INDIVIDUAL LAYING HISTORIES AND THE CLUTCH SIZE AND NUMBERS OF EGGS OF PARASITIC CUCKOOS

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When he discovered a Cuckoo (*Cuculus canorus*) on the Worcestershire Common in 1918, Edgar Chance began a series of detailed field observations revealing that parasitic Cuckoos lay many eggs. Nearly all of the nests containing Cuckoo eggs that were found during several breeding seasons were nests of the Meadow Pipit (*Anthus pratensis*). Worcestershire Common was surrounded on three sides by woods, and the nearest neighboring group of Meadow Pipits was 3 miles away. The isolated nature of the local habitat made it possible for Chance to find all of the eggs laid by Cuckoos on the common (Chance 1922, 1940). By making careful daily observations on his study area over several years, Chance found that a single Cuckoo may lay 11–25 eggs in a season. However, because he collected the clutches as they were parasitized, causing the pipits to nest again, the Cuckoo had perhaps a higher than normal number of nests to lay in than did most Cuckoos in this area. Besides collecting eggs, Chance also provided a dummy nest to promote Cuckoo egg laying (Chance 1922:66). Observations in other areas with less disturbance led Chance to suggest that Cuckoos more often lay 10–15 eggs in a season. Because of disturbances made in his main study, some have questioned whether parasitic cuckoos really do normally lay more eggs than their nesting relatives.

Other studies on egg laying by parasitic cuckoos have involved less disturbance but also less effort on the part of observers to find all of the nests in any one local area. Thus some of the more recent estimates of the numbers of eggs laid by cuckoos each season have been considerably lower (Blaise 1965; Dieselhorst 1955; Labitte 1958; Warncke and Wittenberg 1958). The lower figures have been selected by von Haartman (1971) as more valid, apparently just because they were obtained more recently. The unreliability of some reports (especially those of Baker 1942) is due to the use of collections of eggs that did not contain either random samples of those of locally nesting birds, or eggs that were properly identified to species in areas where several species of parasitic cuckoos coexist. Also, egg collections were divided into their "clutches" at convenient times years after collecting, with little regard to any original data (W. R. P. Bourne, pers. comm.). While these facts make doubtful the validity of certain reports on the number of eggs laid by parasitic cuckoos, other reports are more reliable and are discussed later.

Direct observation of egg laying by cuckoos is difficult. A cuckoo usually lays only a single egg in any one nest of a host, and a female cuckoo ranges widely. In the absence of individually marked cuckoos, or cuckoos recognizable by their color patterns or vocalizations (Chance was able to recognize one of his females), most observers have attempted to determine the area over which a female ranges by plotting the location of the eggs the female lays. It has been assumed that the eggs laid by an individual female are sufficiently distinctive to permit our identification of all her eggs ("Gleiche Weibchen, gleiche Eier," Rey 1892:37). The technique is valid in principle; but it is difficult to find (1) all possible host nests; (2) the eggs a female may lay in nests of alternate hosts; or (3) eggs laid in unsuitable nests when her usual host species is not laying. Also, if two females lay eggs with very similar colors and spots, it might be impossible to be certain that all eggs laid in an area were laid by only one female. From studies by Blaise (1965) in which he ascribed eggs with different markings and colors to different females, it appears that the laying ranges of females sometimes overlap.

Another method of finding the number of eggs of a female was first applied by E. Jenner (1788) in his important pioneer studies of parasitic cuckoos. He wrote (pp. 232–233): "That the Cuckoo actually lays a great number of eggs, dissection seems to prove very decisively. Upon a comparison I had an opportunity of making between the ovarium, or racemus vittelorum, of a female Cuckoo killed just as she had begun to lay, and of a pullet killed in the same state, no essential difference appeared. The uterus of each contained an egg perfectly formed, and ready for extrusion; and

the ovarium exhibited a large cluster of eggs gradually advanced from a very diminutive size, to the greatest the yolk acquires before it is received into the oviduct. The appearance of one killed on the third of July was very different. In this I could distinctly trace a great number of the membranes which had discharged into the oviduct . . . The ovarium still exhibited a cluster of enlarged eggs . . . I would not be understood . . . to advance that every egg which swells in the ovarium . . . is brought to perfection; but it appears clearly, that a bird . . . can either retard or bring forward her eggs. . ."

In the present study the laying patterns through time were determined for parasitic cuckoos by examining the ovaries and oviducts of birds collected in the field. Microscopic examination of the gross ovaries and of serial sections of the ovaries of birds permits counts and age determination of the postovulatory follicles, the ovarian remnants of the eggs that have recently ovulated, for about 2 weeks after each egg has been laid (Payne 1965, 1966, 1969a). The information on laying in this study is more accurate than that of most previous workers because no eggs ovulated and laid within this time have been overlooked; the technique is limited mainly by the fact that the postovulatory follicles can be identified with certainty for little more than 10 days. Seasonal reproductive output by female cuckoos was determined from the short-term laying rates and from the duration of the local laying seasons of the cuckoos in the populations sampled.

MATERIALS AND METHODS

Most cuckoos in the sample of 103 females of the nine species collected were shot during the 1965–66 and 1966–67 breeding seasons in southern Africa. Additional birds were shot or netted in Kenya, Nigeria, and Zambia in 1967, 1968, and 1972. The ovaries and oviducts were examined briefly and fixed in 10% neutral buffered formalin in the field, usually within 5 min of the time the birds were shot. The preserved ovaries were later examined under a dissecting microscope. Postovulatory follicles and the larger growing follicles and atretic follicles were identified and measured. Postovulatory follicles were recognized as yellowish, bag-like, elongated or folded structures in which a slit (the site of ovulation) was visible. The ovulation slit or stigma in the smaller, older postovulatory follicles was usually occluded with a plug of yellowish or creamy material. Atretic follicles were identified as opaque follicles of round shape but with irregularities, and growing follicles were the normal, rounder follicles of various sizes. Most ovaries with two or more evident postovulatory follicles were then embedded in paraffin, serially sectioned at 6 μ or 8 μ, and stained with hematoxylin and eosin. Approximately 60,000 serial sections were examined microscopically for structural continuity of the different postovulatory follicles and for histological characteristics that allowed each postovulatory follicle to be aged. Criteria for identification of postovulatory follicles in serial sections were the presence of an ovulation slit through the thecal layers and the ovarian epithelium, absence of yolk in the lumen, folds in the thecae, and the generally irregular shape of the follicle and its lumen. These characteristics are useful in distinguishing postovulatory from atretic follicles in bird ovaries (Davis 1942; Payne 1966; Erpino 1969; Parmelee and Payne 1973). Because the postovulatory follicles regress rapidly during the incubation period, they are distinguishable from atretic follicles only for about 10–12 days after ovulation (Payne 1966; Erpino 1969); small follicles of apparent older ovulation were disregarded.

A second estimate of the number of eggs laid was made by recording the stage of development of the egg in the oviduct of each female and the proportion of birds with an oviduct egg. The proportion of female cuckoos with eggs in the oviduct on day 1 and day 2 after ovulation was interpreted to indicate the proportion of days on which a typical female cuckoo ovulated or laid its eggs. Numbers of eggs laid in a series, or "clutch," were determined from follicles showing ovulation on successive or alternate days.

It is of interest to compare the number of eggs laid in each series in the parasitic cuckoos because clutch size in nesting birds varies in a highly adaptive manner and has apparently coevolved with behavior of the parents in rearing their young (Lack 1954; Klomp 1970). Parasitic cuckoos usually lay only one egg of this "clutch" in any one host nest. Use of the term "clutch" among poultry workers refers to the number of eggs laid in a series separated in time (often only by a day) from other series of daily layings. Even among birds that normally lay a certain number of eggs and then incubate them, removal of the eggs at the beginning of laying often results in the bird laying its normal "clutch" size again and again in repeated cycles with intervals of a few days of nonlaying between these series (Klomp 1970:5). As seen below in the individual laying histories, parasitic cuckoos also tend to lay their eggs in irregularly repeating cycles in a similar manner. As the usual laying interval of these cuckoos is every 2 days, rather than one, the term "clutch" is used here to refer to the successive eggs laid by the parasitic cuckoos on successive or alternate days; these laying cycles are separated by 2 or more successive days of no laying. In this way, the number of eggs laid in a series or "clutch" by the parasitic cuckoos may be compared with the number of eggs in a series giving rise to a brood in nesting birds that rear their own young.

To estimate the total number of eggs that a female cuckoo lays during a year, the number of eggs laid per week was cumulated over the total breeding season. The timing and duration of the breeding season in each of the study areas were obtained from the local nesting dates of the cuckoos, from my own observations, and from other breeding tallies. This estimate is based in part on the assumption that females lay at a continual rate through their breeding seasons, and this is supported by the constant high proportion of laying females through their breeding period. Cuckoos may lay for only part of the laying season of their hosts, so attention was focused on the laying seasons of the parasites not of their hosts.

This study assumes that each postovulatory follicle of a cuckoo corresponds to a single egg laid and

that each egg laid leaves behind a postovulatory follicle. In birds, functional, ovulating follicles are normally monovular; polyovular follicles are known only in a few parthenogenetic domesticated forms (van Tienhoven 1968) and in some wild birds with some atretic follicles in regressing ovaries at the end of a breeding season (Payne 1965, unpubl. observ.). The only common route of ovulated, large yolks is down the oviduct, there to be encased in albumen and shell before oviposition or laying. Occasionally, perhaps, a large, yolky oocyte may ovulate into the body cavity and there the ectopic yolk may be resorbed. However, I have seen a loose yolk in the body cavity in only one bird (not a cuckoo) and the "ovulated" yolk proved, upon close examination, to be enclosed within its follicle wall, which was severed at the point of attachment to the ovary. Gross and histological examination of cuckoo ovaries showed no instances of binovular or polyovular ovarian follicles.

It is also assumed that the postovulatory follicles of parasitic cuckoos regress rapidly like those of nesting birds. In all birds studied to date, the postovulatory follicles do regress rapidly after ovulation and shrink in size from about half the length of the mature, unovulated follicle to 1–2 mm within 2 weeks. Birds collected through the breeding season, or shot from nests with aged eggs or young, show rapid regression of the postovulatory follicles with total disappearance of macroscopically visible, ruptured follicles from 8 to 20 days after ovulation. This is true in domestic fowl (Pearl and Boring 1918; Floquet and Grignon 1964), Ring-necked Pheasants (*Phasianus colchicus*) (Kabat et al. 1948), Rock Doves (*Columba livia*) (Dominic 1959), corvids (Erpino 1969), and icterids (Payne 1966, 1969a). Serial histological sections of the ovaries of these same birds show that the postovulatory follicles become microscopically indistinguishable from some atretic follicles after 2 weeks. Occasionally, it has been claimed that postovulatory follicles of some birds may remain for a few months (Sleptsov 1948), or from year to year (Wynne-Edwards 1939; Dalke 1963), but these claims have not been supported by study of individual birds whose breeding history was also followed. Thus the conclusion of long-term persistence of the follicles is probably incorrect. In contrast, the postovulatory follicles of mammals and many reptiles usually persist for a few weeks, during which time they secrete hormones and are functional corpora lutea (van Tienhoven 1968).

