ON THE BREEDING BIOLOGY OF SOUTHERN AFRICAN CUCKOOS

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INTRODUCTION

"In no branch of Ornithology is there so much interest to be found, so much need for careful observation in the field and so much liability to error as in the case of the eggs of our parasitic birds." So wrote the father of modern South African ornithology, Austin Roberts, in 1939. Three decades later, it is rather disappointing to find that the study of brood parasites in southern Africa has not progressed too far since Roberts's day, at least partly because of a lack of the careful observation which he stressed.

Herbert Friedmann has made the most carefully detailed analyses of the biology of all African cuckoos (1948, 1949, 1956, 1964, 1967, 1968). His syntheses form a most valuable nucleus of knowledge. However, Friedmann and various other authors summarizing data on African cuckoos were often forced by circumstance to accept definite, possible, and doubtful breeding records with equal readiness. This has been largely due to the distinct scarcity of records of the first-named variety. This work attempts an analysis of all the readily available *authentic* data on breeding of the cuckoos in southern Africa. It is therefore essentially a review and compilation of existing data which have been mercilessly scrutinized for authenticity. Like any work dealing mostly with the data of other people, it can make no claim to include all the authentic records that have been made, but it *is* claimed that no doubtful records have been included in the tables or other data used in forming our conclusions.

MATERIAL AND METHODS

The data used in this study came mainly from the Nest Record Cards (NRCs) of the South African Ornithological Society, housed in the Percy FitzPatrick Institute of African Ornithology. This collection houses nest records for Africa south of the Zambezi and Kunene Rivers (southern Africa as defined in McLachlan and Liversidge 1957, and as here understood). Payne and Payne (1967) based their analyses on the same collection, but included some countries north of the Zambezi, while excluding South-West Africa, the Orange Free State and the northern Cape Province.

All cards present at the Percy FitzPatrick Institute by 15 August 1968 were analyzed. Besides this all our personal records (recorded on NRCs) were included, and some more recent records up to December 1968 were obtained from the files of the Rhodesian Ornithological Society and the Witwatersrand Bird Club. Also, records were culled from the literature and from various personal contacts.

A few of the earliest original records were unavailable to us. Records in the Nest Record Cards and in the literature which gave no substantiation were, for most cuckoos, rejected. Unavoidably, in some cases we have had to use our own judgment as to whether a given observer's observations were reliable or not. In all cases such judgment was on the conservative side. Undated records were used only if particularly significant. The exact criteria for acceptance of records varied from species to species and are given under each.

We have not attempted to give a complete bibliography of all published work dealing with cuckoo breeding in southern Africa. Virtually all the available early records have been transcribed onto S.A.O.S. Nest Record Cards, complete with reference. All of these are also cited in Friedmann's works which give very complete bibliographies. In this connection we mention particularly his recent paper on *Cuculus* (1967) and the monographs on *Clamator* (1964) and *Chrysococcyx* (1968). We have listed all the original references subsequent to 1948 that are cited in the text. For convenience and economy, citations of most works quoted by Friedmann (1948) take the form "Smith in Friedmann, p. 10", although we have in all cases personally checked the original reference.

The aim of the present paper is to indicate the breeding seasons and "biological hosts" of southern African cuckoos by region, as well as to summarize the present extent of our knowledge regarding some other aspects of their breeding biology. The subject of courtship has been largely left out, as has the phenomenon of fledgling feeding by adults of some cuckoos. These are fully dealt with by Friedmann (1948, 1949, 1956, 1964, 1968).

The breeding season is indicated in the tables according to convention, i.e. dates refer to earliest and latest egg dates, actual or computed. Estimates are always on the conservative side. In the majority of our cuckoos incubation, nestling and post-fledging dependence periods are of unknown duration. In such cases we have used conservative estimates based on appropriate periods in congeneric or close relatives, preferably African. The available evidence indicates that the error in this procedure is negligible if dates are grouped by weeks. The month is divided for this purpose into quarters; i /12 refers to egg dates falling in the first "week" of December (1–7). ii refers to the second "week" (8–15), iii the third "week" (16–23) and iv the fourth "week" (24-30/31). Fledglings have in the absence of contrary information been regarded as just out of the nest. Since the post-fledging dependence period is lengthy in cuckoos, and since this is the easiest phase of the cuckoo breeding cycle to observe, we have also mentioned where possible the latest *actual* fledgling records, to indicate to fieldworkers the total period during which cuckoo breeding might be recorded.

We have used data from museum material in only a few cases, since we feel that information from this source is marginal in quantity and usefulness and has largely been covered by other writers. Oviduct egg data, however, are given to supplement meagre information in the case of some species (dates bracketted in tables). It should be borne in mind that oviduct eggs do not necessarily provide the most reliable egg information, as has also recently been pointed out by Ottow and Duve (1965). Such records usually refer to shelled eggs taken from the uterus, where shell formation and pigmentation occurs. Shelled uterine eggs may be obtained at any stage of pigment deposition and indeed of shell formation. There is some evidence from the Neotropical parasitic cuckoo *Tapera* that intensity of pigmentation varies according to the length of time that the full-formed egg spends in the uterus, which interval this species is able to vary at will within certain limits (Neal G. Smith, pers. comm.). Such voluntary retention is also believed to occur in Old World cuckoos (Lack 1968). Little other information is available on egg-laying physiology in cuckoos, but it can be assumed to be basically similar to that in other birds, including the Common Quail *Coturnix coturnix*. Information from the latter (subspecies *japonica*) shows that the egg, which is creamy to greenish heavily blotched and speckled with brown, spends up to 83 per cent of its total formative time (24 hours) in the uterus of the oviduct. The fully calcified egg has received its background colour after approximately seven-eights of its total formative time. In the remaining time before laying it therefore obtains its complete speckle-pattern (Woodard and Mather 1964). The total period involved in the quail is the same as estimated for the glossy cuckoos by Friedmann (1968).

The term "biological host" refers to an ecologically meaningful host, as distinct from casual and accidental hosts. All cuckoos appear to be forced on occasion to lay in nests of birds which can, or will, never rear the cuckoo. Some cuckoo species are more prone to "dump" eggs in this manner than are others. Such an occurrence is, however, biologically insignificant in the economy of the accidental host, and has little significance to the cuckoo in terms of host-parasite relationships over the short term. Unfortunately, our knowledge of cuckoo hosts in southern Africa is still so fragmentary that it is unwise to attempt to distinguish between accidental, unusual and regular hosts, except in a few instances. For this reason we have selected the categories "biological" and "egg" hosts. The former refers to hosts recorded as raising cuckoos past the egg stage. The latter applies to all hosts recorded with cuckoo eggs only. Probably most hosts in the latter category will prove to be casual or accidental hosts, although some will doubtless become "biological" as more information accrues. It should be pointed out that our "biological hosts" may include unusual as well as regular hosts. Also, due to lack of sufficient records from some regions, we have listed a host as "biological" for all regions in which it has been parasitized, even though records of cuckoo young with it may have come from only one of these regions. Only "biological" hosts are listed here; full host listings appear in Payne and Payne (1967) and in various papers by Friedmann.

Incubation and fledging information is included where possible for the sake of completeness, and to demonstrate how scanty it is.

Records are broken down by areas, which are abbreviated according to the key with the table for the Jacobin Cuckoo *Clamator jacobinus*.

Finally before proceeding to the cuckoos themselves we wish to draw attention to a well known fact overlooked by many South African observers when recording cuckoo eggs. Cuckoos are inveterate egg thieves, a fact well documented by overseas observations (Chance 1940, Ingle 1912) as well as in Africa (Chapin 1939; Calder 1951; Swynnerton, p. 163 and van der Plaat, p. 164 in Friedmann; Friedmann 1956 p. 381; pers. obs. R. J. of Jacobin/Black Sunbird, *see* Skead 1967, p. 125). It seems that they may inspect many nests in quest of possible hosts and/or food. The presence of a cuckoo near or even at a nest is by no means proof of (*a*) parasitism or (*b*) parasitism by the cuckoo which was observed. This is particularly pertinent in areas where several cuckoos occur sympatrically.

THE CUCKOOS

Cercococcyx montanus Barred Long-tailed Cuckoo

This species has only recently been found in southern Africa. Nothing whatsoever is known about its breeding within our limits, and little more has been recorded elsewhere. It has been found on the escarpment at the Haroni-Lusitu confluence in Rhodesia, calling during November and January, but apparently absent (or silent) in July and August; and also in the Dondo forest near Beira, Moçambique, in June (Clancey 1968). We are indebted to H. D. Jackson of Salisbury for the above information.

In East Africa a completely authentic egg measured approximately 21×15 mm. (broken) and was white with a faint zone of reddish around the thick end, greatly resembling eggs of akalats *Sheppardia* (Moreau in Friedmann, pp. 111–2). The bird has been suspected of parasitizing akalats and also the Broadbill *Smithornis capensis*.

Pachycoccyx audeberti Thick-billed Cuckoo

Practically nothing definite is known about the breeding of this rare cuckoo. The egg probably resembles speckled eggs of the genus *Cuculus*. An oviduct egg from East Africa was pale greenish-blue with scattered small brown and grey-brown speckles. Only two reliable records are available, from Rhodesia. These refer to fledged young accompanying and being fed by Red-billed Helmet-Shrikes *Prionops retzii* on the Turgwe River, 26/1 and 16/5 (Townley in Friedmann, p. 101).

