART
1907. The oology of Indian parasitic cuckoos, pt. 3. Journ. Bombay Nat. Hist. Soc., vol. 17, pp. 678–696.
1908. Additional cuckoo notes. Journ. Bombay Nat. Hist. Soc., vol. 18, pp. 275–279.
1927. The Fauna of British India including Ceylon and Burma. Birds, vol. 4, 2d ed., pp. 471.
1942. Cuckoo problems. Pp. 207, pls. 12.

---

*Additional host data pertinent to the glossy cuckoos of southern Africa are presented in the following paper that appeared too late for incorporation in this report.

PAYNE, R. B. and PAYNE, B.
1967. Cuckoo hosts in southern Africa.
Ostrich, vol. 38, pp. 135–143.

BANNERMAN, DAVID A.

1933. The birds of tropical west Africa. Vol. 3, pp. 487, figs. 144, pls. 12, map.

1953. The birds of west and equatorial Africa. 2 vols., pp. 1526, pls. 54.

BARNARD, CHARLES A., AND BARNARD, H. GREENSILL

1925. A Review of the Bird Life on Coomooboolaroo Station, Duaringa District, Queensland, During the past Fifty Years. Emu, vol. 24, pp. 252–265.

BARNARD, H. GREENSILL

1914. Northern Territory Birds. Emu, vol. 14, pp. 39–57.

1926. Birds of the Cardwell District, Queensland. Emu, vol. 26, pp. 1–13.

BARRETT, CHARLES LESLIE

1905. Cuckoo notes. Emu, vol. 5, pp. 20–23, pls. 1–3.

BARTELS, MAX

1925. Over de "broedgewooten" van eenige Javaansche parasitische Cuculiden. Jaarbericht Club van Nederl. Vogelkundigen, vol. 15, pp. 54–61.

BATES, GEORGE L.

1905. Field notes on the birds of Efulen in the West-African colony of Kamerun. Ibis, ser. 8, vol. 5, pp. 89–98.

BELCHER, CHARLES F.

1924. Nyasaland notes.—4. Sub-family Ploceinae. Ool. Record, vol. 4, no. 4, pp. 1–10.

1930. The birds of Nyasaland. Pp. 356, map.

1949. Review of "The Parasitic Cuckoos of Africa" Nature in East Africa, ser. 2, no. 2, pp. 14–20.

BENNETT, KENRIC HAROLD

1879. Cuckoos—laughing jackasses. Queenslander, vol. 15 (new series), no. 184, p. 245.

BENSON, C. W.

1940. Further notes on Nyasaland birds, pts. 2 and 3. Ibis, ser. 14, vol. 4, pp. 387–433, 583–629.

1942. Additional notes on Nyasaland birds. Ibis, ser. 14, vol. 6, pp. 197–224.

1946. Field notes from Nyasaland. Ostrich, vol. 17, pp. 297–319.

1952. Notes on some birds' eggs collected by Sir Charles Belcher in Nyasaland. Journ. E. Afr. & Uganda Nat. Hist. Soc., vol. 21 (20), no. 1(91), pp. 443–445.

1953. A check list of the birds of Nyasaland. Pp. 116, map.

BENSON, C. W., AND BENSON, F. M.

1947. Some breeding records from southern Nyasaland. Ool. Record, vol. 21, no. 4, pp. 1–9.

1949. Notes on birds from northern Nyasaland and adjacent Tanganyika Territory. Ann. Transvaal Mus., vol. 21, pp. 155–177.

BENSON, C. W.; BROOKE, R. K.; AND VERNON, C. J.

1964. Bird breeding data for the Rhodesias and Nyasaland. Occas. Papers Nat. Museums of S. Rhodesia, vol. 4, no. 27B, pp. 30–105.

BENSON, C. W., AND PITMAN, C. R. S.

1961. Further breeding records from northern Rhodesia, no. 2. Bull. Brit. Ornith. Club, vol. 81, pp. 156–163.

BENSON, C. W., AND SERVENTY, DOMINIC L.

1957. The feeding of the young Didric Cuckoo *Chrysococcyx caprius*. Ibis, vol. 99, pp. 347–349.

BENSON, C. W., AND WHITE, CHARLES M. N.

1957. Check-list of the birds of Northern Rhodesia. Pp. 166, pls. 28, map.

BENSON, F. M.

1946. Field notes from Nyasaland. Ostrich, vol. 17, pp. 297–319.

BERGER, ANDREW J.

1955. On the anatomy and relationships of Glossy Cuckoos of the genera *Chrysococcyx*, *Lampromorpha*, and *Chalcites*. Proc. U.S. Nat. Mus., vol. 103, pp. 585–597.

BERGH, C. J.

1943. Letter on Wagtail and Didric Cuckoo. Ostrich, vol. 14, p. 121.

BEVEN, GEOFFREY

1943. Some notes from Oudtshoorn. Ostrich, vol. 13, pp. 235–238.

BRADDY, H. J.

1949. Strange behaviour of a cuckoo. Victorian Nat., vol. 65, p. 238.

BRAUN, RUDOLF

1931. Aufzucht von *Chrysococcyx klassi* durch *Pycnonotus tricolor*. Ornithologische Monatsberichte, vol. 39, pp. 148–149.

1943. Biologische Notizen über einige Vögel Nord-Angolas. Journ. f. Ornith., vol. 82, pp. 553–560.

BROMLEY, E. H.

1941. Notes on Malayan birds. Malayan Nat. Journ., vol. 1, pp. 140–146.

BULLER, WALTER L.

1888. A history of the Birds of New Zealand. 2d ed., vol. 1, pp. 250.

BURTON, R. W.