To determine whether cuckoos undergo follicular regression similar to that in other birds, ovaries of three breeding Yellow-billed Cuckoos (*Coccyzus americanus*), collected in southern Oklahoma, were examined and serially sectioned. This species of cuckoo is known to lay its eggs sometimes on successive days and sometimes at less frequent intervals within a single clutch (Bent 1940:57). One (RBP #5015) had a hard, blue egg in the oviduct and three postovulatory follicles (5.8, 3.1, and 2.3 mm) which I judged histologically (compared with ovaries of icterids, see Payne 1966) to be 1, 2, and 4 days postovulatory. The other two cuckoos were shot from nests with young. One nest (5017) contained an egg and four young with their eyes open but with few visible pinfeathers. In the other nest (5016) were one egg and two nestlings with many pinfeathers; a week earlier this nest had four eggs. By their stage of development, the young in these nests were 4–6 days old; incubation takes 10 or 11 days in the species (Bent 1940; Hamilton and Hamilton 1965). Serial sections of ovary 5017 showed four postovulatory follicles that were barely recognizable. The lumen and the ovulation slit were entirely occluded by macrophages and degenerating sloughed, granulous cells. A fifth follicle seen was a questionable postovulatory follicle. Sections of ovary 5016 revealed many degenerating follicles of variable appearance but none that could be identified positively as postovulatory. These results indicate that postovulatory follicles of these cuckoos shrink rapidly and are recognizable for about 2 weeks after which they have regressed beyond the point of recognition by standard histological criteria. Further justification for use of the histological criteria for recognition of postovulatory follicles may be found by comparing the results of Davis (1942) and Payne (1966); the South American cuckoos examined by Davis showed no difference in their ovarian histology from the North American icterids. Because of the agreement in results in these various studies, it seems reasonable that the rapid regression of the postovulatory follicles, and the histological characteristics used to age them up to about 2 weeks, may be applied appropriately to the parasitic cuckoos.

It was possible in some instances to predict that the larger, yolky follicles in the ovary of a breeding parasitic cuckoo would ovulate within a few days, because in most birds that have been examined, the number of large, yolky follicles that develop in a nesting cycle corresponds to the number of eggs in the clutch (e.g., Paludan 1952; Payne 1969a; Kern 1972). A few birds may have a large, yolky follicle in the ovary after they have completed their clutches, but these follicles are generally less than half the diameter of the mature follicles (Cuthburt 1945; Brockway 1968). Nesting cuckoos sometimes do have large, yolky follicles that are likely to be ovulated within a few days. *Coccyzus americanus* 5017, taken from a nest with 4-day young, had two large, yolky follicles measuring 7.0 and 5.8 mm, but these proved to be histologically atretic with pycnotic granulosa cells and with some extruded yolk in the surrounding theca. The other female cuckoo with young had no follicles larger than 3.7 mm. Perhaps the large follicles of the former cuckoo had developed as insurance that the bird could renest quickly if its eggs were lost by late incubation. The follicle sizes of *Coccyzus* suggest that cuckoos that are not laying do not have large, growing, yolky follicles, and therefore it is likely that when large, yolky, nonatretic follicles do occur they will be ovulated within a few days. However, because the one female cuckoo did have large follicles while she was rearing young, I have been conservative about interpreting future ovulation in parasitic cuckoos.

Few studies have attempted to determine whether the number of postovulatory follicles is in exact agreement with the number of eggs in the nests of the same individual birds. Little supporting data from population studies are available, probably because histological sectioning and examination of each ovary is time-consuming and reproductive effort can be determined much more rapidly and simply by examining the nest of a laying or incubating bird. Davis (1958) has examined serial sections of the ovaries of Starlings (*Sturnus vulgaris*) trapped in nest boxes and found good agreement between the mean number of eggs in the nests (4.22) and the mean number of

postovulatory follicles in the ovary (4.38). He found discrepancies in some individual birds for several possible reasons: (a) the bird caught at the nest was not the mother; (b) the birds were examined after their postovulatory follicles had regressed (this is likely in Davis's study especially in his female 922; she was feeding young when she was collected for examination); (c) some individuals had laid in more than one nest; (d) eggs were oviposited outside the nest; and (e) eggs in the nest were lost by interference from predators or other Starlings. In studies of Ring-necked Pheasants, the number of postovulatory follicles corresponded well with the number of eggs known to have been laid (Buss et al. 1951; Kabat et al. 1948). Herring Gulls (*Larus argentatus*) collected during incubation had the same number of postovulatory follicles in their ovaries as eggs in their nests (Paludan 1952). Incubating female Red-winged Blackbirds and Tricolored Blackbirds (*Agelaius phoeniceus* and *A. tricolor*) shot from their nests had the same number of postovulatory follicles as eggs in the nest in all but one instance. The exception was an *A. phoeniceus* with one more postovulatory follicle than egg in the nest; but the nest also had an egg of a Brown-headed Cowbird (*Molothrus ater*), and the cowbird had evidently removed an egg of the blackbird (Payne 1969a). I have collected females of 18 species of birds—including several taxonomic orders—while they were incubating or feeding small young, and in all of these the number of postovulatory follicles has agreed with the number of eggs in the nest. Although there have been few population studies of wild birds that have included examination of the ovarian follicles, in all studies that have been done the number of postovulatory follicles is in good agreement with the number of eggs that a bird lays, and the exceptions do not reflect unfavorably upon the technique of determining laying rates from the ovaries. The technique has long been used for certain mammals such as whales (Harrison 1969), and it has been used with success in reptiles (D. W. Tinkle, pers. comm.).

RESULTS

The laying histories as seen in the ovaries of the cuckoos examined are described graphically. These pictorial histories give the results of temporal patterns of laying and the number of eggs laid in a series for the cuckoos. The growth and regression of ovarian follicles before and after ovulation are shown for some species. Seasonal reproductive rates are interpreted from these samples and from other published works. For the first species, the Diederik Cuckoo (*Chrysococcyx caprius*), the reasoning behind the interpretation of these histories is described in some detail, and for later species the results are interpreted more directly. An example of the histological evidence used in determining the reproductive rates of parasitic cuckoos is given for a Jacobin Cuckoo (*Clamator jacobinus*) in figure 6.

CHRYSOCOCCYX, THE GLOSSY CUCKOOS

Samples were obtained for three of the four African species of glossy cuckoos: the Diederik Cuckoo (*Chrysococcyx caprius*); the Klaas Cuckoo (*C. klaas*); and the Emerald Cuckoo (*C. cupreus*). The glossy cuckoos are the smallest of the African cuckoos; they parasitize a variety of hosts including mainly ploceids and a few other open-country birds (*C. caprius*), small songbirds of open woodland (*C. klaas*), and small songbirds of evergreen forest and thicket (*C. cupreus*) (Payne and Payne 1967; Friedmann 1968; Jensen and Jensen 1969). The fourth glossy cuckoo in Africa (*C. flavigularis*) lives in equatorial evergreen forests and is rarely seen. Because field work was more readily carried out by being able to see the cuckoos in open country, most effort in the present study was concentrated on the open-country species, *C. caprius*. All three species have a similar body size and similar eggs.

CHRYSOCOCCYX CAPRIUS

The largest sample of Diederik Cuckoos taken at any one locality was one of 14 birds at Thorn Grove farm, Waqu Valley, 12 km N of Cathcart, Cape Province, where the habitat was mainly scattered acacia trees and shrubs. Other samples were taken at Committees, Adelaide, and Amanzi in the eastern Cape; Brits, Pretoria-Noord, Lunsklip, Marble Hall, Louw's Creek, and Hans Merensky Nature Reserve in the Transvaal; Sabi Valley Experimental Station and 12 km SE of Salisbury in Rhodesia; Magadi and Kisumu in Kenya; and Zaria in Nigeria. Laying histories of the individual cuckoos, as seen in their ovaries, are shown in figures 1 and 2.

Laying intervals. Laying intervals determined from histological appearance of the follicles indicate that *caprius* lays on alternate days, although sometimes eggs may be laid at longer intervals (3782, 4679). In the few instances where the interval was 1 or 2 days (as in 4204), the larger follicle appeared to be intermediate in tissue degeneration between these days, as aged by comparing ovaries of the cuckoos with the ovaries of nesting icterids (Payne 1966). Sometimes the cuckoos ovulated a single egg with no other egg laid within 3 days (3782, 3991); when this happened, there were sometimes atretic follicles at an apparent similar stage of thecal regression. Perhaps in these birds several follicles enlarged but only one then ovulated while the others became atretic and degenerated.

Laying intervals of 2 days were also estimated by comparing the stage of development of the egg in the oviduct of laying birds. As the cuckoos were sampled at all times of day

TABLE 1. Time of egg formation and laying in *Chrysococcyx caprius*.

Time of day	Stage of laying cycle			
	Ovulating	Soft egg	Semihard egg	Pigmented hard egg
05:00–08:00		3 (05:45–07:30)		1 (07:45)
08:00–10:00		2	1	3
10:00–12:00		1	2	
12:00–14:00			1	1
14:00–16:00	1			1
16:00–19:00		1	1	4

(05:45–18:00) and showed no synchronization in their stage of development at any time (table 1), the proportion of oviduct eggs that were hard provides an estimate of the proportion of time that eggs are carried in the duct after they are fully formed with hard shells. Of the 27 birds with oviduct eggs, 8 had eggs with shells completely calcified and pigmented; soft-shelled eggs were leathery or papery in texture and lacked spotted pigment. Because a third of the birds with eggs had hard eggs, it is likely that *C. caprius* may carry the fully formed eggs ready for laying for half a day or more after the egg has been formed.

Time of laying. Cuckoos were taken with eggs in all stages of development at all times of day (table 1). The process of egg formation in birds generally takes less than 6 hr from ovulation to the beginning of shell secretion in the oviduct (Romanoff and Romanoff 1949); shell calcification and pigmentation is completed in less than a day. Egg development was not in phase at any time of day; the cuckoos evidently may ovulate at nearly any time from before sunrise (one bird had a soft egg at 05:45) until late afternoon (one was ovulating with the egg just entering the upper end of the oviduct at 15:20). Cuckoos with hard eggs were taken from 07:45 to 18:00. These birds had most likely ovulated on the previous day, since generally at least 16 hr are required for eggshells to be calcified and pigmented. Based on the observation that most of the postovulatory follicles exhibited histological evidence of ovulation on alternate days, it appears that hard eggs are usually not carried in the duct for more than a day before they are laid.

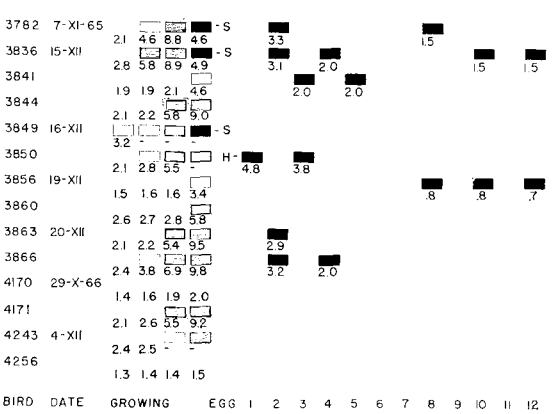

FIGURE 1. Recent laying histories of *Chrysococcyx caprius* at Cathcart "Thorn Grove" farm, eastern Cape Province, South Africa, in 1966. Diameters of the four largest (α-δ) growing ovarian follicles are given. Small yolky follicles yellowish in color but smaller than 5 mm are indicated by open figures, large yolky follicles 5 mm or larger by shaded figures. Shaded figures indicate follicles regarded as very likely to ovulate. Postovulatory follicles are black figures with maximum follicle length (mm) indicated. S = soft egg, H = hard-shelled egg in oviduct; the bar indicates the corresponding postovulatory follicle.

None of the laying *C. caprius* had more than one egg in the duct, so it is likely that the hard egg is laid before the next egg is ovulated, as in other birds (van Tienhoven 1968). In some birds ovulation follows within an hour of laying of the previous day; ovulation is inhibited until the egg is laid (Nalbandov 1959; Romanoff and Romanoff 1949). Thus, the occurrence of soft eggs in all stages of development suggests that the hard eggs of the previous ovulation may be laid nearly any time of day. It is possible, however, that late afternoon laying may not be followed by ovulation of the next egg until the following morning. This manner of photoperiodic control of ovulation has been described for domestic fowl (Nalbandov 1959). Perhaps such inhibition during late afternoon would account for the greater number of soft-shelled eggs before 08:00 in table 1.