Clamator jacobinus Jacobin Cuckoo

One of the two commonest, most widespread and presumably most successful South African cuckoos, this species moves about mostly in noisy pairs during the breeding season. It shows a marked tendency to "dump" a large number of its eggs (e.g. Vernon, in press), a fact reported first, although possibly with some exaggeration, by Bradfield (1931). It appears to lay from one to many (up to seven recorded but probably from more than one female) eggs per nest (NRCs), usually while the host is completing its own clutch, but often before the first host's egg, and sometimes even in deserted nests! One or more host's eggs are removed for every cuckoo egg in most cases.

The eggs in South Africa are invariably pure white, glossy, rounded and much larger than the hosts', to which they bear no resemblance. Records referring to such eggs have been accepted in this study without reservation. It should be mentioned that prior to 1939 such records were frequently attributed to the Black Cuckoo *Culculus clamosus;* these have also been included under this species when a description was given. Eggs measure in the range $23.0–29.0 \times 19.0–24.0$ mm. Table 1 gives the 176 reliable records available to us.

The earliest date for Natal (4/9) is exceptional, and in fact is almost a month before the usual arrival of this species in that province (Vernon, pers. comm.). It is clear that *Pycnonotus* bulbuls are the primary hosts (121 records), while the Fiscal Shrike *Lanius collaris* and, in the Eastern Cape and Natal, Sombre Bulbul *Andropadus importunus* are also major hosts (17 and 14 records respectively). A long list of egg hosts has been recorded, *see* Friedmann (1948, 1964), Payne and Payne (1967) and others. A most unusual biological host is the Fork-tailed Drongo *Dicrurus adsimilis* (one record, Skead 1962).

Table 1: *Clamator jacobinus*

*Area**	*Nestlings*	*Fledglings*	*Eggs Only*	*Biological Hosts*	*Eggs Dates*	*Last Fledgling*
W.P.	—	1	—	*Pycnonotus capensis*	ii/11	5/12
E.P.	25	—	52	*Andropadus importunus* *Pycnonotus capensis* *P. barbatus* *P. nigricans* *Lanius collaris* *Dicrurus adsimilis*	i/10–i/2	—
Natal	2	—	22	*Lanius collaris* *Andropadus importunus* *Pycnonotus barbatus*	i/9 –ii/1	—
Tvl.	1	3	8	*Pycnonotus barbatus* *Lanius collaris*	iii/11–ii/4	20/5
Rhod.	4	5	42	*Pycnonotus barbatus* *Lanius collaris*	i/11–ii/3	—
N.C.–O.F.S.	—	—	6	*Pycnonotus nigricans* *Lanius collaris*	iii/11–i/3	—
S.W.A.	1	—	3	*Pycnonotus nigricans*	iii/12–?/4	?/4
Bots.	—	—	1	†(*Parisoma subcaeruleum*)	iii/1	—

*W.P. – Western Cape Province; E.P. – Eastern Cape Province; Tvl. – Transvaal; Rhod. – Rhodesia; N.C.–O.F.S. – Northern Cape Province and Orange Free State; S.W.A. – South West Africa; Bots. – Bots-wana.

†Bracketted host = egg host, given where no biological host yet recorded.

The incubation period is about 11 days (Liversidge 1961). No accurate nestling period has been recorded, but it seems to be less than 17 days and perhaps as short as 12 days (NRCs). There is no information on the post-fledging dependence period.

The nestling Jacobin does not purposely evict its nest-mates as far as known. However it appears that they usually perish by starvation, jostling out of the nest or trampling. The nestling parasite is at first naked and brownish to orange-brown; the nostrils are oblong rather than round, and are not very prominent. Eyes open by the second day. Mouth is red, with a yellow gape. The back is not flat, but rather rounded. (Description from Skead 1951). The nestlings are said to darken till they are blackish dorsally by the pin-feather stage. They bear considerable resemblance to *Pycnonotus* young dorsally (Peter Steyn, pers. comm.). Feathered young are dull blackish-brown to brown above, slightly crested, and buffy or dark blackish-brown below, depending on phase. Faint white wing windows are discernible.

Clamator levaillantii Striped-breasted Cuckoo

Among the lesser-known cuckoos in South Africa, this species appears to lay only blue-green eggs in our area (but *see* Friedmann 1964, p. 53). Its egg-laying habits seem to resemble those of *Cl. jacobinus*, judging from the few observations available. Authentic records suggest that the egg matches those of its only South African host, Jardine's Babbler *Turdoides jardinei*. It may be paler than the host's eggs, but is invariably rounder and broader. Oviduct eggs average 26.0×20.4 mm. (Friedmann 1948). An authentic egg from Rhodesia measured 25.8×20.2 mm. (Peter Steyn, *in litt.*). This egg was also finely pitted, while the host's single egg was smooth. Other unconfirmed but probable egg records indicate the size range 25.8–27.2×20.2–21.0 mm. Spotted pinkish eggs attributed to this cuckoo (Friedmann 1948) are almost certainly *Cuculus* eggs. Eight authentic records, and two highly probable egg-only records are available to us.

Table 2: *Clamator levaillantii*

Area	*Nestlings*	*Fledglings*	*Eggs Only*	*Biological Hosts*	*Egg Dates*	*Last Fledgling*
Tvl. (E.)	—	1	2	*Turdoides jardineii*	i/12–ii/5	—
Rhod.	4	3	—	*Turdoides jardineii*	i/12–i/5 (6/2, 19/4)	30/5

Other babblers may later also prove to be hosts.

No precise incubation and nestling periods are available, but NRCs indicate a total nest period of over 23 days. Two Rhodesian NRCs indicate that incubation may take about 11 days and fledging 12 to 17 days. Post-fledging period unrecorded. The young cuckoos seem to be more frequently reared with their host's young than is the case in the Jacobin (NRCs).

Nestling and fledgling descriptions are not available, but the young are said to resemble Jacobin young of the white-breasted phase (Jubb 1952; Peter Steyn, pers. comm.).

Clamator glandarius Great Spotted Cuckoo

Fairly common in the savanna and more open bush country of southern Africa, and like its congeners moves about noisily in pairs during the laying season. This species has adapted itself partly to hole-nesters in South Africa. More than one egg is usually laid per nest, often before the first of the host's clutch, sometimes well after the host has completed its own clutch (NRCs). Eggs of the host are often removed, or damaged in the nest, presumably usually one per cuckoo visit. Mountfort (1968) felt that in Spain the host Magpies' *Pica pica* eggs were removed selectively by laying females, while the extremely well-matched cuckoo eggs already present were not molested. In two parasitized Pied Starling *Spreo bicolor* nests in the Eastern Cape we found no host eggs, and one and four cuckoo eggs with three and one cuckoo chicks respectively. All the eggs were rotten, one was cracked and at least two had small holes. If the damage is attributable to cuckoos, it seems that they may be somewhat less selective than in Spain, at least in hole nests.

The record number of cuckoo eggs in our area is 13 from a Pied Crow *Corvus albus* nest in Rhodesia (with four of the host). This set was clearly separable into two groups of six and seven eggs by size and colours, suggesting that two female cuckoos were involved (Neuby-Varty, NRC).

Egg records for this species have been accepted when based on the characteristic egg from nests of hosts with dissimilar eggs. There is usually no confusion of chicks since the normal hosts of this species are different from those of other cuckoos. Greater Honey-guides *Indicator indicator* also regularly parasitise the Pied Starling, however.

The egg is pale greenish, rather rounded, and variably spotted with brown. The brown is usually light to reddish, and speckling is usually profuse, covering the entire egg, but sometimes concentrated at the thick end, sometimes in blotches. The size varies greatly, 30.9–37.0 × 21.0–26.5 mm. Table 3 summarizes 42 reliable records.

Table 3: *Clamator glandarius*

Area	*Nestlings*	*Fledglings*	*Eggs Only*	*Biological Hosts*	*Egg Dates*	*Last Fledgling*
E.P.	4	2	4	*Geocolaptes olivaceus* *Upupa epops* *Onychognathus morio* *Spreo bicolor*	i/9 – ii/1	—
Natal	—	—	3	*Corvus albus* *Onychognathus morio*	ii/[illegible]/10–iii/11	—
Zululand	—	—	1	*Corvus albus*	i/11	—
Tvl.	1	—	7	*Corvus albus* *Spreo bicolor*	ii/10–ii/1	—
Rhod.	3	—	13	*Corvus albus* *Lamprotornis chalybaeus*	i/10–ii/1	—
S.W.A.	1	—	3	*Lamprotornis nitens*	iii/2	—

The largest numbers of records are for the Pied Crow and the Black Crow *Corvus capensis* (12 and 11 respectively). Remarkably, none for the latter species refer to cuckoo young, although it seems probable that this is due merely to small-sample error. Several starlings (hole nesters) appear to be utilized, probably more frequently than would appear from the table. The Ground Woodpecker *Geocolaptes olivaceus* and African Hoopoe *Upupa epops africana* must be highly unusual hosts (3 records *ex* Friedmann 1964).

The incubation period has not been precisely measured in South Africa, but one record (Patten, NRC) was definitely shorter than the 14 days Mountfort (1968) gives for Spanish *Cl. glandarius*. The nestling period was given as 28 days in one instance involving an unusual (hoopoe) host (Courtenay-Latimer, in Friedmann 1964). A hand-reared *Cl. glandarius* in our care began flying at least 20 days after hatching. Other records suggest a similar period (NRCs). Post-fledging dependence lasted at least two weeks in the hoopoe cuckoo mentioned above.