1935. Cuckoo-lore. Journ. Bombay Nat. Hist. Soc., vol. 38, pp. 266–281.

CAMPBELL, ARCHIBALD J.

1898a. Notes on the Bronze Cuckoo. Victorian Nat., vol. 14, pp. 144–146.

1898b. Notes on the Narrow-billed Bronze Cuckoo. Victorian Nat., vol. 14, pp. 151–154.

1901. Nests and eggs of Australian birds, including the geographical distribution of the species and popular observations thereon. Vols. 2, pp. 1102, pls. 116.

1902. Birds of north-eastern Victoria. Emu, vol. 2, pp. 9–18.

1906. Oological notes and further description of new fruit-pigeon. Emu, vol. 5, pp. 195–199.

1913. A Commonwealth collection. Emu, vol. 13, pp. 65–74.

1927. The Belltrees Oological Collection. Emu, vol. 26, pp. 300–301.

CARTER, THOMAS

1903. Birds occurring in the regions of the North-West Cape, pt. 2. Emu, vol. 3, pp. 89–96.

1924. Birds of the Broome Hill District, pt. 2. Emu, vol. 23, pp. 223–235.

CAYLEY, NEVILLE W.

1950. What bird is that? A guide to the birds of Australia. Pp. 359, pls. 37.

CHALK, A. S.

1950. Strange behaviour of a cuckoo. Emu, vol. 49, pp. 219–220.

CHANDLER, L. G.

1910. Cuckoo notes. Emu, vol. 9, p. 245.

CHAPIN, JAMES P.

1939. The birds of the Belgian Congo, pt. 2, vol. 2. Bull. Amer. Mus. Nat. Hist., vol. 75, pp. 632, pls. 21.

1953. The birds of the Belgian Congo, pt. 3. Bull Amer. Mus. Nat. Hist., vol. 75, pp. 821, pls. 14.

CHAPIN, JAMES P.—continued
1954. The birds of the Belgian Congo, pt. 4. Bull. Amer. Mus. Nat. Hist., vol. 75B, pp. 846, pls. 27.
CHENERY, A.
1924. Some Notes on Birds seen during a Holiday Trip in South-West Queensland. So. Austr. Ornith., vol. 7, pt. 7, pp. 215–229.
CHISHOLM, ALEXANDER H.
1920. Bronze-cuckoo and shrike-robin. Emu, vol. 19, pp. 315–316.
1925. The Fairy Warbler: A Re-discovery. Emu, vol. 24, pp. 161–165.
1932. Nature fantasy in Australia. Pp. 196.
1935. Bird wonders of Australia. Pp. 299.
1940. Cuckoo feeding cuckoo. Monthly Notes (Bird Observer's Club, Melbourne), September 1940.
1950. Adult cuckoos' feeding of young. Ibis, vol. 92, pp. 322–323.
CHUBB, E. C.
1914. A descriptive list of the Millar collection of South African birds' eggs. Ann. Durban Mus., vol. 1, pt. 1, pp. 29–106.
CLANCEY, P. A.
1964. The birds of Natal and Zululand. Pp. 511, pls. 58, map.
CLAY, THERESA
1949. Some problems in the evolution of a group of ectoparasites. Evolution, vol. 3, pp. 279–299.
CLELAND, J. BURTON
1924. The Birds of the Encounter Bay district. S. Austr. Ornith., vol. 7, pt. 6, p. 172–184.
COHN, MARC
1924. The Cuckoo and the Red-capped Robins. Emu, vol. 24, p. 76, pl. 13.
COLE, D. T.
1957. Some birds of Chicumbane, P.E.A. Ostrich, vol. 28, pp. 189–192.
CONNELL, ALLAN
1959. Emerald Cuckoo depositing her egg in a Black-eyed Bulbul's nest. Ostrich, vol. 30, p. 140.
CORNWALL, E. M.
1907. Mackay (Queensland) notes. Emu, vol. 6, pp. 192–193.
CURRY-LINDAHL, KAI
1960. Ecological studies on mammals, birds, reptiles and amphibians in the eastern Belgian Congo, pt. 2. Annales du Musée Royal du Congo Belge. Tervueren, Sci., Zool., vol. 87, pp. 7–170, pls. 20.
DEIGNAN, HERBERT G.
1945. The birds of northern Thailand. U.S. Nat. Mus. Bull. 186, pp. 616, pls. 9, maps 4.
DEIGNAN, HERBERT G., AND AMOS, BRUCE
1950. Notes on some forms of the genus *Chalcites* Lesson. Emu, vol. 49, pp. 167–168.
DEWAR, JOHN
1925. Indian bird life. Pp. 276.
DE WARREN, J. J.
1926. Five Nests in Five Months. Emu, vol. 26 pp. 78–79.
DICKISON, D.
1928. Horsfield Bronze Cuckoo and Blue Wren. Emu, vol. 28, p. 151.
DISTANT, W. L.
1897. (Editorial Comments.) Zoologist, ser. 4, vol. 1, p. 143.

DODD, ALAN P.
1913. Foster-parents of cuckoos. Emu, vol. 12, pp. 190–191.

DOVE, H. STUART
1916. Cuckoo notes from Tasmania. Emu, vol. 16, pp. 96–99.
1924. Cuckoo and Emu-Wren. Emu, vol 24, p. 156.
1925. Summer Migrants in Tasmania, 1925. Emu, vol. 25, pp. 43–44.
1928. Bronze Cuckoo and Wrens. Emu, vol. 27, p. 224.