Rate of Laying. The first estimate of laying rate is based on the proportion of birds with an egg in the duct. Half (20) of the 40 females in the total sample had an egg, but since half of these eggs were hard and since eggs are laid on alternate days, only 10 of the 40 females would lay on any given day. From this it seems likely that a female would lay, on the average, 7 × 0.25 or 1.75 eggs per week in the breeding season.

The second estimate of laying rate is based

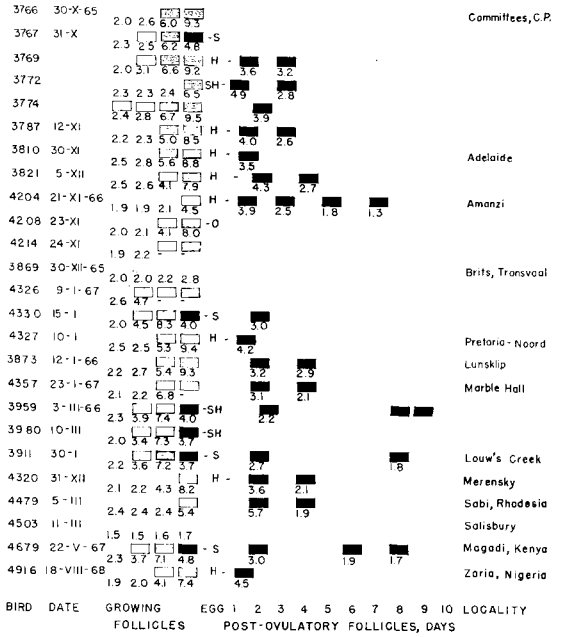

FIGURE 2. Laying histories of additional female *Chrysococcyx caprius*. Symbols and numbers are coded as in fig. 1. O = ovulating (yolk engulfed by infundibulum of oviduct but still inside ovarian follicle), S = soft egg (including albumen and sometimes uncalcified shell membranes), SH = semi-hard egg (incomplete calcification of shell membranes), H = hard egg (shell calcified and pigmented). Also collected were two females on 6 and 12 June 1967 at Kisumu and Magadi, Kenya; both had all follicles less than 1 mm and both were molting.

on the laying histories of the birds in figures 1 and 2. The 40 females had ovulated a total of 54 eggs in 10 days, an individual average of 1.35 eggs per 10 days or about one egg per week. Counting only the eggs ovulated over a week (that is, excluding the 8- to 10-day follicles, which are more difficult to distinguish in histological sections) gives an estimate of 1.23 eggs per week.

The laying rate estimated for a single population is similar to that for the total sample of cuckoos. The sample of 10 females at Cathcart in 1965 (a "normal" year in which local resident farmers M. Beal-Preston and A. R. Dick estimated rainfall to be only somewhat less than usual) had ovulated 13 eggs in the week before collection, giving an estimate of 1.3 eggs per female per week. In this same subsample 4 of the 10 cuckoos had an egg in the duct, indicating 1.4 eggs laid per week by an average female.

Individual females are thought to maintain about the same rate of laying throughout their local breeding season because the proportion of laying females remained nearly the same from the early to the late birds in the sample

TABLE 2. Clutch size in *Chrysococcyx caprius*.

	Frequency distribution of number of eggs in series						
	1	2	3	4	5	Mean	Sample *N*
Completed clutches	2	4	1			1.63	8
Current clutches (including growing follicles >5 mm		4	13	7	1	3.12	25

and because this proportion was consistently high (greater than half) (figs. 1, 2).

Number of eggs in a series or clutch. Glossy cuckoos usually lay only one egg in each parasitized host nest (Friedmann 1968), so each egg in a series or clutch laid by a cuckoo is laid in a different nest. Clutch size was determined in two ways. The first was the count of postovulatory follicles that were histologically identified as resulting from ovulations on successive or alternate days (see figs. 1, 2). Because the cuckoos frequently ovulate at intervals of 2 days, these clutches were known to have been completed only for the series in which the most recent ovulation was 3 or more days before collection, or for those more current ones in which there was no likelihood of additional eggs being laid within 2 days of the most recently ovulated follicle, that is, in ovaries lacking large, growing, yolky follicles. Counts of these completed clutches are summarized in table 2.

A second estimate of clutch size involved adding the large, yolking follicles in the ovary to the number of eggs already ovulated in a clutch currently being laid. The rationale for adding these developing yolks was that in most birds the number of eggs ovulated in a clutch corresponds to the number that develop large, yolky deposits in the ovary. Some birds develop slightly enlarged, yolky follicles at the beginning of laying and then may resorb them after the normal number of eggs has been laid, but if the first egg laid is removed from the nest, these yolky follicles continue to develop. Continual removal of eggs results in continued production of follicles and continued laying of eggs in these "indeterminate layers" (Paludan 1952; Klomp 1970). The mechanism whereby nesting indeterminate-laying birds continue to develop the ovarian follicles or begin to resorb them is thought to be provided by tactile or visual feedback from the number of eggs perceived in the nest. The parasitic cuckoos may be "indeterminate layers" in the sense that the number of eggs ovulated in a single clutch is not determined simply by a predetermined number of follicles that enlarge in the ovary (as in *Agelaius* blackbirds,

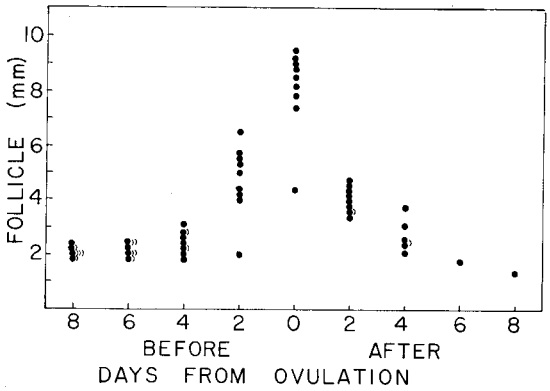

FIGURE 3. Growth of ovarian follicles and regression of postovulatory follicles in *Chrysococcyx caprius*. Growth curves are reconstructed from measurements of the four largest growing follicles in each ovary and from the timing of ovulation on alternate days. The figure includes only those females with a hard egg in the oviduct.

Payne 1969a). Rather they may continue to develop enlarged follicles as long as environmental conditions for laying persist, in parallel to the conditions of incomplete clutches in the nests of nesting indeterminate-laying birds. "Indeterminate laying" in birds is simply a tactic of tracking a variable environment.

The growth rate of ovarian follicles in the ovaries of cuckoos was reconstructed to determine what the critical size of follicles is to make ovulation more or less inevitable. Once larger follicles develop beyond this point of no return, resorbtion is much less likely than ovulation. Because *C. caprius* usually ovulates on alternate days and because histological examination shows that the largest two or three follicles are usually growing and not atretic, the size difference between two large follicles reflects their growth rate over a 2-day period. The diameters of the five largest growing follicles for those laying cuckoos with a hard egg in the oviduct are plotted in figure 3. Because this sample includes only birds with hard eggs, the largest follicles were assumed to have eggs likely to ovulate on the same day. The size of most of these largest α follicles was 8–10 mm, close to the size of six yolks freshly ovulated in the oviducts of other laying females (range 9.0–10.2 mm). The second largest follicles in these nine cuckoos (the 8 follicles) ranged from 2.0 to 6.6 mm; none of the β, γ, or δ follicles were larger than 3.2 mm. It seems from these growth-rate data that ova from any α-follicles larger than about 5.0 mm are very likely to ovulate and that ova from yolky, growing β-follicles are probably scheduled for ovulation 2 days later. A follicle size of 5.0 mm or larger was selected as a "critical size" in these birds for two reasons. First, it is unlikely that either the upper or lower size range of the β-follicles of laying birds represents a critical size because the series of three or four ovulations shown by the postovulatory follicles suggests that more than one egg develop at a time in the ovary. Second, the distribution of sizes of the α-follicles in figure 3 suggests a possible gap in the size range of 5 mm such as would be expected if cessation of laying a series is anticipated by about 2 days in the development of the ovarian follicles. In the "current clutches" in which an egg was in the oviduct, the large, yolky ovarian follicles larger than 5.0 mm would very likely have ovulated in the next few days, hence the number of recent postovulatory follicles plus the number of these large, growing follicles gives a minimal estimate of clutch size. This estimate of current clutch size is minimal because some smaller growing follicles might have developed and ovulated also although some might undergo atresia. This conservative estimate of "current clutch size," including the follicles 5.0 mm or larger in birds with fresh postovulatory follicles, is included in table 2.

In the eight completed clutches, the modal clutch size was 2 and the mean clutch 1.63. The largest clutch was three. In the current clutches, more than half of the females were laying three or more eggs, but no females showed strong evidence of laying clutches larger than four. Mean clutch size for the 25 clutches which females were still laying was 3.12. Adding all 33 clutch sizes indicates a mean clutch size of about 2.71.

Growth of the α-follicles in laying cuckoos with hard eggs in the duct was compared in birds that had already ovulated various numbers of eggs in current clutches (see fig. 3) to determine whether any possible exhaustion of energy resources toward the end of the formation of a clutch could be detected. There was no trend for birds that had just ovulated larger numbers of eggs to have smaller remaining ovarian follicles. The results suggest that no great depletion of energy reserves of a female accompanies the completion of a single clutch of eggs in these cuckoos.

The reason for the discrepancy in mean clutch size determined from completed clutches and from current clutches is probably due to the incomplete counting of postovulatory follicles older than about 8 days in the older clutches, which would include mostly the completed clutches. Because most females were still laying when they were collected, most clutch determinations were made from

the current clutches and were not subject to this technical error.

Breeding seasons and the number of eggs laid in a season. To estimate the total laying performance of a female during a breeding season, the laying rates were summed over the duration of the local laying season.

In the eastern Cape Province the laying season of Diederik Cuckoos is about 12 weeks, beginning in late October and ending in early January (South African Ornithological Society nest record cards; Skead 1952; Jensen and Jensen 1969; Jensen and Vernon 1970; my own observations). I heard males singing frequently in early October at Kei Road in 1965, but the earliest actual laying record available is the oviduct egg on 31 October 1965 (3767, fig. 2) and a postovulatory follicle (3782, fig. 1) aged for the same day. Most records for the eastern Cape are for November and December laying (Skead 1952; present paper). Observations over several breeding seasons are available for one locality: Thorn Grove in the eastern Cape, in 1965, 1966, and 1972 by me and in 1968 by R. A. C. Jensen. Jensen found adults as late as 10 January 1968 and he noted (Jensen and Vernon 1970) eggs and young that indicated laying in late December and early January. I found no Diederik cuckoos at Thorn Grove during visits on 3 and 5 February 1972. One of the latest breeding records for the eastern Cape is that of a young cuckoo being fed by wagtails (*Motacilla* sp.) at Amanzi on 17 February (Niven and Niven 1966); a laying date in mid-January is probable for this fledgling.

If Diederik Cuckoos lay throughout their breeding season at the same rate as the birds in the ovary samples did, then in the eastern Cape Province these cuckoos would lay on the average from 12 × 1.3 to 12 × 1.75 (eggs per week times total weeks) eggs, or about 16–21 eggs in a season.