Purposeful (or "true") eviction is not known to occur in this species. Crows seem to have better chances of surviving with young cuckoos than do starlings because crow nestlings are larger than the parasites. It appears that normally the host's young are trampled, starved or jostled out. Young cuckoos hatched much later than their fellows (a common occurrence) suffer the same fate: we have found trampled, younger cuckoos in parasitized Pied Starling nests. Once we saw a young Cuckoo being pushed out of a Pied Starling nest-tunnel by a larger sibling during a scuffle to reach the food-bringing foster-parent. The starlings continued to feed the young parasite on the ground as well as his erstwhile nest-mates.

The naked chick is yellowish-brown; mouth pinkish- to orange-red, gape pale yellow. The nostrils are oblong, slightly prominent. Feathered chicks resemble the adult, but the crest is not noticeable, top of the head is largely black and the primaries show a rufous area towards the base. The throat and chest are orange-buff. These characters all change rather rapidly after the bird gains independence.

Cuculus canorus gularis African Cuckoo

A little-known cuckoo, in contrast to the European race. It seems that at least some of the African Cuckoos visiting South Africa do not breed here (*see* Mackworth-Praed and Grant 1962). During 1967–8 we noted an influx of African Cuckoos to the farm "Mosdene" near Naboomspruit, Transvaal, in February and March. This cuckoo was neither seen nor heard in October and December. The birds were all adults, all definitely *gularis*, and had departed, presumably on northward migration, by 30 April. A calling *C. c. gularis* pair was recorded in March 1962 in this locality (pers. obs. R.J.). No juveniles have ever been reported from "Mosdene", however, despite the fact that it has been a popular bird-watchers' locality for years. Similar observations have been related to us from other areas.

Nothing has been recorded of the egg-laying habits of this bird. Presumably they do not differ much from those of the European race. *C. c. gularis* seems to be recorded frequently in pairs during the season when calling is heard.

The eggs are practically unknown, but there is evidence that they resemble speckled eggs of the other South African *Cuculus* species. Therefore no egg-only records have been accepted here, apart from one mentioned below. There seems to have been much confusion over the young of this bird also (NRCs, and *see* Payne and Payne 1967); only carefully described records have thus been included.

An oviduct egg from Rhodesia was "pale washed out greeny-blue with pale mauve and brown spots, 24 × 18 mm." (Neuby-Varty 1948). An authentic record (included in table) by Neuby-Varty was of an egg laid by a dying female shot while attempting to parasitize a Fork-tailed Drongo nest (Pitman 1957). The egg was pink-tinged cream, marked with irregular bold blotches and spots of rufous, and underlying mauve, mainly at the thick end, 24.8 × 17.0 mm. It resembled the host's eggs. Two other unconfirmed records by Neuby-Varty from the same locality and based on similar eggs from drongo nests (Pitman *loc. cit.*) have been excluded because of their similarity to the other eggs of the respective clutches in all respects. We follow Payne and Payne (1967) in rejecting Ottow and Duve's (1965) records.

Table 4: *Cuculus canorus gularis*

Area	*Nestlings*	*Fledglings*	*Eggs Only*	*Biological Hosts*	*Egg Dates*	*Last Fledgling*
O.F.S.	1	—	—	*Dicrurus adsimilis*	iii/12	?/1
S.W.A.	—	1	—	*Dicrurus adsimilis*	iv/12	14/1
Rhod.	—	1	1	*Dicrurus adsmilis*	i/11–iii/12 (27/10)	20/1

We have an additional record of a recently independent juvenile near Windhoek, S.W.A., 20 January.

The Fork-tailed Drongo is the only host reliably reported in southern Africa. Reports of White-browed Scrub-Robin *Erythropygia leucophrys* and Black-eyed Bulbul *Pycnonotus barbatus* as hosts could not be verified due to lack of accompanying evidence (Friedmann 1948, 1956).

There are no data on incubation and nestling periods, but these are probably similar to the European Cuckoo's (12½ and 20 days respectively, according to Friedmann 1956). Eviction occurs as in the European Cuckoo *C. canorus canorus* (one observation, Plowes 1948).

The nestling is naked and black. Mouth is orange. Feet are yellow by the time the chick fledges (Plowes 1948). The bill is brown, and apparently only develops the characteristic yellow area shortly before or after fledging (pers. obs.). The young bird shows a "shadow" adult pattern below, being barred throughout, but more narrowly on the throat and chest. Dorsally it is grey, but the feathers are narrowly edged with white, the white being much more extensive on the head which appears strongly mottled. Wings and tail similar to adult. Friedmann (1948 p. 62) describes a hepatic juvenile phase as having the grey and white replaced by brownish and tawny to buff respectively. Juvenile *C. c. gularis* can be confused with the fledgling Red-chested Cuckoo *C. solitarius* (*see* under latter).

Cuculus solitarius Red-chested Cuckoo

A common breeding migrant in the eastern half of the sub-continent, conspicuous by virtue of its call. Liversidge (1955) and Reed (1969) have published fairly comprehensive data on this species. Males establish call-posts to which the females presumably are drawn. One egg is usually laid per nest, between the first and last eggs of the host clutch. Occasionally eggs are laid before the first egg of the host, and even more rarely after the last egg. One host's egg is usually removed on the cuckoo's visit (above information from Friedmann 1948, Reed 1969 and NRCs).

C. solitarius lays uniform as well as spotted eggs in South Africa. By far the commonest egg type is a uniform, usually chocolate-brown (NRCs), but in some areas green or whitish spotted eggs are the rule (Reed 1969; Oatley, in press). Egg-only records involving the characteristic brown eggs are accepted here as fully authentic except in the case of host robins laying very similar eggs. In such cases, and for eggs of other colours, rigorous proof is required. Several other cuckoos lay spotted eggs in the same general size and colour range as spotted *C. solitarius* eggs.

The feathered chick is rather similar to the African Cuckoo chick and possibly to others. Records from areas and hosts which could give rise to confusion have been screened carefully for supporting description (for distinction *see* later).

The brown eggs measure 22.9–26.5 × 17.8–19.5 mm. Oatley's (*op. cit.*) authentic spotted egg measured 23.8 × 19.2 mm. This egg was "pale blue dully freckled with pinkish brown", in a Bearded Scrub-Robin *Erythropygia quadrivirgata* nest. Other similar eggs in Bearded Scrub-Robin nests were found at the same locality (Ndumu), in width down to 17.0 mm. Reed (1969) reported a number of authenticated spotted greenish, whitish and fawn eggs from central Transvaal but none were measured. Other spotted eggs from Rhodesia were not proved to belong to this species (NRCs). Seventy-one authentic records are summarized in Table 5.

The main hosts in southern Africa are Cape Robin *Cossypha caffra* (39 records) and Cape Wagtail *Motacilla capensis* (10 records). Other hosts such as the Bearded Scrub-Robin may turn out to be regularly used.

The incubation period seems to be about two weeks, but reports vary (e.g. Liversidge 1955,

Table 5: *Cuculus solitarius*

Area	*Nestlings*	*Fledglings*	*Eggs Only*	*Biological Hosts*	*Egg Dates*	*Last Fledgling*
W.P.	2	—	3	*Cossypha caffra* *Motacilla capensis*	iii/9–i/11	—
E.P.	6	5	9	*Monticola rupestris* *Turdus olivaceus* *Cossypha caffra* *Saxicola torquata* *Muscicapa adusta* *Motacilla capensis*	iv/10–i/1	7/2
Natal	5	2	9	*Cossypha caffra* *C. natalensis* *Pogonocichla stellata*	iv/10–iii/1	20/2
Zululand	1	—	—	*Erythropygia quadrivirgata*	i/11	
Tvl.	11	2	9	*Cossypha caffra* *Motacilla capensis*	iii/10–iv/1	1/3
Rhod.	1	2	4	*Pogonocichla stellata* *Saxicola torquata* *Pinarornis plumosus* *Cossypha humeralis*	ii/11–i/2	6/3

Reed 1969). The nestling period is about 17–20 days (Liversidge 1955, Reed 1969, NRCs), and Reed (*op. cit.*) shows the post-fledging period to be about four weeks.

Eviction takes place within the first five days, probably not in the first 24 hours (Liversidge 1955, NRCs). The nestling is naked and brownish at first, changing to blackish within the first day or two. Mouth and gape are orange, feet dark flesh. The eyes open at about one week. By the 15th day the feet and skin around eye are yellow. The bill is brownish to blackish (description from Liversidge 1955). Feathered chicks are predominantly slaty-blackish, the feathers of the upperparts and chest narrowly edged with white. Below they show a "shadow-adult" barred pattern. The blackish bars of the underparts are much broader in this species than in the juvenile *C. c. gularis* and there is less white on the throat, chest and crown. The overall dorsal colour is also much darker (blackish in the field, as opposed to grey or grey-brown in *C. c. gularis*).

Cuculus clamosus Black Cuckoo

A poorly known species despite its abundance. No eggs have ever been followed to hatching in our area. This is probably due to its favouring secretive shrikes as hosts. Like some other *Cuculus*, the males appear to have definite calling territories to which females come for mating (pers. obs.).