EDGAR, A. T.
1960. Communal display in the shining cuckoo. Notornis, vol. 9, p. 134.

ERLANGER, CARLO FREIHERR VON
1905. Beiträge zur Vogelfauna Nordostafrikas, pt. 3. Journ. f. Ornith., vol. 53, pp. 433–499.

FARKAS, T.
1962. Contribution to the bird fauna of Barberspan. Ostrich, suppl. no. 4, pp. 39, pls. 4.

FELL, H. BARRACLOUGH
1947. The migration of the New Zealand bronze cuckoo, *Chalcites lucidus lucidus* (Gmelin). Trans. Royal Soc. New Zealand, vol. 76, pp. 504–515.

FISCHER, G. A.
1880. Briefliche Berichte aus Ost-Afrika. Journ. f. Ornith., vol. 28, pp. 187–193.

FITZGERALD, M.
1960. Communal display and courtship feeding in the shining cuckoo. Notornis, vol. 9, pp. 9–10.

FLETCHER, J. A.
1915. Cuckoos in Tasmania. Emu, vol. 14, p. 166.

FRIEDMANN, HERBERT
1928. The origin of host specificity in the parasitic habit in the Cuculidae. Auk, vol. 45, pp. 33–38.
1949a. The parasitic cuckoos of Africa. Washington Acad. Sci. Monograph, no. 1(1948), pp. 204, pls. 10.
1949b. Additional data on African parasitic cuckoos. Ibis, vol. 91, pp. 514–519.
1956. Further data on African parasitic cuckoos. Proc. U.S. Nat. Mus., vol. 106, pp. 377–408.
1963. Host relations of the parasitic cowbirds. U.S. Nat. Mus. Bull. 233, pp. 276.
1964. Evolutionary trends in the avian genus Clamator. Smiths. Misc. Coll., vol. 146, no. 4, pp. 127.
1967. Evolutionary terms for parasitic species. Systematic Zoology, vol. 16, p. 175.

FRY, C. H.
1961. Notes on the birds of Annobon and other islands in the Gulf of Guinea. Ibis, vol. 103a, pp. 267–276.

FULTON, ROBERT
1910. The Pipiwharauroa, or Bronze Cuckoo (*Chalcococcyx lucidus*), and an account of its habits. Trans. New Zealand Institute, vol. 42, pp. 392–408.

GALBRAITH, IAN C. J., AND GALBRAITH, EBBA H.
1962. Land birds of Guadalcanal and the San Cristoval Group, Eastern Solomon Islands. Bull. British Museum (Nat. Hist.), Zool., vol. 9, pp. 86.

Gilbert, P. A.
1935. The seasonal movements and migrations of birds in eastern New South Wales. Emu, vol. 35, pp. 17–27.

Gilbert, P. A., and Keane, H.
1913. The black-eared cuckoo (*Mesocalius palliolatus* Lath.). Emu, vol. 13, pp. 80–82.

Givens, T. V.
1925. Fantail Cuckoo (*Cacomantis flabelliformis*) and Brown Thornbill (*Acanthiza pusilla*). Emu, vol. 25, p. 28, pl. 9.

Graham, D. H.
1940. Notes on the shining bronze cuckoo. Forest and Bird Bulletin of the Forest and Bird Protection Society of New Zeland, vol. 55, p. 4.

Gray, Annie P.
1958. Bird hybrids. Commonwealth Agricultural Bureaux, Farnham Royal, England. Pp. 390.

Grote, Hermann
1912. Beitrag zur Ornis des südöstlichen Deutsch-Ostafrika. Journ. f. Ornith., vol. 60, pp. 501–529.
1925. Zum brutparasitismus von *Vidua serena* (L.) Beitr. Fortpflanzungsbiol. Vögel, vol. 1, p. 34.

Guichard, K. M.
1950. A summary of the birds of the Addis Ababa region, Ethiopia. Journ. E. Afr. Nat. Hist. Soc., vol. 19, pp. 154–178.

Haagner, Alwin K., and Ivy, Robert H.
1906. Notes on the nidification of the members of the genus Chrysococcyx. Journ. S. African Ornith. Union, vol. 2, pp. 35–39.

Hall, Robert
1898. Notes on the birds of the Box Hill district. Victorian Nat., vol. 15, pt. 1, pp. 70–72; pt. 2, pp. 75–80.
1901. Foster parents to the Bronze Cuckoo. Victorian Nat., vol. 17, p. 128.

Hanscombe, S. A.
1915. Cuckoos and their offspring. Emu, vol. 14, pp. 160–161.

Hartert, Ernest, and Stresemann, Erwin
1925. Ueber die indoaustralischen glanzkuckucke (*Chalcites*). Novit. Zool., vol. 32, pp. 158–163.

Harvey, Len
1961. Field Notes. The Bird Observer (Bird Observers' Club, Victoria, Australia), October 1961, p. 3.

Haydock, Edward L.
1950. Supplementary notes on African cuckoos. Ibis, vol. 92, pp 149–150.
1951. Extracts from a Northern Rhodesian diary. Babbler (the Journal of the Rhodesia Bird Club), no. 6, pp. 1–3.

Heinroth, Oskar
1922. Die Beziehungen zwischen Vogelgewicht, Eigewicht, Gelegegewicht und Brutdauer. Journ. f. Ornith., vol. 70, pp. 172–285

Heuglin, Martin Theodor von
1871. Ornithologie Nordost-Afrikas. Vol. 1, pt 2, pp 417–854, pls. 15.

Hill, G. F.
1907. Birds of Ararat District, pt. 2. Emu, vol. 7, pp. 18–23.