Local and seasonal differences in the weather and in the availability of host nests may create considerable differences in the clutch size of individual cuckoos, with some birds laying more eggs and some few or none in some years. Particularly in droughts, *C. caprius* may fail to lay for much of its "breeding season." During 1965, 8 of the 10 females taken in November and December had been laying at Thorn Grove. That year the weather, though considered somewhat dry by local farmers (M. Beal-Preston and A. R. Dick, long-time residents), was wet enough that the streams at Cathcart were flowing, and nests of several host species were found by me, Karen Payne, and Gordon Ranger. In contrast, 1966 was drier, much of the local acacia thicket along the dry creek was cut to provide food for the goats because the grass was so scanty, and fewer weaver nests were found. Mr. Dick informed us that the Waqu Valley was drier by early December that year than it had been for the previous 20 years. We did find active nests with eggs of the Karroo Robin (*Erythropygia coryphaeus*) and the Masked Weaver (*Ploceus velatus*), both of these birds hatch and rear young Diederik Cuckoos (Payne and Payne 1967). In this dry year only two of the four female cuckoos collected had enlarged ovaries, and none had laid recently. The following season was apparently even drier, and the local *C. caprius* did not breed in the area in 1967–68 until late December (Jensen and Vernon 1970). Further field work is necessary to precisely measure the yearly changes in egg production by the cuckoos; the ovary samples were collected both in the eastern Cape and elsewhere over 2 years without regard to local weather conditions or the presence of certain host species, so that the data are presumably representative of seasons typical of the areas where the birds are common.

In Transvaal the breeding season extends from November through mid-March (Hunter 1961; Reed 1968; Tarboton 1968; Jensen and Jensen 1969). The Merensky Reserve in the northwestern Transvaal lowveld was visited no earlier than late December in 1966, and observations were continued until 2 April 1967. No young were seen in late December, suggesting that little laying had occurred well before that time. Reed (1968) estimates that the laying season near Johannesburg extends over 15 weeks, but he comments that females that lay blue eggs in the nests of the Red Bishop (*Euplectes orix*) begin and end their breeding a month after those females that parasitize hosts with spotted eggs and lay mainly in November and December. This suggests that the season for an individual female may not exceed 10 or 12 weeks. Although the breeding season for cuckoos throughout the Transvaal extends over 5 months, at any one locality the season appears to be more restricted, and probably for any female it is no longer than in the more temperate eastern Cape Province. The 10 female cuckoos collected in Transvaal showed altogether 16 postovulatory follicles as recent as 7 days, suggesting a local laying rate of 1.6 eggs per week by an average female. At this laying rate, a female would lay an average of about 19 eggs per season in the Transvaal, about the same number as in the Cape.

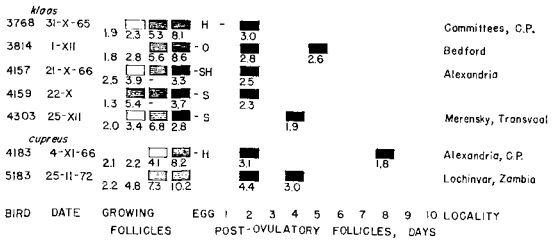

FIGURE 4. Laying histories of *Chrysococcyx klaas* and *C. cupreus*. Symbols, numbers, and letters as in figs. 1–2.

As in the eastern Cape, severe drought in summer curtails the breeding of the Diederik Cuckoos in the Transvaal. One bird with a small ovary was taken in late December in 1965 at Brits, during a prolonged drought that was said by the resident farmer J. C. Ras to have been the most severe drought on his farm for at least 10 years. The earth was cracked, the acacias were wilting and dropping leaves, and we found no host nests in the area where cuckoos were calling. In 1972 I revisited the farm in early January. The area was green that year, and I found many active nests of the host species *Euplectes orix* and *Ploceus velatus*, and the cuckoos were singing.

In more tropical regions the cuckoos were sampled less intensively. Except in Rhodesia, the local breeding seasons are not well known and indeed they may be poorly defined in local cuckoo populations. In Kenya one breeding Diederik Cuckoo had ovulated four times in about 8 days, suggesting that in this equatorial country a prolonged breeding season for the species was not associated with a decreased frequency of laying for any one cuckoo. The other two cuckoos from Kenya were not breeding and may have been "wintering" birds from southern Africa (fig. 2). Diederik Cuckoos in southern Africa are thought to migrate out of their breeding area after the breeding season in the austral spring and summer (Friedmann 1968).

The variation among birds, the lack of information about local breeding seasons, and the occurrence of nonbreeding migrants make it difficult to compare reproductive effort and clutch size in different latitudes. No differences in frequency of laying or in clutch size are evident between samples of the temperate, subtropical, and tropical populations (figs. 1 and 2).

Age-specific reproductive effort. Determining the age is difficult once these cuckoos have passed their postjuvenal molt, but some variation in the older birds suggests the retention of juvenal feathers. Males sometimes retain a few brown-barred feathers of the juvenal plumage through their first year and then can be aged at 1 year. Unbarred males all are probably 2 years or older. In the collections of the University of Michigan Museum of Zoology and the Field Museum of Natural History, 61 adult males are unbarred and 8 have a few loose-textured, juvenal feathers retained on the wing. The very low proportion of unbarred males suggests a complete postjuvenal molt in some males in their first year. If the females with barred, brown, loose-textured upper wing coverts are younger than the unbarred females, on the average, it should be possible to detect any gross difference in the reproductive performance of the first-year female cuckoos. Adult female *C. caprius* in the FMNH sample included 21 barred females and 23 unbarred females. In 11 of the barred females, the barred coverts appeared to be worn, loose-textured juvenal feathers; in the remaining barred females the coverts appeared not to be retained from the juvenal plumage.

Of the 37 females saved as study skins in the present study, 19 have brown bars and 18 are unbarred. The proportion of barred females is higher than that of barred males, so probably some of these barred females are older than a year. Probably the barred sample has a younger average age as this group includes the first-year females. In the barred females, 15 of 19 birds were laying (postovulatory follicles or large, yolky follicles) and, in the unbarred females, 15 of 18 were laying. When only the females with the most juvenal-like barred features are considered, seven of the eight were laying. Similarly, the proportion of females with eggs in the oviduct was nearly identical in the barred and unbarred groups. The data suggest that first-year female *C. caprius* lay eggs as often in a season as do the older (unbarred) female cuckoos.

CHRYSOCOCCYX KLAAS AND *CHRYSOCOCCYX CUPREUS*

The samples of Klaas Cuckoo (*Chrysococcyx klaas*) and Emerald Cuckoo (*C. cupreus*) give the individual histories of recent laying in figure 4. In both species eggs are most often laid on alternate days. In *C. klaas* ovulation may occur at nearly any time of day; 3814 was ovulating at 17:15, and 4157 had just ovulated and was secreting albumen around the yolk at 08:10. Less information is available for *C. cupreus*; the Alexandria bird was taken in late afternoon as it was drying itself during the first pause in 3 days of hard, cold rain. The Lochinvar bird was netted at 09:00

perhaps after having just laid an egg; the appearance of the α-follicle indicated its ova was ready for release.

Only one Klaas Cuckoo had recently completed a clutch; it had ovulated a single egg about 4 days before the next egg was ovulated. The development of the yolking follicles (counting those 5.0 mm or larger) suggests frequent clutches of three or four eggs. Mean clutch size of nine clutches of *C. klaas* was 2.67, and the most common clutch size was four. A protracted series of layings in Emerald Cuckoos is suggested by the ovary of the Lochinvar bird. The female was about to ovulate the third egg in a series, and she had a fourth large, yolky follicle.

At a rate of laying two eggs per week (post-ovulatory follicle counts in *C. klaas*), a female would lay about as many eggs as a female *C. caprius*. The laying rate of *C. cupreus* in the data available appears to be similar.

Breeding seasons of *C. klaas* in the eastern Cape extend from late October through early January (SAOS nest record cards; Skead 1952; Jensen and Jensen 1969; fig. 4) although along the wetter coast, *C. klaas* may breed in winter when some host sunbirds nest (Skead 1952, 1972; Quickelberge 1967). During late spring and early summer, an individual cuckoo may lay for about 12 weeks, and if it lays at the observed rate of two eggs per week for this time, it would produce about 24 eggs in a season. Breeding seasons in Transvaal (SAOS nest record cards; Tarboton 1968) appear to be similar to those published for Rhodesia (Benson et al. 1964) where more records are available and where *C. klaas* breeds from October to December. At Merensky in eastern Transvaal, a live, newly fledged *C. klaas* was given to us by G. T. Roux in mid-January 1966, suggesting early December laying. We heard Klaas Cuckoos singing there through March in 1966, so the local laying season probably extended over 12 weeks. Again, a comparison of the laying rates and the local breeding season suggests no great difference in laying rates or seasonal egg production in the temperate eastern Cape and subtropical northeastern Transvaal.

The breeding season of Emerald Cuckoos in South Africa is not well known, and the Lochinvar female provides the first breeding date for any Emerald Cuckoo in Zambia (Benson et al. 1971). In Malawi it breeds in September and November (Benson et al. 1964). If its breeding season is about the same duration as that of the other glossy cuckoos in southern Africa, then *C. cupreus* probably lays about as many eggs in a season.

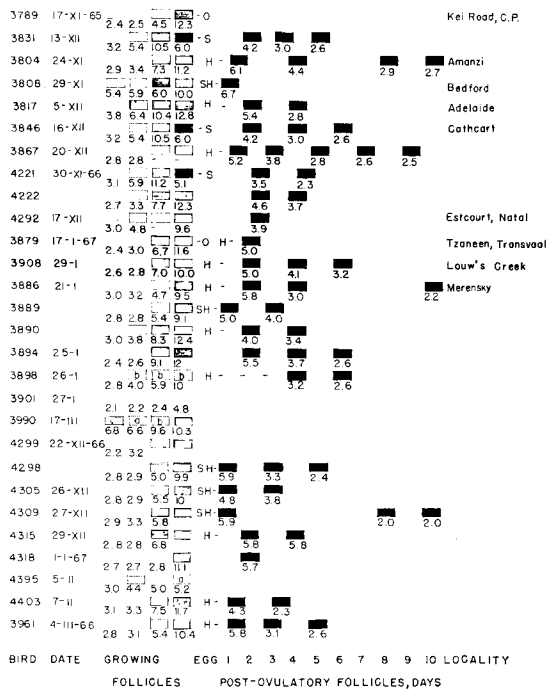

FIGURE 5. Laying histories of *Clamator jacobinus*. Symbols, numbers, and letters as in figs. 1–2, except that only follicles larger than 6 mm are shaded.

CLAMATOR, THE CRESTED CUCKOOS

The three African representatives of *Clamator* are large birds of savanna and open woodland. Two are among the largest of the African parasitic cuckoos. The biology of the crested cuckoos has been summarized by Friedmann (1964). The largest sample of laying females was taken from the smaller species, the common Jacobin Cuckoo (*Clamator jacobinus*). In southern Africa it lays its eggs mainly in the nests of bulbuls, the Fiscal Flycatcher (*Sigelus silens*), and *Lanius* shrikes. The same cuckoo species occurs in India. The Striped Cuckoo (*C. levaillantii*) was collected in the Transvaal lowveld, eastern Rhodesia, and Malawi, in generally more dense woodland and thickets where its main host in this region, the Arrow-marked Babbler (*Turdoides jardinei*), lives. The Great Spotted Cuckoo (*C. glandarius*), a species which inhabits dry acacia savanna in Africa and the European Mediterranean, was taken along the thorny stream-side vegetation near Cathcart, eastern Cape, where starlings nested and reared the young, and also in acacia country in Kenya, where their hosts are mainly corvids (Friedmann 1948, 1964).

CLAMATOR JACOBINUS

Recent laying histories were determined for 28 Jacobin Cuckoos, all of them *C. j. serratus*

TABLE 3. Time of egg formation and laying in *Clamator jacobinus*.