Black Cuckoos appear to remove an egg of the host for each cuckoo egg laid (Masterson, in Friedmann p. 88; NRCs). Only one egg per nest is deposited (Friedmann 1948; NRCs). Black Cuckoos have been seen at nests, and it seems that males may play a part in nest visits (Friedmann, *op. cit.* and NRCs; *see* introductory remarks, however).

The eggs resemble speckled eggs of several other cuckoos as far as is known. Egg-only records have therefore been excluded here, except for two from Rhodesia found under circumstances suggesting a high probability of correct identification (details in Friedmann 1948, p. 88). The feathered chick is distinctive.

An oviduct egg collected by Hoesch (Hoesch and Niethammer 1940) in South-West Africa was whitish tinged grey, with small light-brown and brown-violet speckles and flecks, measuring approximately 23.5 × 17.0 mm. (broken). The eggs mentioned in the previous paragraph, from Boubou-Shrike *Laniarius ~~ferrugineus~~* nests, were pale reddish-brown "with smallish speckles of reddish-brown and bluish-grey" concentrated at the large end, 24 × 17 and 24 × 17.5 mm. Only 14 reliable records are available (Table 6).

Table 6: *Cuculus clamosus*

Area	*Nestlings*	*Fledglings*	*Eggs Only*	*Biological Hosts*	*Egg Dates*	*Last Fledgling*
E.P.	1	6	—	*Laniarius ferrugineus*	ii/11–iii/1	21/2
Tvl.	1	1	—	*L. ferrugineus*	iii/1–ii/3	30/4
				L. atrococcineus		
Rhod.	1	1	2	*L. aethiopicus*	iii/12–iv/1	15/2
				L. atrococcineus		
S.W.A.	—	1	—	*L. atrococcineus*	ii/1, (6/2)	11/2

The main hosts are the boubou shrikes *L. ferrugineus* and *aethiopicus* (11 records). The Crimson-breasted Shrike *L. atrococcineus* may be found to serve as a regular host also in the drier areas. The Boulder Chat *Pinarornis plumosus* and Heuglin's Robin *Cossypha heuglini* have been suggested as egg hosts with circumstantial evidence in Rhodesia (NRCs and Friedmann 1967), but the eggs were larger than authentic eggs of this cuckoo, and in the absence of further proof, cannot be accepted from an area where several other cuckoos with similar eggs may occur.

The incubation period is unknown. Fledging takes between 16 and 21 days according to one record (Skead 1951). Post-fledging dependence lasts at least 19 to 26 days (two records, Neethling 1968, 1969).

The newly-hatched chick evicts its nest-mates within the first few days. It possesses the typical *Cuculus* features, but the mouth is said to be pink (description in Skead 1951). The feathered chick is apparently always all-black (Skead *op. cit.*) and lacks yellow feet and orbital skin, but otherwise resembles other *Cuculus* young.

Chrysococcyx cupreus Emerald Cuckoo

A remarkably mysterious species in southern Africa, from where few acceptable breeding records are available. Much misinformation exists due to extensive confusion with other *Chrysococcyx* species, particularly *Ch. klaas* (this applies also to other parts of Africa).

The female is apparently often accompanied by the male during oviposition (Connell 1959, and extralimital records in Friedmann 1948, 1968). Only one egg is laid per nest. In other aspects of egg-laying and territorial behaviour, it seems to be much like Klaas's Cuckoo (Friedmann 1948, 1968; pers. obs.).

As far as is known, the Emerald Cuckoo's eggs can be, and have been, easily confused with those of other *Chrysococcyx* (examples in Friedmann 1948, NRCs). Egg records of this genus from areas where the Emerald occurs, and from other than well established Didric or Klaas's hosts, should be particularly carefully observed and documented. There is some *suggestion* that the eggs of this cuckoo are smaller than Didric eggs and mainly white or pale blue in our area. The nestling, fledgling and juvenile stages have undoubtedly been extensively confused with the corresponding stages of Klaas's Cuckoo, both in our area and elsewhere. In consequence numerous records for *Ch. klaas* and a large proportion of the few for this species have had to be omitted (cf. Payne and Payne 1967).

The few available authentic records do not warrant tabulation. Two oviduct eggs from Natal taken in the last century, in October and December, are plain white and white sparsely speckled with purple (Friedmann 1948, p. 121). One dateless record from Natal reports a pair of Emerald Cuckoos parasitizing a Black-eyed Bulbul *Pycnonotus barbatus* nest (Connell 1959). The cuckoo's egg was pure white, 18×15 mm. Friedmann (1968) gives measurements of 20.5×13.0 and 17.8×12.2 mm., but the locality and authenticity of these records is unknown to us.

We mention four other records from Natal. Two (unproven) involve pale blue cuckoo eggs, one from a nest of Yellow-throated Warbler *Seicercus ruficapillus* (Oatley and Pinnell 1968) and a slightly larger one (within Didric egg size range) from a nest of Bleating Bush-Warbler *Camaroptera brachyura* (Vernon, in prep.). The remaining two involve definite records of young birds. On 5 February 1968 C. J. Vernon and the senior author found a nestling *Chrysococcyx* in a *Camaroptera brachyura* nest near Pietermaritzburg, and a fledgling *Chrysococcyx* fed by another pair of Bleating Bush-Warblers nearby (Vernon, in prep.). The fledgling cuckoo was without doubt an

Emerald, since it could be critically compared with a nearby Klaas's Cuckoo fledgling at the time (*see* Vernon, *loc. cit.*). Subsequent examination of extensive museum material and correspondence with J. G. Williams and C. R. S. Pitman confirmed this identification and revealed the diagnostic characters presented later.

The nestling cuckoo was removed for hand-raising, but died when about a week old. Fortunately, we were subsequently able to confirm its identity beyond doubt by comparison of the preserved specimen and colour photographs taken during its development with comparable stages of a hand-raised Klaas's Cuckoo from South-West Africa (for differences *see* below).

Other hosts listed for South Africa have here been rejected as indeterminately identified (cf. Payne and Payne 1967). Vincent 1934 has recorded the Puff-backed Shrike *Dryoscopus cubla* as a fosterer from just north of our limits in Moçambique. Elsewhere in Africa the paradise flycatchers *Terpsiphone* spp. (J. G. Williams, *in litt.*) and sunbirds are said to be regular hosts. It is interesting to note that the Thick-billed Weaver *Amblyospiza albifrons* has been retained as a host in Friedmann (1968, p. 55) although the eggs on which the record is apparently based have been rejected (p. 74). This record (Friedmann 1948, plate 6, fig. 1) is an obvious error; the "cuckoo" eggs are normal weaver eggs, while the "weaver" egg is probably a Didric's.

Incubation, nestling and post-fledging periods are unrecorded. Eviction occurs as in other *Chrysococcyx* (recorded for the *Camaroptera* cuckoo nestling mentioned above).

The naked nestling has not been described previously. The recently hatched nestling (less than 48 hours) from the *Camaroptera brachyura* nest referred to above was pinkish-yellow. It was smaller than a Didric of comparable age, and had a comparatively shorter bill and flatter head. Two days later it was much darker, yellowish-brown and violet-blackish. At about one week of age the first feathers were breaking out of their sheaths. The eyes were still closed. These stages greatly resemble those of Klaas's Cuckoo but the Emerald nestling is more yellowish and yellowish-brown, and less blackish, than either Klaas's or Didric chicks at all stages.

The feathered young is very like Klaas's. It is barred throughout except on the under tail coverts. There is variation in the amount of barring on the outer tail feathers (as in Klaas's), which are predominantly white. Friedmann (1948, p. 116) has given an inadequate but widely used key for separating juvenile *Chrysococcyx klaas* and *cupreus*. Personal observation, examination of skins and correspondence or discussion with numerous ornithologists from southern and East Africa demonstrated the existence of widespread confusion. Capt. C. R. S. Pitman kindly examined the extensive material in the British Museum and confirmed our findings regarding the separation of juveniles. The white-barred forehead character given by Friedmann refers only to juvenile *male* Emerald Cuckoos. J. G. Williams (pers. comm.) confirms the validity of Friedmann's upper tail covert character. Feathered young of the Emerald Cuckoo are separable from young Klaas's Cuckoos as follows: they are slightly larger, and have the outer upper tail-coverts entirely green or bronzy, with at most a narrow white fringe. Klaas's juveniles are smaller and have the outer webs of the upper tail-covert feathers white. These characters are of value only in the hand. However, young Emeralds are also heavily barred below with *bronzy green*, males showing a "shadow adult" pattern with closer, greener barring on the chest, and a wash of faint yellow on the belly. Klaas's Cuckoo juveniles are usually less heavily barred, with few or no bars on the lower belly, and the lower (belly) bars are *bronzy brown*. These differences are subtle in the field, and require careful examination in a good light. In addition juvenile Klaas's Cuckoos almost invariably show a whitish ear patch which is absent in the Emerald Cuckoo. Some Klaas's show the ear patch very faintly, however. Juvenile female Emerald Cuckoos are barred brownish and bronzy-green on the crown and forehead, as are juvenile Klaas's, although some of the latter have some white on the forehead, approaching the condition in male juvenile Emeralds. Juveniles change gradually towards the adult plumage from the time of fledging, the most conspicuous change being the loss of barring on the underparts (partial or complete depending on sex).

Chrysococcyx klaas Klaas's Cuckoo

This species is widespread but rather uncommon in southern Africa. It seems to have habits similar to *Cuculus* during the breeding season: males call from a given territory, to which females come (pers. obs.).