Hill, H. E.
1903. Some notes from the Geelong and Otway Districts. Emu, vol. 2, pp. 161–167.

HOBBS, J. N.

1961. The birds of south-west New South Wales. Emu, vol. 61, pp. 21–55.

HOESCH, WALTER, AND NIETHAMMER, G.

1940. Die Vogelwelt Deutsch-Südwestafrikas. Journ. f. Ornith., vol. 88 (spec. ed.), pp. 404, pl. 1.

HOLMAN, F. C.

1947. Birds of Gold Coast. Ibis, vol. 89, pp. 623–650.

HOOGERWERF, A.

1949. Bijdrage tot de oölogie van Java. Limosa, vol. 22, pp. 1–279.

HOWE, FRANK E.

1905. Field notes on cuckoos. Emu, vol. 5, pp. 35–36.

1910. A cuckoo day. Emu, vol. 9, pp. 163–164.

1913. Cuckoo records. Emu, vol. 12, p. 190.

1928a. Cuckoo Notes: New Combination Clutches. Emu, vol. 27, p. 216.

1928b. Notes on some Victorian birds. Emu, vol. 27, pp. 252–265.

HUME, ALAN O.

1875. A first list of the birds of Upper Pegu. Stray Feathers, vol. 3, pp. 1–194.

HUNTER, H. C.

1961. Parasitism of the Masked Weaver *Ploceus velatus arundinaceus.* Ostrich, vol. 32, pp. 55–63.

HURSTHOUSE, E. W.

1944. *In* Summarized notes. New Zealand Bird Notes, vol. 1, p. 78.

HUTTON, F. W

1900. Our migratory birds. Trans. New Zealand Institute, p. 215.

INGLE, ARTHUR P.

1912. Cuckoos as nest robbers. Emu, vol. 11, pp. 254–255.

INGLIS, CHARLES M.

1908. The oology of Indian parasitic cuckoos. Journ. Bombay Nat. Hist. Soc., vol. 18, pp. 681–682.

IREDALE, TOM

1956. Birds of New Guinea. Vol. 1, pp. 230, pls. 15.

IVY, R. H.

1901. Notes on the nesting and other habits of some South African birds. Ibis, ser. 8, vol. 1, pp. 18–28.

JACKSON, CAROL

1949. Cuckoo feeding young. Emu, vol. 48, p. 176.

JACKSON, FREDERICK JOHN

1938. The birds of Kenya Colony and the Uganda Protectorate. 3 vols., pp. 1592, pls. 24.

[JACKSON, S. W.]

1908. Review of "Catalogue and Data of the 'Jacksonian Oological Collection.' " Emu, vol. 7, pp. 201–205.

JAMES, H. W.

1921. Notes on birds occurring in the Cradock and Tarkastad Districts, Cape Province, with nesting dates. S. Afri. Journ. Nat. Hist., vol. 3, pp. 174–198.

JEROME, C. H.

1943. Difficulties of amateur ornithologists in identifying the eggs of parasitic birds. Ostrich, vol. 14, pp. 99–103.

JOUBERT, H. J.

1943. Some notes on birds. Ostrich, vol. 14, pp. 1–7.

KEULEMANNS, JOHN G.

1907. The golden cuckoo. Bird Notes, vol. 5, pp. 245–247.

Kikkawa, J., and Dwyer, P. D.
1962. Who feeds the fledged Pallid Cuckoo? Emu, vol. 62, pp. 169–171.
Layard, Edgar Leopold
1875–84. The Birds of South Africa, new ed. (rev. by R. B. Sharpe). Pp. 890, pls. 12.
Leach, Hugh A. C.
1928. The Birds of Central Northern Victoria. Emu, vol. 28, pp. 83–99.
1929. Honeyeaters and Cuckoos. Emu, vol 28, pp. 177–182.
Learmonth, Noel F.
1949. Monthly Notes from Portland, F.N.C. (*Cuculus pallidus* feeding its own young). Victorian Nat., vol. 65, p. 258.
Le Souëf, D.
1898. On some birds and eggs lately collected at Cape York, Queensland, by Mr. H. G. Barnard. Ibis, ser. 7, vol. 4, pp. 51–59.
Linton, E. H.
1930. Some notes concerning two of the cuckoos. Emu, vol. 29, pp. 304–307.
Littlejohns, R. T.
1943. Different cuckoo eggs in same nest. Emu, vol. 42, pp. 250–251.
Littler, Frank Mervyn
1910. A handbook of the birds of Tasmania and its dependencies. Pp. 242.
Lynes, Hubert
1934. Contribution to the ornithology of southern Tanganyika Territory. Journ. f. Ornith., vol. 82, supp., pp. 147, pls. 15.
Macgillivray, W.
1914. Notes on some North Queensland birds. Emu, vol. 13, pp. 132–186.
1924. A Spring Excursion into South-Western Queensland. Emu, vol. 24, pp. 13–24.
Mack, G.
1930. Notes and descriptions of some rare eggs of Australian birds. Emu, vol. 29, pp. 302–303.
Mackworth-Praed, Cyril W., and Grant, Claude H. B.
1952. Birds of Eastern and North Eastern Africa. Vol. 1, pp. 836, pls. 59.
1957. Birds of Eastern and North Eastern Africa. Vol. 1, 2d ed., pp. 845.
Maclaren, P. I. R.
1952. Feeding by the Didric Cuckoo. Ibis, vol. 94, pp. 684–685.
1953. Bird notes from Nigeria. Nigerian Field, vol. 18, pp. 165–171.
MacLeod, J. G. R., and Hallack, M.
1956. Some notes on the breeding of Klaas's Cuckoo. Ostrich, vol. 27, pp. 2–5.
MacLeod, J. G. R.; MacLeod, E. M.; and Murray, C. d'C.
1952. The birds of the Hottentots Holland, pt. 2. Ostrich, vol. 23, pp. 16–25.
Makatsch, Wolfgang
1955. Der Brutparasitismus in der Vogelwelt. Pp. 236.
Markus, M. B.
1961. Diederik cuckoo eggs in masked weaver's nest. Bokmakierie, vol. 13, p. 33.
1963. Egg of *Chrysococcyx caprius* (Boddaert). Ostrich, vol. 34, p. 47.
1964. Egg polymorphism in the Diederik Cuckoo (*Chrysococcyx caprius* [Boddaert]) at Pretoria. Ostrich, vol. 35, p. 123.
Masterson, H. B.
1953. Klaas' Cuckoo (*Chrysococcyx klaas*) parasitising Red-headed Weavers (*Anaplectes rubriceps*). Ostrich, vol. 24, p. 51.