Time of day	Stage of laying cycle			
	Ovulating	Soft egg	Semihard egg	Hard white egg
05:00–08:00		1 (07:15)		1 (08:00)
08:00–10:00			2 (08:30–09:00)	3
10:00–12:00	2 (10:00–10:20)[a]	1 (10:30)	2	2[a]
12:00–14:00			1	3
14:00–16:00				1
16:00–19:00				1 (16:40)

[a] Includes one bird with a hard egg in shell gland and another ovulating egg in infundibulum of the oviduct.

in South Africa. The largest sample is of 16 from Merensky Reserve, Transvaal (fig. 5). Omitted from figure 5 is a female *C. j. jacobinus* in fresh plumage, taken in March in Rhodesia; this form, characterized by its short winglength, winters in Africa and migrates to southern India to breed (Ali and Ripley 1969; Friedmann 1964).

Laying intervals. The most common laying interval was 2 days (fig. 5). Some consecutive eggs may have been laid less than 48 hr apart because several cuckoos had a post-ovulatory follicle series that appeared between 1 and 2 days postovulation. The proportion of hard eggs in the oviduct (11 of 20 birds that had oviduct eggs) suggests that the cuckoo usually carries a hard egg in its duct for a day after it has been fully formed. The histological interpretation and the hard-egg frequency data both are in agreement with the direct observation of Liversidge (1971: 125) that Jacobin Cuckoos lay most often at 2-day intervals, though sometimes on successive days and occasionally with breaks of several days between eggs.

The only instance of any cuckoo having an oviduct egg with no postovulatory follicle 2 days old or less postovulation was a pathological case of an egg-bound bird. Cuckoo 3898 had a hard egg in the oviduct and a corresponding postovulatory follicle in the ovary measuring 3.2 mm, smaller than the largest post-ovulatory follicle of any other laying *jacobinus*. Histologically, the follicle appeared to have ovulated 3 or 4 days earlier. The oviduct had become occluded and the bird was eggbound. It was drinking at a dam, where it died without disturbance within a half-hour of first being observed. The breast muscle was atrophied, the feathers fouled, the viscera enflamed and full of acrid fluids. The hard shell of the egg was very brittle and had cracks and weak areas, possibly due to calcium resorbtion from the general acidosis of the bird. The yolky ovarian follicles were atretic and histological sections showed that they had burst through the theca.

Time of laying. Females with hard eggs were taken from early morning through late afternoon. Ovulation may occur nearly any time of morning; the time that eggs were ovulating, undergoing albumen deposition, or developing a soft shell (table 3) suggests that ovulation occurs as early as 06:00 or as late as 10:00. If these cuckoos ovulate within an hour or two after laying the preceding egg, then they may lay from early morning (05:00) to late morning; no birds collected were ovulating in the afternoon. Field observations of host nests parasitized by Jacobin Cuckoos in the eastern Cape have shown that cuckoos lay mainly in mid-morning between 07:00 and 09:00 (Liversidge 1961, 1971:124).

Number of eggs laid in a series or clutch. Individual laying histories suggest little regularity in the number of eggs in each series of alternate-day layings (fig. 5). Only two females had sets of postovulatory follicles clearly separated from the series currently being ovulated. These two birds had completed clutches of two and three eggs; the former was from the egg-bound bird which probably would have laid a longer series if it had not become eggbound. Two other cuckoos (3808, 3886) had a possible series of six older postovulatory follicles, but some of these follicles were more than 10 days old and could not be distinguished without question as postovulatory.

To determine the size of the growing ovarian follicles that were very likely to ovulate, the growth curve was plotted for follicles and postovulatory follicles in birds that had a hard egg in the duct (and that had no yolky follicles ruptured by shot). The curve (fig. 6) suggests that follicles larger than 6 mm would most likely be ovulated within 3 or 4 days. On this basis, minimal estimates of clutch size for current clutches were determined (table 4).

The number of eggs in completed clutches ranged from 1 to 4 and averaged 2.0 eggs; in current clutches the number ranged from 2 to 6 and averaged 3.78 eggs. For all 28 clutches the average size was 3.46 eggs.

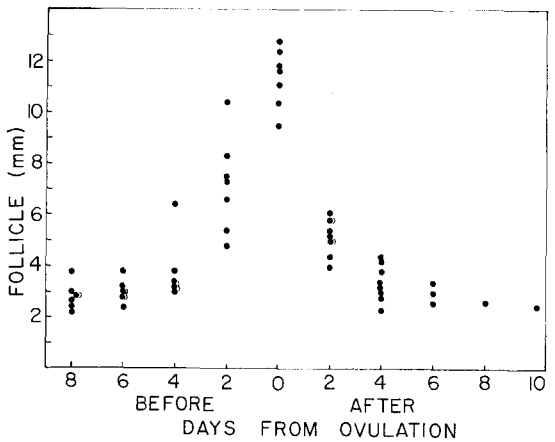

FIGURE 6. Growth of ovarian follicles and regression of postovulatory follicles in *Clamator jacobinus* (females with hard egg in oviduct). Growth and regression curves are reconstructed from sizes of follicles and from known ovulation rates as in fig. 3.

In his field study of Jacobin Cuckoos, Liversidge found it difficult to ascribe eggs to individual females since all birds laid plain white eggs; however, he found he could distinguish them using shell texture (Liversidge, pers. comm.). He had the impression that females did not lay in "clutch rhythms," but rather showed some variation in their day-to-day laying patterns (Liversidge 1971:125). The variation found among the ovaries in the present sample is in agreement with this impression. The variation in number of eggs laid in a "clutch" indicates that there is no constant single clutch size, but that eggs are laid in series as in the other cuckoos. Ovarian sections of a representative laying Jacobin Cuckoo are shown in figure 7.

Rate of laying. The proportion of laying females, with an egg in the oviduct, was 20 out of 28. Since Jacobin Cuckoos lay on alternate days, the frequency of eggs in the oviduct suggests that a female lays $^{20}/_{28} \cdot \frac{1}{2} \cdot 7$ eggs a week, about 2.5 eggs per week. The estimate of laying rate indicated by the recent laying histories determined by measurement of postovulatory follicles is 1.86 eggs per week. Both of these estimates appear to be somewhat higher than the similarly determined rates in the glossy cuckoos.

Local breeding seasons and the number of eggs laid in a season. In the eastern Cape the laying season extends from late October to early February, with 26 of the 30 egg dates in the SAOS nest record cards falling in a 10-week period from November to January. Local breeding seasons may be shorter. In the present study no evidence of laying before mid-November was found, but the laying dates

TABLE 4. Clutch size in *Clamator jacobinus*.

	Frequency distribution of number of eggs in series						
	1	2	3	4	5	6	Mean
Completed clutches	2	2[a]		1			2.0
Current clutches		3	6	8	5	1	3.78

[a] Includes one egg-bound bird.

in figure 5 suggest a season extending from about 14 November to late December. No Jacobin Cuckoos were seen or heard at Thorn Grove or at Kei Road during the first week of February 1972. Perhaps the laying season there is as long as 10 weeks. Near Port Elizabeth, in coastal eastern Cape Province, Liversidge (1971) found that in a local area most eggs were laid during 6 weeks from late October to early December, though he records laying also on 7 October, suggesting a laying period of perhaps 8 weeks.

The breeding season in Natal extends from October to January (Dean 1971); a series of dates for a single locality is not available. In Transvaal only nine nest records of eggs were reported in the SAOS nest record cards and these fell from late November to late January. Tarboton (1968) noted eggs from December through February in south-central Transvaal. At Merensky the local Jacobins laid from 18 December through 7 February; although no birds were taken in the next weeks, they were present and calling, and a bird on 17 March appeared ready to ovulate. The local laying season at Merensky in the Transvaal lowveld lasts about 12 weeks. With an average local breeding season of 10 weeks, a female would lay an average of either 19 or 25 eggs, depending on which estimate of the rate of laying is more appropriate.

It seems likely that individual females continue to lay through the season. The evidence from the birds sampled indicates that the proportion of laying birds remained high and was very nearly constant throughout the various months (fig. 5).

No local differences in reproductive performance were noted. The two females taken during the 1966 drought at Thorn Grove, Cathcart, were laying. Possibly the host species of *Clamator jacobinus* in acacia country are less dependent on optimal local weather conditions for their own nesting than are the weaver hosts used by *Chrysococcyx caprius*. In Rhodesia the Black-eyed Bulbul (*Pycnonotus barbatus*) breeds nearly all year (Benson et al. 1964), and this bulbul was the most common species known to be a host of *C. jacobinus* in the Waqu Valley. Likewise, the gonads of

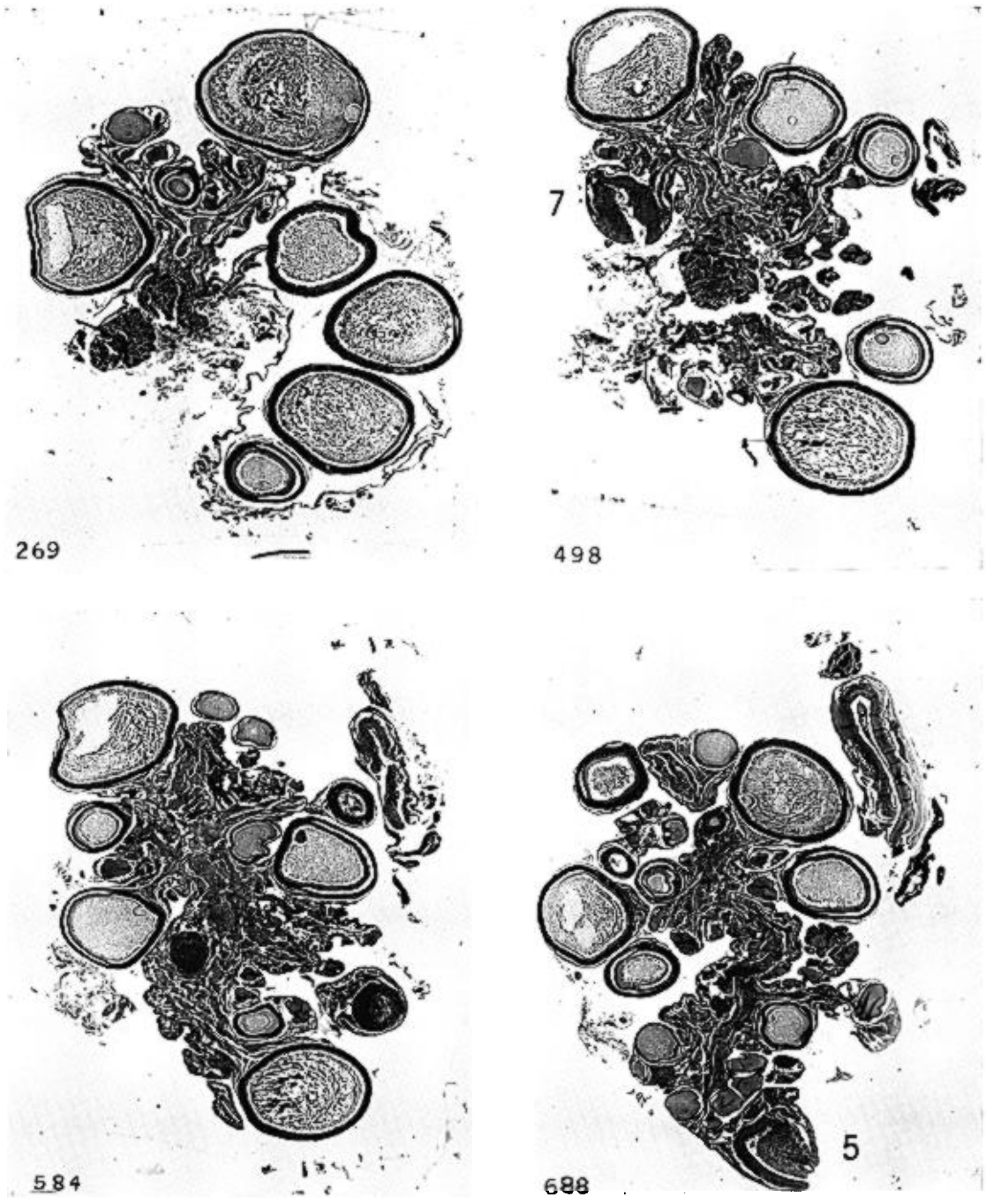

FIGURE 7, part 1.

the host Cape Bulbul (*P. capensis*) near Port Elizabeth are in breeding condition all year (R. Liversidge, pers. comm.), though the bulbul's nesting is restricted locally from August to December (Liversidge 1966).