The eggs of this species seem to be smaller than the Didric Cuckoo's, with authentic eggs showing a "product factor" (length × maximum width) always less than 270. Most eggs are probably separable by length (less than 20 mm.) or width (less than 13.5 mm.) alone, since all Didric eggs accepted in this paper have larger dimensions than these. Since at least the main hosts are quite different also, egg-only records conforming to the above dimensions, from localities or habitat ruling out the Emerald Cuckoo (*see* ranges in McLachlan and Liversidge 1957) and with well established hosts, have been accepted. The range of egg variation in *Ch. klaas* and *caprius* makes it impossible to accept egg-only records from unusual hosts.

The young bird is easily distinguished from the Didric juvenile, allowing ready acceptance of such records when outside possible Emerald Cuckoo range. Where confusion with the latter could arise, records have been carefully evaluated on the basis of substantiating evidence (usually none) and treated accordingly.

Oviduct eggs from tropical Africa have been white with red flecks, and pale greenish-blue blotched with light rufous, concentrated at the thick end. An authentic record by C. J. Vernon in Rhodesia (NRCs) described a creamy-white egg speckled with red at the thick end, indistinguishable in size and colour from the Crombec *Sylvietta rufescens* host's eggs. The identity of the parasite egg only became evident four days later, after hatching. Other authentic eggs from Cape Batis *Batis capensis* nests in the Western Cape are similar but "pinky white" rather than cream (MacLeod and Hallack 1956).

Two acceptable egg-only records from the Transvaal (NRCs) in Crombec nests give measurements of 18.8×13.5 and 20.2×12.5 mm. The eggs were white and greenish-white, with brown and slate speckles concentrated at the thick end. To two egg-only records (Friedmann 1948) from nests of the Grey Sunbird *Nectarinia veroxii* we have regretfully added a third of our own. These eggs, from Natal and Zululand, were whitish to greyish-white heavily speckled with light brown to grey-brown, and (one egg) "lighter, more blotchy than host egg" which is uniform chocolate. Measurements were 18.3–19.4×13.1–13.4 mm. These are considered acceptable on the basis of size and colour. At least one of these was in habitat not frequented by Emerald Cuckoos (low xeric sand forest), which were in any case absent from the area during a dry spring (Ndumu, November 1967). Forty-eight reliable records are analyzed in Table 7.

Table 7: *Chrysococcyx klaas*

Area	*Nestlings*	*Fledglings*	*Eggs Only*	*Biological Hosts*	*Egg Dates*	*Last Fledgling*
W.P.	6	3	2	*Muscicapa adusta* *Batis capensis* *Apalis thoracia* *Nectarinia famosa*	iii/8–iv/11	6/12
E.P.	6	11	—	*Apalis thoracica* *Nectarinia afra*	ii/7–iv/7 ii/10–ii/1	16/8* 1/2
Natal	—	1	1	*Batis molitor*	iv/11–ii/1	5/2
Zululand	~~1~~	—	2	*Sylvietta rufescens* (*Nectarinia veroxii*)	ii/10–iv/11	—
Tvl.	2	4	1	*Sylvietta rufescens* *Nectarinia mariquensis*	ii/10–iii/2	20/3
Rhod.	4	1	—	*Sylvietta rufescens* *Eremomela icteropygialis* *Nectarinia amethystina* *N. senegalensis*	iv/10–iv/11	30/12
S.W.A.	1	2	—	*Batis pririt* *Nectarinia fusca*	iii/12–iii/3	10/4

*Further work may or may not substantiate a double season.

It is difficult to designate main hosts, since these seem to vary geographically. In the south, Cape Batis *Batis capensis*, Bar-throated Apalis *Apalis thoracica* and, in the Eastern Cape, Greater Double-collared Sunbird *Nectarinia afra* are the main hosts (7, 6 and 13 records). In the Transvaal and Rhodesia the Crombec seems to be the main host (9 records). *Batis* spp. account for 10 records, *Nectarinia* spp. for 21.

Several notable omissions of published records must be explained. An account of a "Klaas's" female caught while attempting to parasitize a White-browed Sparrow-weaver *Plocepasser mahali* colony probably rests on a misidentification. The captive bird laid two white eggs on succeeding days, the measurements of which are within Didric size range and therefore larger than other eggs reported for Klaas's (Wragg 1960). Another record lists the Red-headed Weaver *Anaplectes rubriceps* as a host on the basis of an egg and a fledgling seen out of the nest (Masterson 1953). The size again places this egg in the Didric range. The fledgling subsequently seen (not necessarily the one from the described egg) could have been misidentified. Friedmann (1968) listed these hosts, but rejected the eggs from the above records as too large for Klaas's cuckoo. We do not know whether other records for these hosts were available to him. Finally a recent record (Brooke 1967) of a fledgling "Klaas's" cuckoo being fed by Puffback Shrikes *Dryoscopus cubla* has here been left out as indeterminate, since no attempt was made to eliminate possible confusion with *Ch. cupreus* (Brooke *in litt.*). In view of Vincent's (1934) record of *D. cubla* as a host of the Emerald Cuckoo in Moçambique, further substantiation is needed to establish *D. cubla* as a Klaas's host in our area. While it is not impossible that Klaas's Cuckoo in Rhodesia may lay larger eggs and parasitize hosts different from those recorded elsewhere, proof is necessary.

No accurate figures for incubation and nestling periods are available, but several records give indications. One from Rhodesia in a nest of the Scarlet-chested Sunbird *Nectarinia senegalensis* suggests approximately 11 or 12 days for incubation (NRCs). Another Rhodesian record suggests a nestling period of about 15 days (NRCs). A third from the Transvaal indicates a total nest time of not more than one month (Schmidt 1963). A hand-reared Klaas's Cuckoo in our care flew at 20–21 days.

Eviction occurs invariably in this species. The naked nestling is, like that of the Emerald Cuckoo, smaller than a Didric from the start, but it greatly resembles the latter in colouration. The bill, however, is smaller and dark, never pale yellowish or orange as in the Didric. Feathered young *Ch. klaas* are scarcely separable from young Emeralds in the field (*see* previous species). There is some variation in juvenile Klaas's Cuckoos (partly sexual?), chiefly in the amount of underpart barring, of green, of white on the forehead, and of intensity of the "ear" patch.

Chrysococcyx caprius Didric Cuckoo

This is much the commonest and best known South African cuckoo. Breeding males call and display in definite territories, to which the females presumably are attracted (pers. obs.). Usually one egg is laid per nest, but up to three have exceptionally been recorded (Pringle in Friedmann, p. 163; Jensen and Vernon, in press). Usually one host egg is removed for every cuckoo's but sometimes none are removed (Friedmann 1968, Reed 1968, NRCs). Eggs are normally laid between the first and last eggs of the host's clutch, rarely before the first and not infrequently after the last. Males are said sometimes to assist the ovipositing female with distraction displays (e.g. Zim in Friedmann, p. 162). At least four eggs form a "clutch" in this species (Friedmann 1948) although it is not known whether a given female lays more than one "clutch" per season. There is circumstantial evidence that given females are host specific as in the European Cuckoo (Friedmann p. 158–9, Plowes p. 161, Pringle p. 163, in Friedmann; Markus 1964; Ottow and Duve 1965; source data of Jensen and Vernon, in press).

Present evidence suggests that Didric eggs are always larger than Klaas's ("product factor" over 270) but further data may disprove this. They cannot be certainly distinguished from Emerald Cuckoo eggs for lack of data on the latter. The Didric's usual hosts differ from those of the other two species, however. A further complication in identifying Didric eggs lies in the facts that (1) they resemble host eggs frequently, (2) many of the ploceid hosts lay extremely variable eggs themselves (e.g. Hunter 1961); this variability even occurs *within* clutches (*see* Jensen and Vernon, in press). Accordingly, egg-only records have been rejected for the most part, but the following

categories have been allowed here, *provided* they also conform to established Didric egg measurements, and are recorded by experienced observers:

(*a*) From nests of Red Bishop-bird *Euplectes orix*, blue eggs which are larger and usually less glossy and paler than those of the host's clutch.
(*b*) From Cape Weaver *Ploceus capensis* nests, blue eggs which are smaller, paler and usually more glossy than those of the host.
(*c*) Blue eggs of the above type from nests of other well known Didric hosts, or any such eggs from areas where Emerald Cuckoos do not occur.
(*d*) Eggs of a light blue-white colour, finely speckled all over with brown, from Cape Sparrow *Passer melanurus* nests as described by Reed (1968). Such eggs are acceptable only when they differ from the other eggs in the clutch.
(*e*) Certain classes of greenish or whitish eggs speckled finely but densely all over, from nests of *Ploceus* spp. Such eggs are acceptable only when they *differ markedly* from the other eggs in the clutch in *both* size and colour. They must furthermore be out of possible *Chrysococcyx cupreus* range.

It follows that the accepted egg records will be biased towards non-matching Didric eggs, since closely matching egg-only records would either have been overlooked in the field in the first place, or rejected for the purposes of this study. In addition, numerous records lacking the detail necessary for evaluation have had to be ignored. The nestling and fledgling are distinctive and such records have been accepted even with no substantiating evidence in the case of well known hosts; for the more unusual hosts we have judged the record on the basis of any substantiation available.