MATHEWS, GREGORY M.

1914. A list of the birds of Melville Island, Northern Territory, Australia. Ibis, ser. 10, vol. 2, pp. 91–132.

1918. The Birds of Australia, vol. 7, pt. 4, pp. 321–384, pls. 352–362.

MATTINGLEY, A. H. E.

1906. A cuckoo's egg at midwinter. Emu, vol. 6, p. 66.

MAYR, ERNST

1932. Birds collected during the Whitney South Sea Expedition. Pt. 19, Notes on the Bronze Cuckoo *Chalcites lucidus* and its subspecies. Amer. Museum Novitates, no. 520, pp. 1–9.

1939. The winter quarters of *Chalcites malayanus minutillus* (Gould). Emu, vol. 39, pp. 128–129.

1941. List of New Guinea birds. A systematic and faunal list of birds of New Guinea and adjacent islands. Amer. Mus. Nat. Hist., pp. 260, map.

1944. The birds of Timor and Sumba. Bull. Amer. Mus. Nat. Hist., vol. 83, art. 2, pp. 123–194.

1945. Birds of the southwest Pacific. A field guide to the birds of the area between Samoa, New Caledonia, and Micronesia. Pp. 316.

1953. On the origin of bird migration in the Pacific. Proc. VIIth Internat. Pacific Sci. Congress, 1949, vol. 4, pp. 387–394.

1963. Animal species and evolution. Pp. 797.

McGILP, J. NEIL

1921. Cuckoos' eggs. Emu, vol. 20, p. 240.

1923. Birds of Lake Frome District, South Australia. Emu, vol. 22, pp. 274–287.

1925. Bird notes – Records – Cuckoos. S. Austr. Ornith., vol. 8, pt. 1, p. 5,

1926. Cuckoo Eggs. A. Austr. Ornith., vol. 8, pt. 7 p. 278.

1929. Should Cuckoos' Eggs Be Destroyed? Emu vol. 28, p. 298.

1935. Nesting of the Brown Weebill (*Smicrornis brevirostris*). Emu, vol. 35, pp. 11–13.

1956. Notes on cuckoos in South Australia. S. Austr. Ornith., vol. 22, pt. 1, pp. 9–12.

McLACHLAN, G. R., AND SPENCE, J. M.

1957. Didric Cuckoo laid egg on way to museum. Ostrich, vol. 28, p. 126.

MEINERTZHAGEN, RICHARD

1954. The Birds of Arabia. Pp. 28, pls. 624, figs. 53, maps 35.

MELLOR, J. W.

1917. Notes on hatching of Cuckoo and Wren. S. Austr. Ornith., vol. 3, pt. 1, p. 18.

MENEGHETTI, FERUCCIO

1944. Further notes on the nesting of Paradise Flycatchers and on parasitism by Klaas' Cuckoo. Journ. E. Afr. Nat. Hist. Soc., vol. 18, p. 96.

MICHIE, R. H.

1948. Habits of shining cuckoo. New Zealand Bird Notes, vol. 2, p. 196.

MILES, H. M.

1951. The cuckoos in Southern Rhodesia. Babbler (the journal of the Rhodesia Bird Club), no. 6, pp. 3–6.

MILLAR, HAROLD M.

1926. Golden cuckoo, *C. cupilus*. S. Afr. Journ. Nat. Hist., vol. 6, pp. 28–29.

1943. The Emerald Cuckoo. Ostrich, vol. 14, p. 118.

Moltoni, Edgardo, and Ruscone, Giuseppe Gnecchi

1940. Gli uccelli dell' Afr. Orient. Ital., pt. 1. Pp. 261, pls. 38.

Moreau, Reginald E.

1944. Food-bringing by African Bronze Cuckoos. Ibis, vol. 86, pp. 98–100.

1949. Special Review—Friedmann on African Cuckoos. Ibis, vol. 91, pp. 529–537.

Moreau, Reginald E., and Moreau. Winifred M.

1939. Observations on some East African birds. Ibis, ser. 14, vol. 3, pp. 296–323.

Mouritz, L. Beresford

1910. Ornithological notes from the south-west border of Rhodesia. Proc. Rhodesia Scient. Assoc., vol. 10, pp. 46–84.

Nicholson, F. G.

1897. Egg of South African Golden Cuckoo in nest of Cape Wagtail. Zoologist, ser. 4, vol. 1, pp. 142–143.

North, Alfred J.

1893. On the nest and eggs of *Gerygone magnirostris*, Gould. Ibis, ser. 6, vol. 5, pp. 373–375.

1894. Notes and exhibits. [Exhibition of cuckoos' eggs from neighbourhood of Sydney.] Proc. Linn. Soc. New South Wales, ser. 2, vol. 8, p. 327.