Comparison of laying in black-phase and white-phase jacobinus. Unique among breeding cuckoos in southern Africa is the occurrence in the Jacobin Cuckoos of a conspicuous plumage dimorphism independent of sex. The black-phase birds are completely black except for a white wing patch, and the white-phase birds have white underparts and white spots on the tail as well as the white wing patch.

Black-phase birds are the most common color form in the southern and eastern Cape Province, comprising about 90% of all birds seen there in this field study, whereas nearly all of the birds north of Natal are white-phase. In the females whose ovaries were sampled, all of the Transvaal cuckoos, the Natal cuckoo,

FIGURE 7, part 2.

FIGURE 7. Representative serial sections of the ovary of *Clamator jacobinus* 3867, showing follicles from recent ovulations on days 1, 3, 5, 7 and 9 before the bird was collected on 20 December 1965 at Thorn Grove, near Cathcart, eastern Cape Province. Approximate ages in days are indicated by numbers beside the follicles; the section numbers are shown below the sections. The large open follicle at upper right of sections 733, 782, and 898 is a growing yolky follicle that was ruptured by shot; it has yolk visible in the lumen.

and 3789 (mated with a black male) at Kei Road were white-bellied cuckoos; the other eastern Cape cuckoos were black-phase. No differences are evident in the timing of laying, clutch size, or total numbers of eggs laid in these two phases (fig. 5). The white-phase bird at Kei Road was the earliest breeding female collected there, even though in most of the range of the white-phase birds, the *jacobinus* breeding season averages somewhat later than in the eastern Cape (Jensen and Jensen 1969). There is no reason to suppose that the two phases breed at different times where they occur sympatrically. Near Estcourt, Natal, I observed eight pairs of *jacobinus* in December 1966. Four were pairs of black birds and four were pairs of white-bellied birds; no mixed pairs were seen. All appeared to be breeding as they were calling and spending time in pairs.

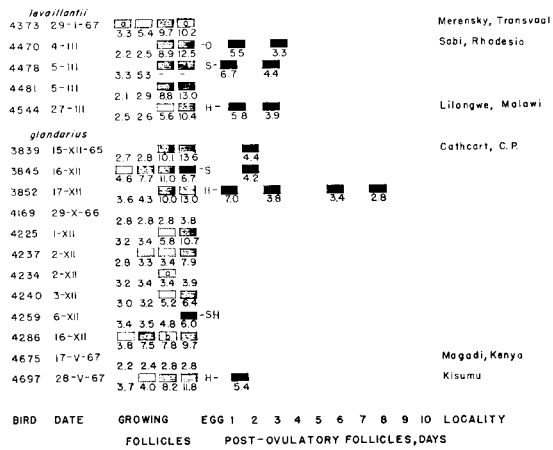

FIGURE 8. Laying histories of *Clamator levaillantii* and *C. glandarius*. Symbols, numbers and letters are keyed in figs. 1–2, except that only follicles larger than 6 mm are shaded.

CLAMATOR LEVAILLANTII

Striped Cuckoos (*Clamator levaillantii*) ovulate at intervals of 2 days (fig. 8). Two of the five females collected had an oviduct egg, a third female was ovulating. None had long series of postovulatory follicles, though the development of the growing follicles in 4470 and 4478 suggests that these cuckoos may sometimes lay in series of at least four eggs. The total of six postovulatory follicles in the five cuckoos suggests that a female may lay on the average about 1.2 eggs in a week; the proportion of females with yolk in the duct suggests a larger number.

Breeding seasons of Striped Cuckoos are not well known. In Rhodesia, Zambia and Malawi the season extends from November to March, about the same as in Jacobin Cuckoos (Benson et al. 1964); locally the Striped Cuckoos may lay until May (Jensen and Jensen 1969).

CLAMATOR GLANDARIUS

The laying histories of the 12 female Great Spotted Cuckoos (*Clamator glandarius*) sampled are summarized in figure 8. As in other *Clamator* species, the histological appearance of sets of postovulatory follicles in each ovary indicates ovulation (and laying) on alternate days, though occasionally 2 days may pass between ovulation days. Field observations at nests of their host, the Pied Crow (*Corvus albus*), in Nigeria have shown directly that Great Spotted Cuckoos lay on alternate days (Mundy and Cook 1971). The series of postovulatory follicles and large, yolky follicles in cuckoo 3852 suggests at least occasional clutches of six eggs.

If performance of the cuckoos in the eastern Cape in 1965 was typical of an average year, then *C. glandarius* may lay on the average 2.3 eggs in a week, at least in a good week.

The breeding season in the eastern Cape extends from September to January (Jensen and Jensen 1969); the nine egg dates available in the SAOS nest record cards, when I examined them in 1966, fell between early November to late December. At Thorn Grove in the Waqu Valley, the cuckoos may begin laying by late October, and continue laying until mid-January. On 14 December 1965, I collected a fully grown juvenile there feeding on hairy caterpillars; since the incubation period is 12–14 days and the young fledge with a short tail at day 19 to 21 (von Frisch 1969; Valverde 1971), the egg from which this *C. glandarius* hatched was probably laid in late October. I found a young bird about 9 days of age there alone in a nest of a Pied Starling (*Spreo bicolor*) on 1 February 1972, indicating laying on about 10 January. These extreme dates indicate a laying period at Thorn Grove of about 10 weeks. During this period, if a female *glandarius* lays at the rate observed in the 1965 sample, she would lay about 23 eggs in a season.

Because they breed in semiarid acacia country, Great Spotted Cuckoos experience very dry conditions in years of little rain, and in some years their breeding is sharply curtailed. Only one of the seven females taken at Thorn Grove in 1966 was laying. Of the nonlaying females, one had a small ovary, three had atretic yellow, yolky follicles that had grown and then degenerated, and two other birds might have ovulated in the next few days but had not during the previous 10 days. The 1966 season was extremely dry in the Waqu Valley, in contrast to 1965 and to the 1971–72 seasons. No rains fell in spring in 1966 until 4 December; that night 36 mm were recorded but too late to make the area as green in mid-December as it had been at that time the previous year. Some hosts of this cuckoo were breeding in 1966, though two stream banks that had housed colonies of *S. bicolor* in 1965 had none nesting there in 1966. This starling is the most frequently parasitized host in southern Africa (Friedmann 1964). Other birds known to be hosts of *C. glandarius* that were seen nesting in 1966 were the Hoopoe (*Upupa epops*), the Ground Woodpecker (*Geocolaptes olivaceus*), the Pied Crow (*Corvus albus*), and the Cape Glossy Starling (*Lamprotornis nitens*). We found two eggs of *C. glandarius* on the ground, pecked and empty, near the dry stream bed on 30 No-

vember and 2 December. No young *C. glandarius* were seen out of the nest in 13 days of observation in 1966, though in 1965 during 8 days of observation several juveniles were seen with their foster parent *S. bicolor* and *L. nitens*. Probably the drought of 1966 adversely affected breeding in the cuckoos though it did not completely stop them, and the dry conditions did not stop all of their hosts from breeding. The proportion of "unusually" dry years in this area is not known; the 1971–72 season produced streams and green vegetation more lush than in 1965.

One of two *C. glandarius* taken in May in Kenya was laying. The other was excessively fat and molting. Since it is impossible to distinguish any geographic races in the species, it is not known whether the second bird was from a population that breeds in East Africa or a "wintering" bird from southern Africa. Most South African *C. glandarius* disappear except during the breeding season and apparently migrate to equatorial Africa though a few occur in the eastern Cape during the austral winter (Payne 1969b).

The first-year birds of either sex can be distinguished from older birds in the field as well as in the hand by the retention of rufous flight feathers in the wing and by a dark-gray crest; the older birds have grayish-brown flight feathers and a pale gray crest (Friedmann 1948). One of the four younger birds was laying; she was the only laying bird taken at Thorn Grove in 1966. Unaged birds include one laying bird taken in 1965 and a bird with a 7.9 mm follicle taken in 1966. The data suggest that some females breed when they are a year old.

THE *CUCULUS* CUCKOOS

Laying histories based on examination of the ovaries of the *Cuculus* cuckoos that breed in Africa indicate that they ovulate most often on alternate days (fig. 9), as did Chance's (1922) *Cuculus canorus* in England. The only species of African *Cuculus* with a sample adequate to estimate an average reproductive performance is the Black Cuckoo (*Cuculus clamosus*; = *C. cafer* of some authors). Four of the six females had an egg in the oviduct. These cuckoos evidently often carry a hard egg for a day before the egg is laid. The six Black Cuckoos had ovulated a total of 13 eggs in a week for an average of 2.17 eggs per week for a female. Series of at least four or five eggs may be laid (3763, 3792), though singletons are also indicated (4232, 4366).

Duration of the breeding season of *C. clamosus* in the eastern Cape, where most of

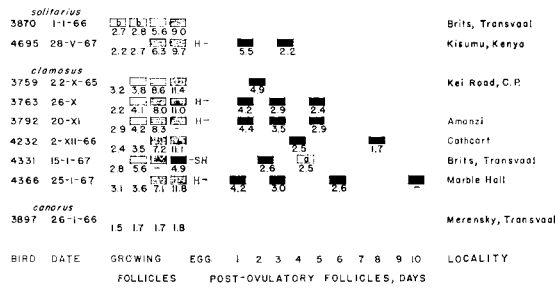

FIGURE 9. Laying histories of *Cuculus canorus*, *C. solitarius*, and *C. clamosus* (= *C. cafer*). Symbols, numbers and letters as in figs. 1–2, except that only follicles larger than 6 mm are shaded.

the sample was taken, is reported to be from November to January (Jensen and Jensen 1969), though the 1965 samples indicate that birds at Kei Road may start by 22 October. At Kei Road in 1972 I watched a juvenile being fed by a Boubou Shrike (*Laniarius ferrugineus*) from 31 January to 4 February in Gordon Ranger's garden; Ranger first recorded it shortly after it had fledged, about 2 weeks earlier. This bird was probably hatched around 1–4 January (Skead 1951 gives fledging at day 16–21) and the egg laid around 20 December; the exact incubation period is unknown. These dates suggest a laying period of at least 9 weeks at Kei Road. In the Transvaal, nestlings have been seen north of Rustenburg in February and April (Tarboton 1968), suggesting a laying season of 3 months. Assuming an average laying season of 10 weeks in any one local population, a female Black Cuckoo would lay an average of about 22 eggs in a season.

The lack of recent breeding in Transvaal in the lone African Cuckoo (*Cuculus canorus gularis*) and in the Red-chested Cuckoo (*Cuculus solitarius*) was probably related to local droughts, though some other cuckoos (notably *Clamator jacobinus*) were breeding then, as was *Cuculus clamosus* during the drought at Thorn Grove. A *C. solitarius* taken in Kenya appeared to have laid on alternate days and to be midway through a clutch of four eggs. The clutch would probably be no larger than that because the γ follicle was smaller than that in the *C. cafer* sample of laying cuckoos (in these two species the birds are nearly the same size, and so are their eggs).