There are numerous authentic egg records available for southern Africa (e.g. Hunter 1961; Markus 1961, 1964; Reed 1968). Measurements range widely, 20.0–25.1 × 13.7–16.0 mm. Colour varies from immaculate white and immaculate blue to whitish, cream, greenish or bluish variably speckled or blotched with any shade of brown. Friedmann (1968) has listed five main types and other variants known from Africa. Three main classes of Didric eggs in southern Africa match to some degree those of the three primary hosts (Jensen and Vernon, in press). Table 8 summarizes 275 authentic records available to us.

There are three main hosts in southern Africa: the Masked Weaver *Ploceus velatus* (44 records), the Cape Sparrow (62 records) and Red Bishop-bird (114 records). The Cape Weaver (25 records) is also a primary host in the areas where it occurs. Other regular biological hosts include various weavers *Ploceus* spp., and the Cape Wagtail. Friedmann (1968) and Payne (1967) give comprehensive listings including all the other recorded hosts.

Incubation and nestling periods of the Didric have yet to be agreed upon: barring Skead's (1952, and in Rowan and Broekhuysen 1962), precise observations are lacking. Incubation seemingly takes about 11 or 12 days, fledging about 20. Post-fledging dependence lasts at least three or four weeks (Reed 1968).

Eviction takes place whenever this is possible, between one and five days of age, and never in the first 24 hours (the chick is then too weak). In cases where the host's eggs hatch well before the cuckoo, eviction may be impossible for the young parasite, which may die or be raised with the host's young. According to our observations, young Didrics evict chicks preferentially to eggs at least in ploceid nests (Jensen and Vernon, in press).

The newly-hatched Didric is pink (Jensen and Vernon, in press). It may or may not have the orange-red bill colour developed at this stage. Otherwise it resembles chicks of the genus *Cuculus*, but is smaller. By 48 hours of age, it becomes largely black and the red colour of the bill deepens (occasionally the bill remains rather pale). It is immediately distinguishable from all other cuckoo nestlings by the bill colour, which persists until at least 17 days after fledging (Reed 1968). The eyes begin to open at seven days. Feathered young are distinguishable from the other *Chrysococcyx* juveniles by clear white spotting on the wing coverts (Klaas's may show a few small white flecks) and dark spots or blotches (not bars) on the whitish underparts, as well as by bill colour. The outer tail feathers are largely dark with white blotches or bars.

Table 8: *Chrysococcyx caprius*

Area	*Nestlings*	*Fledglings*	*Eggs Only*	*Biological Hosts*	*Egg Dates*	*Last Fledgling*
E.P.	21	4	4	*Erythropygia coryphaeus*	iv/10–iv/1	23/2
				Prinia maculosa		
				Motacilla capensis		
				Passer melanurus		
				Ploceus capensis		
				P. velatus		
				P. ocularis		
Natal	37	3	23	*Motacilla capensis*		
				Passer melanurus		
				Ploceus capensis		
				P. cucullatus	ii/11–ii/3	14/4
				P. subaureus		
				P. ocularis		
				Euplectes orix		
Zululand	—	1	—	*Ploceus subaureus*	i/2	6/3
Tvl.	114	18	18	*Motacilla capensis*		
				Passer melanurus		
				Ploceus capensis		
				P. cucullatus	ii/10–ii/3	14/4
				P. velatus		
				P. intermedius		
				Euplectes orix		
				E. albonotatus		
Rhod.	11	3	9	*Ploceus velatus*		
				P. xanthops	iii/12–ii/3	30/3
				Euplectes orix		
N.C. – O.F.S.	1	2	1	*Motacilla capensis*		
				Passer melanurus	iii/11–ii/3	13/4
S.W.A.	3	1	1	*Passer griseus*		
				Ploceus velatus	i/12–ii/2	14/3

DISCUSSION AND CONCLUSIONS

There are remarkably few precise breeding records for most southern African cuckoos. Much confusion between the eggs, and in some cases between the young, of many cuckoos has occurred and continues to occur. Furthermore, the inclusion of inadequately-supported records in comprehensive listings (Friedmann 1948, 1949, 1956, 1964, 1967, 1968; Payne and Payne 1967) tends to obscure much of the authentic information available.

We now discuss several important aspects of cuckoo breeding biology on which our data have a bearing.

(*a*) *Hosts*

The data here analyzed are admittedly biased on the conservative side, since records for other than well known hosts have automatically been more critically and suspiciously appraised, resulting in a "higher–than–average" rejection rate for such records. Nevertheless, these data suggest a far greater degree of alloxenia (Friedmann 1968, p. 103) than other works on African cuckoos have shown (Friedmann 1967, 1968; Payne and Payne 1967). For example, only the Dusky Flycatcher *Muscicapa adusta*, Fork-tailed Drongo and Cape Wagtail have been recorded in the capacity of biological hosts to more than one cuckoo species (two in each case, *see* Tables 1, 4, 5, 7, 8). Only the Cape Wagtail can be considered to do so regularly, and in all three cases the competitors belong to different genera.

Our host lists (in tables) bear a remarkable resemblance to Moreau's (1949) which were based on a reappraisal of Friedmann's (1948) data.

(*b*) *Host Specificity and Egg-matching*

Payne (1967), Reed (1968) and Jensen and Vernon (in press) have presented considerable evidence for the existence of *gentes* (host-specific tribes) in the Didric Cuckoo. The existence of egg-types matching different host eggs is likewise well documented in this species (above references plus Hunter 1961, Markus 1961, 1964, Ottow and Duve 1965). For other *Chrysococcyx* the position is not clear, but it seems that Klaas's Cuckoo lays matching eggs with certain hosts in at least some areas.

In *Cuculus* there seems to be strong specialization by each species on a very few hosts. In *C. solitarius*, some eggs are partly matched, while the majority are unmatched. The scanty data on the other two species suggest that their eggs are reasonably- to well-matched to their hosts'.

In *Clamator*, one species shows complete matching (size and colour), one shows partial matching with one (ancestral?) host (colour only) and the third shows no matching at all. In neither of the last two genera are *gentes* currently known from our area, but their existence is likely in some species at least.

(*c*) *Eggs and Egg-laying*

There now appears to be sufficient evidence to state that all South African *Chrysococcyx*, *Cuculus* and *Clamator* cuckoos remove host eggs when adding their own. *Clamator glandarius* seems to make frequent exceptions to this rule, however (NRCs). Usually only one egg is removed, at the time of laying, but again exceptions are frequent.

Eggs are laid in most cases during the interval when the host is completing its own clutch, but again deviations from this "normal" pattern are common. Most South African cuckoos seemingly lay one egg per nest, but up to three have been found for *Cuculus* and *Chrysococcyx*, while multiple parasitism with three or more eggs is frequent in *Clamator jacobinus* and perhaps the rule in *Cl. glandarius*. The Jacobin Cuckoo seems to lay more indiscriminately than any other, although this observation may partly reflect the ease with which its eggs are recognized.

The eggs of our cuckoos are still poorly known. Some are easy or fairly easy to recognize (most *Clamator* eggs, typical brown *C. solitarius* eggs). The greatest difficulties occur with the eggs (usually speckled) of *Cuculus* and *Chrysococcyx*. The eggs of *Pachycoccyx* and *Cercococcyx* probably also are similar to these. *Ch. klaas* seems to be distinguished by the smallest eggs, but there are some, mostly unconfirmed, reports of Didric-sized eggs for this species, and of smaller (under 20 mm. length) eggs for *Ch. cupreus* and *Ch. caprius*. At present it seems safest to disregard such unconfirmed records.

(*d*) *Laying Interval*

There is no detailed work as yet on the "clutch" size of any African cuckoos, but there is evidence on the laying interval. The larger cuckoos are generally thought to lay every second day, following the careful observations of Chance (1940) and Baker (1942). Friedmann (1948) had some evidence for two-day periods in *Cuculus solitarius* and a shorter interval in *Chrysococcyx caprius*. There is one record of a *Chrysococcyx* (*see* p. 174) which laid an egg on two succeeding days after capture, confirming the postulated 24-hour minimum interval (Baker 1942, Friedmann 1968) for this genus. It is of course well established that longer breaks in a cuckoo's laying sequence can occur (Chance 1940) and are in fact probably quite frequent under natural conditions. Ottow and Duve's (1965) findings on the Didric fit this explanation.

(*e*) *Incubation, Nestling and Post-fledging Periods*

The diversity of recorded incubation and fledging periods may be at least partly real. We have observed differing development rates of two Didrics in different host nests (Jensen and Vernon, in Press). The time of laying of a cuckoo egg with respect to the host's clutch must inevitably affect the incubation period even if all other factors are constant. Hosts with differing incubation patterns may well be responsible for part of the intraspecific variation of cuckoo incubation periods also. Furthermore, Liversidge (1961) has presented some evidence for pre-laying development in Jacobin Cuckoo eggs, an additional factor in the length of incubation.

The data on incubation, nestling and post-fledging periods are still scanty, but tentative general-

izations emerge if intrageneric variation is assumed to be minimal. These periods in *Cuculus* and *Chrysococcyx* are around 12, 20 and 20–30 days respectively. Incubation and fledging in the European Cuckoo takes 12–13 and 20 days respectively (Friedmann 1956). In *Clamator*, there appears to be a slight dichotomy, *Cl. glandarius* agreeing with *Cuculus* and *Chrysococcyx* in incubation and nestling periods, while nestlings of the other two species apparently develop faster and fly sooner (about 15–17 days?). The post-fledging period has not been determined for *Clamator* (one record of at least two weeks in *glandarius*).