1895. Oological notes. Proc. Linn. Soc. New South Wales, ser. 2, vol. 10, pp. 215–220.

1897. A list of the insectivorous birds of New South Wales. Dept. Agr. Sydney, New South Wales, Misc. Publ. no. 128, pt. 2, pp. 31.

1912. Nests and eggs of birds found breeding in Australia and Tasmania. Vol. 3, pp. 362.

Oliver, Walter R. B.

1955. New Zealand birds. 2d ed., pp. 661.

Olivier, Georges.

1957. Jeune Coucou de Didric (*Chrysococcyx caprius*) nourri par un de ses parents. Oiseau, vol. 27, p. 382.

Orton, C. L. E., and Sandland, P. T.

1913. Birds of Moora (W. A.) and district. Emu, vol. 13, pp. 75–80.

Ottow, Johann, and Duve, Gebhard

1965. Zur Kenntnis der Fortpflanzung von *Chrysococcyx caprius* und *Cuculus canorus gularis* in Süd-Africa. Journ. f. Ornithologie, vol. 106, pp. 431–439, pl. 1.

Packenham, R. H. W.

1948. Field notes on the birds of Zanzibar and Pemba Islands. 5th ser. Ibis, vol. 90, pp. 98–102.

Parkes, K. C.

1965. Character displacement in some Philippine cuckoos. The Living Bird, vol. 4, pp. 89–98.

Parkin, Charles

1954. Three shining cuckoos fed by one grey warbler. Notornis, vol. 5, p. 207.

Parsons, F. E.

1918. Cuckoo eggs in Blue Wren's nest. S. Austr. Ornith., vol. 3, pt. 5, p. 145.

Paterson, Hugh

1945. Notes on birds at Natal Coast. Ostrich, vol. 16, pp. 225–227.

Peters, James L.

1940. Check-list of the birds of the world. Vol. 4, pp. 291.

PETIT, LOUIS

1899. Ornithologie congolaise. Mem. Soc. Zool. France, vol. 12, pp. 59–106.

PITMAN, CHARLES ROBERT S.

1929a. The occurrence of *Chrysococcyx c. cupreus* (Shaw)—the Yellow-bellied Emerald Cuckoo at Entebbe, Uganda. Bateleur, vol. 1, pp. 98–99.

1929b. The habits of the Didric Cuckoo *Lampromorpha caprius* (Bodd). Bateleur, vol. 1, p. 99.

1934. A report on a faunal survey of Northern Rhodesia. Pp. 175–292.

1957. *Prinia subflava* as the host of the Cuckoo *Chrysococcyx klaas* in Northern Rhodesia. Ool. Record, vol. 31, pp. 3–6.

PLOWES, DARRELL C. H.

1945. Data of birds' eggs collected. Ostrich, vol. 16, pp. 109–117.

1946a. Additional notes on the birds of Bloemhof District. Ostrich, vol. 17, pp. 131–144.

1946b. Data of birds' eggs in my collection, pt. 3. Ostrich, vol. 17, pp. 258–272.

PRIEST, CECIL DAMER

1929. A guide to the birds of Southern Rhodesia and a record of their nesting habits. Pp. 233.

1936. The birds of Southern Rhodesia. Vol. 4, pp. 420, pls. 10.

1948. Eggs of birds breeding in Southern Africa. Pp. 180, pls. 20.

PRINGLE, N. L.

1946. Cuckoo eggs. Ostrich, vol. 17, pp. 368–369.

PRINGLE, V. L.

1948. Egg records of Cuckoos. Ostrich, vol. 19, pp. 155–156.

RAND, AUSTIN L.

1942. Results of the Archbold Expeditions. No. 112. Birds of the 1936–1937 New Guinea Expedition. Bull. Amer. Mus. Nat. Hist., vol. 79, art. 5, pp. 289–366.

REED, R. A.

1953. Some observations on the Didric Cuckoo (*Chrysococcyx caprius*). Ostrich, vol. 24, pp. 138–140.

REICHENOW, ANTON

1881. Eier des Glanzkukuks. Ornith. Centralbl., vol. 6, p. 16.

1894. Die Vögel Deutsch-Ost-Afrikas. Pp. 250.

1902. Die Vögel Afrikas. Vol. 2, pp. 752.

RENSCH, BERNHARD

1931. Die Vögelwelt van Lombok. Sumbawa und Flores. Mitteil. Zool. Mus. Berlin, vol. 17, pp. 451–637.

ROBERTS, AUSTIN

1913. Egg collecting in the bushveld. Journ. S. African Ornith. Union, vol. 9, pp. 1–45.

1926. Descriptions of some S. African birds' eggs. Ann. Transvaal Mus., vol. 11, pp. 226–244.

1939. Notes on the eggs of parasitic birds in South Africa. Ostrich, vol. 10, pp. 1–20.

1940. The birds of South Africa. Pp. 463, pls. 41.

1963. The birds of South Africa, rev. ed. Pp. 542, pls. 64.

ROBINSON, A. W.