The ages of *Cuculus clamosus* are unknown. Plumage variation in South Africa involves variation of barring of the underparts; some birds are heavily barred and others are unbarred. Both barred and unbarred females in the sample were laying. The fact that all six females collected were laying suggests that

C. clamosus females breed when a year old. The nonbreeding *C. canorus gularis* was a first-year bird as it retained a barred juvenal secondary. The laying *C. solitarius* was evidently a first-year bird because it had only a trace of rufous below and it was distinctly barred with black on the upper breast. According to Friedmann (1948) and my confirmatory examination of museum specimens, this plumage appears to be typical of yearling Red-chested Cuckoos.

DISCUSSION

The individual laying histories of the eight species of laying parasitic African cuckoos, as determined from their ovaries, are similar in several features to the laying histories of *Cuculus canorus* in England, as described by Chance and others who have followed individual cuckoos by finding their eggs through a breeding season. Like the European Cuckoo, the cuckoos in Africa lay mainly on alternate days, they vary considerably in the number of eggs in a series or clutch, and they lay a rather large number of eggs in a season.

The laying interval for all brood parasitic cuckoos sampled is most frequently 2 days. Through field observations on unmarked individuals whose eggs appeared distinctive, Chance (1922, 1940) and Niethammer (1938: 129) determined that the European Cuckoo (*Cuculus c. canorus*) lays eggs on alternate days. Other field workers have suggested longer laying intervals (Blaise 1965; Čapek 1896; Diesselhorst 1955; Groebbels 1957; Makatsch 1955; Labitte 1948; Ottow and Duve 1963; Paulussen 1957; Rey 1892; Warncke and Wittenberg 1958). The African species do sometimes lay at longer intervals as there is a gap of 3–8 days between some series of layings although within a series the eggs are ovulated on alternate days in most instances. The European field workers based their estimates of low reproductive rates on their own infrequent discovery of cuckoo eggs. However, they may have overlooked some host nests or may have found the nests after the cuckoo eggs were ejected by the hosts. The original data of some of these workers suggest laying on alternate days; eggs of those individuals for which the largest number of eggs were found were located in some instances at intervals of 2 days (female 32 in Čapek 1896; female 1 in Warncke and Wittenberg 1958). On the other hand, no one has ever reported any convincing evidence that parasitic cuckoos normally lay every day, although in a few instances a female may lay at intervals between 24 and 48 hr (figs. 1, 2, 5). Friedmann (1968:87) has guessed at daily layings in *Chrysococcyx caprius*, based upon his gross examination of the ovaries of laying birds. He noted that the size difference between the largest ruptured follicles was less than in the ovaries of *Cuculus*, but this smaller difference may be simply a correlate of the smaller size of the eggs of *Chrysococcyx*. The follicles of the *Chrysococcyx* species are only about half the volume of the ovulating follicles of the *Cuculus* species (figs. 1, 2, 4, 9) and the postovulatory follicles that remain when the follicles have ovulated are correspondingly smaller in the glossy cuckoos. The relative differences in the sizes of the largest postovulatory follicles in these birds are the same (figs. 1, 2, 4, 9). Friedmann (1948:161, 1968: 86) credited Pringle (1946) with seeing a female *Chrysococcyx caprius* visit a nest of a host Cape Sparrow (*Passer melanurus*) "on three successive days, and each day depositing an egg in the nest." Pringle, however, stated that the cuckoo returned for 3 days, "each time removing a sparrow egg and leaving its own," the phrase "its own" referring to a single cuckoo egg that he had marked on the day of the first visit. Possibly some parasitic cuckoos may lay at other intervals upon occasion. However (1) evidence from the African species using the histological picture from the ovaries and the proportion of hard eggs in the oviduct as well as (2) field evidence on *Cuculus canorus* from Chance (1922), who actually observed individual cuckoos from blinds or hides at the host nests while they laid their eggs, both show that cuckoos usually lay their eggs at intervals of 2 days.

Egg laying on alternate days by cuckoos agrees with the observation that freshly laid cuckoo eggs have undergone considerable embryological development at the time they are laid in a host nest. Liversidge (1961) compared the embryo on the surface of the yolk to that of a chicken embryo of known age and judged the embryonic primitive streak in the egg of *Clamator jacobinus* to be about a 25 hr development. Other freshly laid eggs of a *C. jacobinus* were noted by Vernon (1970) to have visible embryos. I have noted primitive-streak embryos in the yolks of three hard eggs taken from the oviduct (two of *Clamator jacobinus*, one of *Cuculus clamosus*). Probably the yolks of many other hard eggs had developed embryos but these were obscured by the albumen coagulated in the fixation process. Perrins (1967) collected a fresh clutch of cool, unincubated eggs of the Great Reed Warbler (*Acrocephalus scirpaceus*) that had a *Cuculus canorus* egg. He found that,

in testing the eggs in water, the fresh warbler eggs sank quickly while the cuckoo egg sank less quickly; upon examination the cuckoo egg had a visible embryo.

By being retained in the oviduct and incubated internally, the cuckoo eggs have a head start on the host eggs in embryonic development when they are laid. This development may be responsible for the shortened incubation period of the eggs of parasitic cuckoos (mentioned by Hamilton and Orians 1965 and by Jensen and Jensen 1969). It allows the young cuckoo to hatch either before the host young (if the cuckoo egg were laid while the host was laying) or at the same time (if the cuckoo egg were laid after incubation of the host clutch had just begun). By shortening the time required for its incubation in the nest, the prelaying development of the cuckoo egg may increase the chances that the young will hatch early and thus be a winning competitor for parental care in the nest of the foster species. Retention of the egg in the oviduct for an extra day may also allow the female cuckoo time to find an opportune moment to approach and lay in the host nest, or time to find a suitable host nest in which to lay if the nests she had been watching were destroyed. Some nesting, nonparasitic cuckoo species also lay on alternate days or at longer intervals. Laying at intervals longer than a day has been reported at least on occasion for *Coccyzus americanus* (Hamilton and Hamilton 1965), *Coccyzus erythropthalmus* (Bent 1940; Spencer 1943), *Geococcyx californianus* (Woods 1960), *Crotophaga ani* (Köster 1971), and *Crotophaga sulcirostris* (Skutch 1959). The long interval may (1) permit the energy expended in forming the large eggs of these nesting cuckoos to be spread over several days or (2) facilitate asynchronous hatching with subsequent chance of brood reduction by the feeding parents or (3) perhaps decrease conspicuousness of the nest to a predator during laying. Regardless of the adaptive significance of alternate-day laying in the nesting cuckoos, the laying interval in the parasitic cuckoos appears to allow time for laying in a suitable host nest as well as for early development of the embryo and a shortened incubation period in the host nest.

Clutch size in all of the African species studied appears to be variable, with the number of eggs ovulated in a series or clutch varying as much as one to six eggs even in a single bird (figs. 1, 2, 4). Although the number is variable, the eggs appear to be laid in recognizable clutches. To test whether cuckoos laid successive eggs at short intervals or at random, the observed laying intervals of *Chrysococcyx caprius* and of *Clamator jacobinus* were compared with the number of successive layings to be expected if laying were equally likely at any interval between 1 to 10 days. Intervals for *C. caprius* were 1 day (6 instances), 2 (20), 4 (1), 5 (2), and 6 days (1), and for *jacobinus* they were 1 day (4), 2 (3), 4 (1), and 7 days (1). For statistical analysis the laying intervals of $N + 0.5$ days were truncated to N days (see figs. 1, 2, 4) and alternate days were lumped to satisfy χ^2 requirements of no expected values less than 5 (Siegel 1956). For each species there was a significant tendency for laying intervals to be nonrandom ($\chi^2 = 21.7$, $P < 0.001$ for *caprius*, $\chi^2 = 21.6$, $P < 0.001$ for *jacobinus*). The laying pattern in the parasitic cuckoos thus proves to be one of laying a series of eggs at short intervals, with the time between series marked by longer intervals between successive eggs of 4 days or more. Because egg laying does occur in demarcated series, the use of the term "clutch" as defined earlier in the paper is appropriate.

The observation that parasitic cuckoos in Africa lay in series or clutches agrees with the laying dates of *Cuculus canorus* in Europe, where Chance (1940) found series of two to five eggs. Most egg collectors have not checked nests every day to determine the temporal pattern of laying. Estimates of clutch size of three or four have been made for several African species based upon gross examination of the number of yolky follicles in the ovaries of birds collected, occasionally including also any ruptured follicles. Friedmann (1948:30) states for *Clamator jacobinus* that "examination of the ovaries of breeding birds indicates that the number is at least 4." In two small weaver colonies, Friedmann (1948:161) checked nests for contents and found three eggs of a *Chrysococcyx caprius* in one colony and four eggs in the other colony. A female was then shot from the former colony and found to have three "discharged egg follicles." Ottow and Duve (1963) report that *Chrysococcyx caprius* lays four to five eggs, presumably in a series, though their descriptions of times involved are vague and they may have meant four to five eggs in a season. In a field study in Natal, Friedmann closely observed six nests of the Cape Robin (*Cossypha caffra*) and found four of them to be parasitized by *Cuculus solitarius*. The cuckoo eggs were laid on alternate days, all apparently by one individually recognizable female in the area. At least one female cuckoo with five dis-

charged follicles was collected there (Friedmann 1948:70–71). Other estimates of clutches of three and four eggs made from counts of yolky follicles plus an oviduct egg are listed for other cuckoo species (Friedmann 1948:45, 56, 87, 100). In the present study I have been cautious in assuming that all yellow, yolky follicles are destined to ovulate; rather, the fact that the completed clutches are often smaller than the incomplete current clutches (including only the largest one or two follicles in counts for incomplete clutches) suggests that some of the yolky follicles (those from 3 to 5 mm in *Chrysococcyx caprius*) are less likely to ovulate than to degenerate. In the earlier studies no information was available on the rates of development of growing follicles or for the rates of degeneration of ovulated follicles; these have been estimated for two species in the present study and are close to the rates assumed by the early collectors. In spite of these differences, the field observations of nest-finders, the gross ovarian examinations of careful collectors who noted ovarian development (Friedmann, Bates, and Lynes, all cited in Friedmann 1948), and the gross and histological examination of ovaries of the present study all indicate that parasitic cuckoos usually lay clutches of two to four eggs, though longer series are sometimes laid.

A noteworthy result of the present study is that parasitic cuckoos were found to lay more eggs in a breeding season than the average nesting cuckoo would lay in the same time. Although mean clutch size is not particularly large in the parasitic cuckoos but is rather similar to that in many nesting cuckoos (Payne unpubl. data), several series or clutches are laid in a season. Even in a season as short as 10 weeks, most species of parasitic cuckoos appear to lay an average of 20–25 eggs.