(f) Nestlings and Fledglings

The similarity between naked *Chrysococcyx* and *Cuculus* nestlings (except in size) does not seem to have been sufficiently emphasized in the past. All stages have not yet been adequately described for all species, but extrapolation seems safe in the light of what is known. The nestlings are apparently always pink at first, darkening to blackish in a day or two. All have flat backs, prominent rounded, protruding nostrils, and a strong evicting instinct till the fifth day or so. Feathered young are barred in four of the six species.

Clamator nestlings also are probably all pinkish at first, but darken to brownish rather than black. They have less prominent, oval nostrils, rounder backs, and lack the strong evicting impulse (no morphological description of *Cl. levaillantii* available, however). Feathered young of *Cl. glandarius* are distinctive, but young of the other two species apparently resemble one another.

As with eggs, the greatest field identification difficulties arise within genera, but these are largely surmountable (unlike some egg problems).

(g) Breeding Seasons

It is commonly assumed that breeding seasons of the cuckoos exactly follow those of the hosts. Lack (1963, 1968) discussed the erroneous nature of this assumption for the European Cuckoo and suggested sound reasons for the non-identity of host-parasite breeding seasons. It is beyond the scope of the present paper to discuss this situation in South Africa, where far less information is available. Nevertheless, an examination of Tables 1–8, and other reports (e.g. Hoesch 1934, Reed 1968, Jensen and Vernon, in press) makes it clear that many of our cuckoos do not utilize the full length of their hosts' breeding seasons, whether because of absence on migration, or for other unknown reasons (Jensen and Vernon *op. cit.*). Our own recent observations in South-West Africa (study in progress) confirm this for at least four cuckoo species. At present we are inclined to accept Lack's (1963) food-lack theory as the most likely explanation for this phenomenon.

The *Clamator* cuckoos show the earliest and latest breeding dates (excluding Klaas's Cuckoo in the Western and Eastern Cape). Among the crested cuckoos, only *Cl. jacobinus* has sufficient data to show seasonal trends: a tendency to later records in the north and west (Table 1). *Cl. levaillantii* starts and ends much later than the other two (Table 2).

The Red-chested Cuckoo lays earlier than its congeners (earliest date 20 September), and its laying season seems to end earlier in the south than the north (Table 5). The few records for the other two *Cuculus* show only that they lay between November and February (one March record for *C. clamosus*), with the African Cuckoo perhaps ending earlier than the Black (Tables 4 and 6).

The glossy cuckoos show considerable variation in breeding season. The Didric breeds from about October to March, and the large number of records shows a trend towards slightly earlier starting dates in the south, and an earlier cessation in the Eastern Cape than further north (Table 8; *see* also Jensen and Vernon, in press). *Ch. klaas* is the only cuckoo showing winter breeding, in the southern and eastern Cape. This appears to be an adaptation to utilize winter breeding sunbirds in this area. Elsewhere, Klaas's Cuckoo seems to have a season similar to the Didric's, with perhaps a higher proportion of early summer (October–November) records.

(h) Migration

Very little is known concerning the departure dates of cuckoos in southern Africa, or of local movements within the sub-continent. The fact that juveniles tend to change rapidly towards the adult plumage not long after fledging in many if not all species makes the task of separation of adult and juvenile migration even more difficult. Local movements are not well understood either. Our own observation suggests that Didrics may be plentiful in an area one year and very scarce the

next. Corroboration comes from Pooley and Dixon (1966) who state that the populations of Klaas's and Didric Cuckoos at Ndumu fluctuate considerably from year to year; and from Hoesch (1955), who spoke of "guten Kuckucksjaren" (p. 134) in South-West Africa.

In the Cathcart district, Eastern Cape, in 1968 we found three species of cuckoos (*Clamator glandarius*, *Cuculus cafer* and *Chrysoccyx caprius*) laying their eggs till 10 January and then deserting the area entirely. Subsequently the first young cuckoos were seen out of the nest only on 16 January Skead (1951, 1952) found a similar exodus of adult cuckoos in January in the Albany district of the Eastern Cape. More recently, Reed (1968) has stated that adult Didrics probably leave his area (near Johannesburg, Transvaal) by mid-February although young of the year are present until April. We recorded Didrics in 1968 near Pietermaritzburg, Natal, laying and indulging in active courtship on 5 February; and we failed to record eggs or nestlings of Didrics as late as early December in Zululand (Jensen and Vernon, in Press) and South-West Africa (unpublished) although courting Didrics were then present at the colonies concerned. Taken together, these observations (and others) as well as the tabular data in this paper suggest that Didrics and some other South African cuckoos may lay earlier in the southern parts of their ranges, moving out of these areas by January to join other cuckoos already established further north. The "southern" cuckoos may or may not continue laying as they go. Furthermore, it seems likely that in at least the drier areas, cuckoos "invade" different localities in different years, following abundant food supplies or for other reasons. It is also clear that some if not all young leave on migration without the guidance of adults in at least some of our cuckoo species; a situation long ago proved for certain Australian and New Zealand *Chrysococcyx* (Dove 1925, Mayr 1932), and well known in the European Cuckoo (e.g. Chance 1940).

SUMMARY

Applying stringent selection criteria to ensure the use of only authentic breeding records, all such available data on breeding in southern African cuckoos was analyzed. Despite the paucity of information, some tentative generalizations emerge from the study:

1. *Cercococcyx* and *Pachycoccyx* are virtually unknown.
2. *Cuculus* and *Chrysococcyx* share many characteristics in their breeding biology, including similar developmental characters and periods, laying habits and evicting impulse.
3. *Clamator* differs in most of these characters; particularly, it lacks the true evicting instinct, and two species apparently develop faster than *Cuculus*/*Chrysococcyx*.
4. Egg matching is absent in *Cl. jacobinus*, partial in *Cl. glandarius*, excellent in *Cl. levaillantii*. In *Cuculus* it is variable (usually poor in one species, *C. solitarius*). In *Chrysococcyx* matching varies from partial to excellent, even within individual species (*klaas*, *caprius*).
5. Field identification of cuckoo eggs and young is given particular attention (text), and we conclude that intrageneric confusion is most frequent, but can be avoided in some cases involving eggs, and in most cases involving feathered young.
6. Biological hosts (hosts recorded with cuckoo young, as opposed to egg-only hosts) are listed, and we conclude that utilization of different hosts by different cuckoo species (alloxenia) is more general than previously thought.
7. The breeding season of South African cuckoos coincides with the summer rainy period, except in some winter-rain area Klaas's Cuckoo populations. As in the European Cuckoo, however, they do not utilize the full length of their hosts' breeding periods.
8. Many if not all South African juvenile cuckoos migrate well after the adults, as in the case of some Australian, New Zealand and Palaearctic species.

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REFERENCES

BAKER, E. C. STUART 1942. *Cuckoo Problems*. London: H. F. & G. Witherby.
BRADFIELD, R. D. 1931. The crested cuckoos of South Africa. *Ostrich* 2: 7–9.
BROOKE, R. K. 1967. A new host of Klaas' Cuckoo. *Ostrich* 38: 202.
CALDER, D. R. 1951. A note on the Didric Cuckoo, *Chrysococcyx caprius* (Boddaert). *Ostrich* 22: 36.
CHANCE, E. P. 1940. *The Truth about the Cuckoo*. London: Country Life.
CHAPIN, J. P. 1939. The Birds of the Belgian Congo. Pt. 2 Vol. 2 *Bull. Amer. Mus. Nat. Hist.* 75.
CLANCEY, P. A. 1968. Miscellaneous taxonomic notes on African birds 26. *Durban Mus. Novitates* 8, Pt. 13: 183–198.
CONNELL, A. 1959. Emerald Cuckoo depositing her egg in a Black-eyed Bulbul's nest. *Ostrich* 30: 140.
DOVE, H. S. 1925. Summer migrants in Tasmania, 1925. *Emu* 27: 224.
FRIEDMANN, H. 1948. *The Parasitic Cuckoos of Africa*. Washington Acad. Sci. Monogr. No. 1. Washington, D.C.
——— 1949. Additional data on African parasitic cuckoos. *Ibis* 91: 514–19.
——— 1956. Further data on African parasitic cuckoos. *Proc. U.S. Nat. Mus.* 106: 377–408.
——— 1964. Evolutionary trends in the avian genus *Clamator*. *Smithson. Misc. Coll.* 146 (4): 1–127.
——— 1967. Alloxenia in three sympatric African species of *Cuculus*. *Proc. U.S. Nat. Mus.* 124: 1–14.
——— 1968. The evolutionary history of the avian genus *Chrysococcyx*. *U.S. Nat. Mus. Bull.* 265. Washington, D.C.
HOESCH, W. 1934. Lamprocolius nitens bispecularis als Wirtsvogel von Clamator glandarius. *Ornith. Monatsber.* 42: 68–70.
——— 1955. *Die Vogelwelt Südwestafrikas*. Windhoek: S.W.A. Wissenschaftliche Gesellschaft.
——— and NIETHAMMER, G. 1940. Die Vogelwelt Deutsch-Südwestafrikas *J.f. Ornithol.* 88 Sonderheft. Berlin.
HUNTER, H. C. 1961. Parasitism of the Masked Weaver *Ploceus velatus arundinaceus*. *Ostrich* 32: 55–63.
INGLE, A. P. 1912. Cuckoos as nest robbers. *Emu* 11: 254–255.
JENSEN, R. A. C. and VERNON, C. J. (in press). On the biology of the Didric Cuckoo *Chrysococcyx caprius* in southern Africa. *Ostrich*.
JUBB, R. A. 1952. Some notes on birds of Southern Rhodesia. *Ostrich* 23: 162–164.
LACK, D. 1963. Cuckoo hosts in England (with appendix by T. Royama). *Bird Study* 10: 185–202.
——— 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen & Co.
LIVERSIDGE, R. 1955. Observations on a Piet-my-vrou and its host, the Cape Robin. *Ostrich* 26: 18–27.
——— 1961. Pre-incubation development of *Clamator jacobinus*. *Ibis* 103a: 624.
MCLACHLAN, G. R. & LIVERSIDGE, R. 1957. Roberts Birds of South Africa. Johannesburg: C.N.A.
MACKWORTH-PRAED, C. W. & GRANT, C. H. B. 1962. Birds of the southern third of Africa. Vol. 1. London: Longmans, Green and Co.
MACLEOD, J. G. R. & HALLACK, M. 1956. Some notes on the breeding of Klaas's Cuckoo. *Ostrich* 27: 2–5.
MARKUS, M. B. 1961. Diederik cuckoo eggs in Masked Weaver's nest. *Bokmakierie* 13: 33.
——— 1964. Egg polymorphism in the Diederik Cuckoo (*Chrysococcyx caprius* (Boddaert)) at Pretoria. *Ostrich* 35: 123.
MASTERSON, H. B. 1953. Klaas' Cuckoo (*Chrysococcyx klaas*) parasitizing Red-headed Weavers (*Anaplectes rubriceps*). *Ostrich* 24: 51.