1950. Observations on courtship feeding in some Australian birds. West Australian Nat., vol. 2, p. 107.

Ross, J. A.
1913. Cuckoo notes. Emu, vol. 12, pp. 280–281.
1919. Cuckoo seen with egg. Emu, vol. 18, p. 302.
1926. Recollections of an oologist. Emu, vol. 25, pp. 137–146.
1946. Cuckoo depositing egg by the bill. Emu, vol. 45, pp. 246–247.
Rowan, M. K., and Broekhuysen, G. J.
1962. A study of the Karoo Prinia. Ostrich, vol. 33, no. 2, pp. 6–30.
Rowley, Ian
1965. The life history of the Superb Blue Wren (*Malurus cyaneus*). Emu, vol. 64, pp. 251–297.
Royama, T.
1966. A re-interpretation of courtship feeding. Bird Study, vol. 13, pp. 116–129.
Ryves, V. V.
1959. An emerald cuckoo's foster parents. Journ. East African Nat. Hist. Soc., vol. 23, p. 175.
Sandland, P. T.
1909. More new foster-parents. Emu, vol. 8, pp. 150–151.
Sandland, P. T., and Orton, O. L. E.
1922. List of birds found breeding in and around the swamps near Moora, W. A., during 1921. Emu, vol. 22, pp. 134–137.
Schmidt, R. K.
1963. Marico Sunbird *Cinnyris mariquensis* as host of Klaas's Cuckoo *Chrysococcyx klaas*. Ostrich, vol. 34, p. 176.
Schönwetter, M.
1964. Handbuch der Oologie (edit. W. Meise). Nos. 9, 10, pp. 513–640.
Sclater, William L.
1906. The migration of birds in South Africa. Journ. South African Ornith. Union, vol. 2, pp. 14–21.
Sclater, William L., and Moreau, Reginald E.
1932–33. Taxonomic and field notes on some birds of northeastern Tanganyika Territory. Pt. 1, Ibis, ser. 13, vol. 2, pp. 487–522; pt. 5, Ibis, ser. 13, vol. 3, pp. 399–440.
Seaton, Cleo
1962. The Yellow-breasted Sunbird as a host to the Rufous-breasted Bronze-Cuckoo. Emu, vol. 62, pp. 174–176.
Sedgwick, Eric H.
1955. Display of Bronze-Cuckoos. Emu, vol. 55, p. 254.
Selby, A. D.
1946. Note on the Narrow-billed Bronze-Cuckoo. Emu, vol. 46, p. 186.
Serle, William
1950. A contribution to the ornithology of the British Cameroons. Ibis, vol. 92, pp. 343–376.
1954. A second contribution to the ornithology of the British Cameroons. Ibis, vol. 96, pp. 47–80.
Serventy, Dominic L.
1929. Ornithological Notes on the Irwin Valley, Western Australia. Emu, vol. 28, pp. 192–197.
Serventy, Dominic L., and Whitell, Herbert M.
1948. A handbook of the birds of Western Australia. Pp. 365.
1962. Birds of Western Australia. Pp. 427.

SHARPE, RICHARD B.

1873. On the Cuculidae of the Ethiopian region. Proc. Zool. Soc. London, pp. 578–624.

SHELLEY, GEORGE E.

1879. Descriptions of two new species of African birds. Proc. Zool. Soc. London, pp. 679–680.

SHEPPARD, D. M.

1958. Bird notes from Molo. 2. The garden. Journ. E. Afr. Nat. Hist. Soc., vol. 23, pp. 6–8.

SKEAD, C. J.

1947. A study of the Cape weaver (*Hyphantornis capensis olivaceus*). Ostrich, vol. 18, pp. 1–42.

1951. Recent cuckoo records of interest. Ostrich, vol. 22, p. 197.

1952. Cuckoo studies on a South African farm, pt. 2. Ostrich, vol. 23, pp. 2–15.

1954a. A study of the Larger Double-collared Sunbird (*Cinnyris afra afra* [Linnaeus]). Ostrich, vol. 25, pp. 76–88.

1954b. A study of the Cape Wagtail *Motacilla capensis*. Ibis, vol. 96, pp. 91–103.

1956. A study of the red bishop bird, *Euplectes orix orix* (Linnaeus). Ostrich, vol. 27, pp. 112–126.

SKINNER, KENNETH L.

1929. Short notes. Bull. Brit. Ool. Assoc. no. 20 [vol. 2, no. 8], pp. 110–111.

SMITH, K. D.

1957. An annotated check list of the birds of Eritrea, pt. 2. Ibis, vol. 99, pp. 307–337.

SMITH, W. W.

1926. Cuckoos' eggs in sparrows' nests. Emu, vol. 25, p. 296.

SMYTHIES, BERTRAM E.

1953. The birds of Burma. 2d ed., pp. 668, pls. 30.

1960. The birds of Borneo. Pp. 561, pls. 99.

SOUTHERN, H. N.

1954. Mimicry in cuckoos' eggs. *In* Evolution as a process, edit. Huxley, Hardy, and Ford. Pp. 219–232.

SPARROW, RICHARD

1936. Exhibition of a series of eggs of South African parasitic birds. Bull. Brit. Ool. Assoc., vol. 5, pp. 5–7.

STANFORD, J. K., AND TICEHURST, CLAUD B.

1939. On the birds of northern Burma, pt. 5. Ibis, ser. 14, vol. 3, pp. 1–45.

STIDOLPH, R. H. D.

1939. The Grey Warbler and New Zealand cuckoos. Emu, vol. 39, pp. 84–93.

STONEHAM, HUGH F.

1926. Field notes on a collection of birds from Uganda, pt. 1. Ibis, ser. 12, vol. 2, pp. 26–91.

1929. Field notes on a collection of birds from Uganda, pt. 3. Ibis, ser. 12, vol. 5, pp. 267–292.

1952. Annual Report of the Stoneham Museum. 18 pp.

SWYNNERTON, CHARLES F. M.

1916. On the coloration of the mouths and eggs of birds. Pt. 1, The mouths of birds. Pt. 2, On the coloration of eggs. Ibis, ser. 10, vol. 4, pp. 264–294, 529–606.

Thomas, D. K.
1960. Birds-Notes on breeding in Tanganyika: 1958–1959. Tanganyika Notes and Records, no. 55, pp. 225-243.
Tinbergen, Nikolaas
1951. The study of instinct. Pp. 228.
1954. The origin and evolution of courtship and threat display. *In* Evolution as a process, edit. Huxley, Hardy, and Ford. Pp. 233–250.
van Bemmel, A. C. V.
1948. A faunal list of the birds of the Moluccan Islands. Treubia, vol. 19, pp. 323–402.
van Someren, Vernon D.
1958. A bird watcher in Kenya. Pp. 270, illus. 32.
van Someren, Victor G. L.
1916. A list of birds collected in Uganda and British East Africa with notes on their nesting and other habits. Ibis, ser. 10, vol. 4, pp. 193–252, 373–472.
1918. A further contribution to the ornithology of Uganda (West Elgon and district). Novit. Zool., vol. 25, pp. 263–290.
1922. Notes on the birds of East Africa. Navit. Zool., vol. 29, pp. 1–246, pls. 1–7.
1925. What is the true relationship of Klaas's Cuckoo to *Chrysococcyx cupreus* and *Lampromorpha caprius?* Ibis, ser. 12, vol. 1, pp. 660–662, pls. 12 and 13.
1932. Birds of Kenya and Uganda, being addenda and corrigenda to my previous paper in "Novitates Zoologicae" 1922. Novit. Zool., vol. 37, pp. 252–380, pls. 4.
1939. Reports on the Coryndon Museum Expedition to the Chyulu Hills. Pt. 2, The birds of the Chyulu Hills. Journ. E Afr. & Uganda Nat. Hist. Soc., vol. 14, pp. 15–129.
1956. Days with birds, studies of the habits of some east African species. Fieldiana, Zool., vol. 38, pp. 1–502.
van Someren, Victor G. L., and van Someren, G. R. C.
1945. Evacuated weaver colonies and notes on the breeding ecology of *Euodice cantans* Gmelin and *Amadina fasciata* Gmelin. Ibis, vol. 87, pp. 33–44.
1949. The birds of Bwamba. Uganda Journ., vol. 13, special supp., pp. 111, map.
van Tyne, Joselyn, and Berger, Andrew J.
1959. Fundamentals of ornithology. Pp. 624.
Vaughan, John H.
1930. The birds of Zanzibar and Pemba, p. 2. Ibis, ser. 12, vol. 6, pp. 1–48, pls. 1–3.
Verheyen, Rene
1953. Oiseaux, *in* Exploration der Parc Nat. de Upemba, Mission G. F. de Witte fasc. 19, pp. 687, pls. 5, figs. 45.
Vincent, Alfred W.
1946. On the breeding habits of some African birds. Ibis, vol. 88, pp. 48–67.
1947. On the breeding habits of some African birds (cont.). Ibis, vol. 89, pp. 163–204.
Vincent, Francois
1965. Le Coucou Emeraude (*Chrysococcyx cupreus intermedius* Hartlaub 1857) parasite d'un nid de souimanga (*Nectariniidae*) au Congo (Brazzaville). L'Oiseau, vol. 35, no. 2, pp. 81–86.

VINCENT, JACK
1934. The birds of northern Portuguese East Africa . . ., pt. 5. Ibis, ser. 13, vol. 4, pp. 757–799.
WALDEN, ARTHUR, VISCOUNT
1874. On a further collection of birds made by Lieutenant Robert Wardlaw Ramsay, F.Z.S., in the Andaman Islands. Ibis, ser. 3, vol. 4, pp. 127–149.
WATSON, J. S., AND BULL, P. C.
1950. Communal display of the shining cuckoo. New Zealand Bird Notes, vol. 3, p. 226.
WHITE, CHARLES M. N.
1965. A revised check list of African non-passerine birds. Pp. 299.
WHITE, H. L.
1908a. Foster-parents of cuckoos. Emu, vol. 8, p. 31.
1908b. Scone (N. S. W.) notes. Emu, vol. 7, pp. 157–158.
1910. A curious clutch. Emu, vol. 10, p. 49.
1915. Australian cuckoos. Emu, vol. 14, pp. 144–154.
WHITE, S. R.
1950. Cuckoo notes from the Morawa District. West Australian Nat., vol. 2, pp. 77–80.
WHITLOCK, F. LAWSON
1910. On the East Murchison. Emu, vol. 9, pp. 181–219.
WILLIAMS, NIGEL
1946. *Alseonax minimus pumilus* and *Lampromorpha klaasi*. Journ. E. Afr. Nat. Hist. Soc., vol. 19, p. 138.
WILSON, F. ERASMUS
1914. New foster-parent. Emu, vol. 14, p. 170.
1918. New cuckoo foster-parent. Emu, vol. 17, p. 235.
WINTERBOTTOM, JOHN M.
1939. Miscellaneous notes on some birds of Northern Rhodesia. Ibis, ser. 14, vol. 3, pp. 712–734.
1951. Common birds of the bush. Pp. 40, pls. 4.
WOODWARD, R. B., AND WOODWARD, J. D. S.
1899. Natal birds. Pp. 215, pl. 1.
WORMAN, A. G.
1930. Male emerald cuckoo (*Chrysococcyx cupreus intermedius*) feeding young. Ool. Rec., vol. 10, pp. 76–77.

Index

U.S. GOVERNMENT PRINTING OFFICE: 1968