MAYR, E. 1932. Birds collected during the Whitney South Sea Expedition. Pt. 19, Notes on the Bronze Cuckoo *Chalcites lucidus* and its subspecies. *Amer. Mus. Novitates* 520: 1–9.
MOREAU, R. E. 1949. Special Review. Friedmann on African Cuckoos. *Ibis* 91: 529–537.
MOUNTFORT, G. 1968. *Portrait of a Wilderness* (2nd Edition). England: David & Charles.
NEETHLING, J. H. 1968. In "Letters" (to the Editor). *Bokmakierie* 20: 50.
———1969. Ibid. *Bokmakierie* 21: 48.
NEUBY-VARTY, B. M. 1948. Some nests and eggs. *Ostrich* 19: 158–160.
OATLEY, T. B. (in press). Robin hosts of the Red-chested Cuckoo in Natal. *Ostrich.*
——— & PINNELL, N. R. 1968. The birds of Winterskloof, Natal. *S. Afr. Avifauna Ser. No.* 58. Cape Town: Percy FitzPatrick Inst.
OTTOW, J. & DUVE, G. 1965. Zur Kenntnis der Fortflanzung von *Chrysococcyx caprius* and *Cuculus canorus gularis* in Süd Africa. *J. f. Ornithol.* 106: 431–439.
PAYNE, R. B. 1967. Interspecific communication signals in parasitic birds. *Amer. Natur.* 101: 363–375.
———& PAYNE, K. 1967. Cuckoo hosts in southern Africa. *Ostrich* 38: 135–143.
PITMAN, C. R. S. 1957. On the egg of the African Cuckoo *Cuculus canorus gularis* Stephens. *Bull. B.O.C.* 77: 138–139.
PLOWES, D. C. H. 1948. Young African Coockoo in Drongo nest. *Ostrich*: 99–100.
POOLEY, A. C. & DIXON, J. E. W. 1966. A check-list of the birds occurring in the Ndumu Game Reserve in northern Zululand. *S. Afr. Avifauna Ser. No.* 39. Cape Town: Percy FitzPatrick Inst.
REED, R. A. 1968. Studies of the Diederik Cuckoo *Chrysococcyx caprius* in the Transvaal. *Ibis* 110: 321–331.
——— 1969. Notes on the Red-chested Cuckoo in the Transvaal. *Ostrich* 40: 1–4.
ROBERTS, A. 1939. Notes on the eggs of parasitic birds in South Africa. *Ostrich* 10: 1–20.
ROWAN, M. K. & BROEKHUYSEN, G. J. 1962. A study of the Karoo Prinia. *Ostrich* 33: 6–30.
SCHMIDT, R. K. 1963. Marico Sunbird *Cinnyris mariquensis* as host of Klaas's Cuckoo *Chrysococcyx klaas. Ostrich* 34: 176.
SKEAD, C. J. 1951. Cuckoo studies on a South African farm (Part I). *Ostrich* 22: 163–175.
——— 1952. Cuckoo studies on a South African farm (Part II). *Ostrich* 23: 2–15.
——— 1962. Jacobin Crested Cuckoo *Clamator jacobinus* (Boddaert) parasitising the Fork-tailed Drongo *Dicrurus adsimilis* (Bechstein). *Ostrich* 33: 72–73.
———1967. *Sunbirds of Southern Africa*, etc. Cape Town: A. A. Balkema.
VERNON, C. J. (in prep.). New host species for three cuckoos. *Ostrich.*
VINCENT, J. 1934. The birds of northern Portuguese East Africa. Pt. 5. *Ibis*, ser. 13, Vol. 4: 757–99.
WOODARD, A. E. & MATHER, F. B. 1964. The timing of ovulation, movement of the ovum through the oviduct, pigmentation and shell deposition in Japanese Quail (*Coturnix coturnix japonica*). *Poultry Sci.* 43: 1427–32.
WRAGG, D. A. 1960. *Rhodesian Orn. Soc. Bull.* 30:2.

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ON THE BIRDS OF THE SANDVELD KALAHARI OF SOUTH WEST AFRICA

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This is the report on the sixth Percy FitzPatrick Institute of African Ornithology expedition to South West Africa. Analysis of avian distribution in that country showed that by far the least-known part of it was along the eastern border, in what has been called the Sandveld Kalahari (McLachlan & Liversidge, 1957; Winterbottom, 1966a). Our 1968 expedition was accordingly planned to investigate this area. Several previous expeditions had traversed the road from Windhoek via Gobabis to Fort Rietfontein, *en route* to Ghanzi, in western Botswana (de Schauensee, 1931; Roberts, 1936; Macdonald, 1957) but the investigations had been superficial and no work had been done elsewhere in the Sandveld in South West Africa, though the much larger extent of this habitat in Botswana had been well covered by Smithers (1964).

Professor and Mrs. Winterbottom, with the Rondevlei taxidermist Mr. Nathaniel August, left Cape Town on 23 November 1968 and travelled via Springbok, Mariental and Stampriet to Gobabis, where they were joined on the 17th by Mr. P. N. F. Niven and proceeded to the farm Sturmfeld, some 65 miles north of Gobabis. They remained there until 2 December, when they moved to Sindi, about 70 miles south of Gobabis. The last camp, at De Waal, 8 miles north of Leonardville, was reached on 7 December. Mr. Niven left for home on the 9th via Auros and Matamata and the rest of the party on the 12th by the same route as they had come, arriving back in Cape Town on the 14th. (*See* Fig. 1).

Owing to circumstances into which it is unnecessary to enter, the expedition was very short of ammunition, especially 410 ammunition, and our collecting was consequently severely limited except for those species which could be caught in mistnets. However, we managed to secure examples of most of the critical species, such as the larks. A selection of the skins was sent to the State Museum, Windhoek, and the rest are in the South African Museum, Cape Town.

In the systematic list, I have included all species reported from the Sandveld Kalahari in South West Africa, whether recorded by us or not. Apart from the published sources mentioned in the first paragraph and Hoesch & Niethammer (1940), I have used information given me by the Tölkens (father, mother and two sons) in respect of Sturmfeld, and by Mr. Kolberg in respect of Sindi. There are also a few Sandveld records in Prozesky's paper (1963).

The present expedition took place much later in the year than any of the others except the second. This had the big advantage that most of the Palaearctic migrants had arrived and enabled us to fill in gaps in the recorded distribution which would have been impossible two months earlier. The most abundant of these migrants were *Merops apiaster*, *Apus apus*, *Hirundo rustica*, *Muscicapa striata*, *Phylloscopus trochilus* and *Lanius collurio*. A number of African migrant species, chiefly cuckoos, were also met with.

The total number of species we recorded for the Sandveld (i.e., between Mariental and Sturmfeld) was 143, of which 31 were recorded from this section of South West Africa for the first time. One hundred-and-thirty-six specimens of 52 species were collected.

In discussing bird distribution in South West Africa previously (Winterbottom, 1966a), I commented that "information about the Sandveld Kalahari is particularly inadequate". This, largely owing to the present expedition, is no longer so true as it was and it is now possible to examine the relationships of the Sandveld avifauna on the basis of South West African records alone, without supplementing them from Botswana. In this comparison, I have omitted water-birds and raptors, which are nearly all too wide-ranging to contribute useful data. If this is done, the Coefficient of Community between the Sandveld and Damaraland is only 53.9; but this is entirely due to the much greater richness of the latter fauna. Simpson's Coefficient (number of species in common x 100 ÷ number of species in the Sandveld fauna) is 98.5, indicating that the Sandveld fauna is merely an impoverished version of that of the plateau to the west. This confirms the results of my previous analysis, in which the Coefficient of Community was 51 and Simpson's Coefficient 90.