These estimates of high seasonal laying rates agree with those of Chance (1922, 1940) but differ from those of several other workers. The contradictory conclusions of many of the European observers can probably be explained by the difficulty the workers had in finding all host nests in an area frequented by an individual female cuckoo and by the even greater difficulty of finding each nest at the moment when a cuckoo had just laid but before the host had an opportunity to eject the cuckoo egg or to abandon the nest. The area over which an individual cuckoo lays is not well known. Although Chance apparently accounted for all the eggs laid by two *Cuculus canorus* females by finding all the nests of their hosts on the Worcestershire Common, no one has ever individually marked a female cuckoo and followed her to find the extent of her movements and layings through a laying season. Rather, all observers have identified the movements of their individual females simply by estimating the distances between host nests that held cuckoo eggs of characteristic color and markings. If a female wanders over a range with a radius of more than about 2 km, it seems unlikely that all of her eggs would be found. Yet Blaise (1965), in one of the most thoroughly documented of all cuckoo field studies, reports one female in France (CR2 in 1956 in the Secteur de Croismare) laying in the nest of Great Reed Warblers and leaving eggs over a stretch of 4 km of riverside marsh. Most of the cuckoos reported by Blaise each laid within an area no longer than 2 km. Because he studied cuckoos laying in a single host species in nests restricted to patches of riverine vegetation, Blaise likely found most of the host nests in those restricted areas where he worked most intensively. On a coastal sand dune-salt marsh area Williamson (1967) found four cuckoos active within 200 acres (81 hectares). Schiermann (1926) in similar strand habitat found a female to lay over at least 1200 m. In Labitte's (1948) study of cuckoos there were probably three or four females within 15 km^2, about 3–5 km^2 per female or perhaps a larger area since the laying ranges of females may overlap by several hundred meters (Blaise 1965). Most workers have not adequately described the local habitat or the range over which all of their eggs were found, nor do they discuss the possibility of laying over distances greater than those within which the egg collections were taken. Chance (1939:9) reported one female cuckoo having laid "within a two-mile radius" in the nests of Yellowhammers (*Emberiza citrinella*), although this may have been a printing error since he later described apparently the same female in the same year having laid "within a quarter of a mile" (Chance 1940:130). The eggs in the collection of Rey (1892, 1894) were found within a 2-km area near Leipzig; several females laid in more than one "territory" (*Revier*) even in a single year. Within the 2-km area over a few years, Rey (1892) identified eggs of 34 different individual cuckoos, and the females overlapped considerably in their ranges. In 1893, out of 70 cuckoo eggs recorded, 28 were taken in nests with an egg of another individual cuckoo (Rey 1894). The ranges of activity of some cuckoos are probably restricted to the hosts that nest in isolated patches of marsh vegetation or on islands. Ruthke (1951) studied cuckoo laying for

several years on an island 2 × 0.5 km that was isolated by 2–3 km from other land, and he found two or three females on the island each year. By the nature of the habitat and his intensive searching efforts, it seems likely that his estimates of seven and nine eggs laid in a year represent all eggs that could be located that were laid by those females. In the absence of detailed local maps, it is impossible to evaluate whether the cuckoos laying within the patches of marsh as reported by Diesselhorst (1955), Groebbels (1957), Warncke and Wittenberg (1958) and others were in fact restricted there. Because female cuckoos by most accounts use areas of 1 km or more, it is indeed a challenge to find all of the parasitized nests within their ranges of laying activity.

The low estimates of mean number of eggs laid by individual cuckoos in several studies may reflect the failure of the observer to find all host nests, particularly the nests that were deserted or destroyed at an early stage. It is impossible to determine directly without an intensive banding study of both adults and fledged young whether all nests within an area are found. However, it is possible to estimate the degree to which observers may have overlooked nests with cuckoo eggs by calculating the chances of loss of the eggs before the host nests were found. From studies of nests laying to hatching is about 62% (273 instances of parasitism, Čapek 1896) and survival from hatching to fledging is 43% (109 instances of hatched young, Owen 1912–21; Niethammer 1938). These data indicate about 27% survival of *Cuculus canorus* from laying to fledging. The figures permit an estimate of the extent of loss of eggs and young before they were found. In his study in northeastern France, Blaise (1965) obtained 82 cuckoo-years of data on reproduction rates. Most (36) females were reported to have laid only one egg in a year (rather, only one egg was *found*, a figure improbably low to be representative of actual laying rates of cuckoos in the population), 17 laid two, 17 laid three, 7 laid four, 1 laid five, 3 laid six, and 1 laid seven. In addition to these eggs, several instances of parasitism were discovered only when the young were found in the nest or recently fledged but still within the area where they could be matched with the eggs of a certain female cuckoo. A total of 23 young was found without their eggs having been seen. These young then represented the survival product of perhaps nearly 100 eggs laid by the cuckoos. (The estimates of hatching and nestling survival may be somewhat greater than the actual values because some loss of eggs and of nestlings before the observer found them in the nest may have occurred.) The ratios of cuckoos found first as young to those found as eggs was no lower in the areas where Blaise made his most frequent visits to the marshes (6/36 at Domjevin-Fremenil, 9/33 at Manoviller-Benamenit, 6/37 at Marainviller-Thiebaumenil) averages 19.8/100, whereas for the total sample the ratio averages 19.5/100. Thus it seems likely that his visits to the marshes (the visits were usually at least a week apart) were too infrequent to detect many of the eggs that were laid but then lost.

From field observations (mainly involving egg-collecting) the estimates of annual reproductive output in eggs laid by individual *Cuculus canorus* are summarized in table 5, together with estimates of African cuckoos from the present work. Chance (1940) obtained many of his yearly laying figures by increasing the availability of host nests to the cuckoos and although this resulted in 25 eggs being laid in 7 weeks, he estimated that undisturbed wild cuckoos probably lay 10–14 eggs. Niethammer in 1938 accepted as the most valid data at that time seasonal reproductive efforts of 16–22 eggs, reportedly based on Schiermann (1927), Rey (1892), and Heinroth and Heinroth (1926–28), though Schiermann reported smaller averages and the Heinroths (p. 301) state that the mean is 18 eggs. It seems probable to me that most of the records of individual cuckoos laying one to three eggs per season are of doubtful validity because of the chance that not all eggs laid were found. On the other hand, the variable number of eggs laid by many cuckoos points out that no set number is appropriate to describe laying in the parasitic cuckoos, but rather that cuckoos lay in proportion to the number of suitable host nests that they find during a season. Some may lay few and some, many.

Experimental evidence that increasing the number of available host nests will increase the number of eggs laid is amply provided by Chance's (1922, 1940) field work in which he collected eggs of cuckoos and hosts as the host clutches were completed. This forced the host pipits to nest and lay again and again, and each time they received again another parasitic egg from the cuckoo.

A possible trend in more recent publications and evident in table 5 is for lower values of the maximum number of eggs of *Cuculus canorus* to be recorded in a season. One wonders whether this is due to increased destruction

TABLE 5. Estimates of eggs laid in a season by parasitic cuckoos.

Species	Sample size (*N* birds)	No. of eggs laid	References
Cuculus canorus	31	7 (1 instance), 6 (3), 5 (1), 4 (10), 3 (16), 2 or 1 (numerous instances)	Blaise 1965[a]
	7	9; 8; 5, 4, 4; 7, 6	Čapek 1896
	13[b]	11, 18, 21, 15, 25; 4, 2, 1; 2; 8; 7; 15; 14	Chance 1940[c]
	7	3, 3, 2, 2, 4, 1, 1	Diesselhorst 1955
	5	1, 1, 1, 2, 3	Groebbels 1957
	–	4–6 in most, to 10	Harbø (in Makatsch 1955)
	2	"a great number"	Jenner 1788
	3	8, 15, 19	Krüger-Velthusen (1892)
	11	1 (5), 2 (2), 3 (2), 5, 6	Labitte 1948, 1954, 1958
	3	9, 10, 10	Moebert (in Groebbels 1957)
	1	5	Owen 1921
	4	5, 6, 6, 8	Paulussen 1957
	33[b]	1–29, mean 4 (calculated, average normally 17–22	Rey 1892
	18	1 (8), 2 (3), 3 (2), 5, 7, 9, 13, 16	Rey 1894
	2	7, 9	Ruthke 1951
	7	4, 6 (4), 7, 8,	Schiermann 1926
	2	8, 19	Scholey 1921[c]
	6	3, 3, 5, 5, 6, 6	Warncke and Wittenberg 1958
Cuculus clamosus	6	22 estimated, South Africa	present study[d]
Cuculus solitarius	2	? same as *clamosus*	present study[d]
Chrysococcyx caprius	25	16–21 estimated, eastern Cape Province	present study[d]
Chrysococcyx klaas	5	? same as *caprius*	present study[d]
Chrysococcyx cupreus	2	? same as *caprius*	present study[d]
Clamator jacobinus	28	19–25 estimated, South Africa	present study[d]
Clamator levaillantii	5	? same as *jacobinus*	present study[d]
Clamator glandarius	12	23 estimated, Eastern Cape	present study[d]
	2	15, 16 (captive, Germany)	von Frisch 1969

[a] These values are based on eggs plus young found in cuckoo's area. For values based on eggs alone, see p. 433.
[b] Several of Rey's birds were studied for more than one season, and one of Chance's females was recorded for five seasons.
[c] High values reported by Chance and Scholey resulted from artificially increased layings.
[d] Estimates in present study are calculated from mean observed ovulation rate and from duration of local breeding seasons, not from eggs found in nests.

of the habitats where cuckoo hosts build their nests (as at Deinvillers in Blaise's 1965 study) or to less diligent and thorough field work by the more recent observers. There is no biologically sound basis for von Haartman's (1971: 419) prejudice that the most recent data are the most reliable by virtue of their timeliness. The classic work of Jenner (1788) is of interest not only because he first mentioned several "cuckoo problems" but also because his observations were carefully made and well described.

The field data may best be summarized by saying that 5–10 eggs laid by a female *Cuculus canorus* may be found by an ornithologist who searches diligently throughout a season, but that a female sometimes lays as many as 10–20 eggs.

The observation in the present field study that breeding was curtailed in *Chrysococcyx caprius*, *Clamator glandarius*, and probably *Cuculus solitarius* in drought situations indicates that the number of eggs laid in a season by parasitic cuckoos is highly dependent on local conditions and on seasonal changes. In the first two of these species, the local hosts appeared to have curtailed their own breeding effort during the dry period; they may have in the case of the third species also, but the colonial nesting of the hosts of the first two species makes a comparison of their nests in wet and dry years more feasible. When host nests are available, the cuckoos appear to lay more or less continuously with occasional breaks of a few days. Similar results have been reported for captive breeding *Clamator glandarius*. Von Frisch has had females lay repeatedly in an aviary in a nest of a Magpie (*Pica pica*). Within 7 weeks one captive female laid 15 eggs, the other laid 16, an average weekly rate of two to three eggs (von Frisch 1969). This laying rate is the same as in the wild population at Thorn Grove, Cape Province, observed in the present study in 1965. On the other hand, cuckoos typically found in more mesic habitats than the acacia savanna of *Chrysococcyx caprius* and *Clamator glandarius* showed no such inhibition of ovarian development and laying. Birds found breeding in dry situations include *Clamator jacobinus* and *Cuculus clamosus*. Perhaps it is most advantageous for cuckoos and hosts of the

more arid regions to avoid breeding during the periods of extreme drought. Alternatively, birds of mesic areas are adapted to following the average conditions of their more stable environments and may breed regardless of short-term vagaries of the weather.

SUMMARY

Ovaries and oviducts of 103 females of nine species of brood parasitic cuckoos collected in Africa were examined in gross aspects and in serial histological sections. Using morphological techniques developed from studies of nesting birds of known recent breeding history, including nesting cuckoo species, the recent laying history of each individual cuckoo was determined by counting and aging the postovulatory follicles in its ovary. Samples of more than 20 laying females each were analyzed in *Chrysococcyx caprius* and *Clamator jacobinus* and smaller samples of laying female *Chrysococcyx klaas*, *Chrysococcyx cupreus*, *Clamator levaillantii*, *Clamator glandarius*, *Cuculus clamosus*, and *Cuculus solitarius* were available.

Eggs were usually laid on alternate days in all species examined. A few instances of successive ovulations were found between 24 and 48 hr, and some longer intervals of 3–8 days were recorded. Alternate-day laying is associated with embryonic development of the egg within the oviduct and this shortens the number of days required for incubation of the parasitic cuckoo eggs; egg retention may also enable cuckoos to time suitable layings in the nests of their hosts.

Clutch size was determined in two ways: (1) number of postovulatory follicles ovulated within series of alternate days and completed more than 2 days prior to sampling; and (2) number of postovulatory follicles in clutches currently being ovulated plus the number of growing, yolky postovulatory follicles likely to ovulate within a few days.

Clutch size of parasitic cuckoos was highly variable. Clutch size observed ranged from one to four in *Chrysococcyx klaas*, *Clamator levaillantii*, *C. glandarius*, and *Cuculus solitarius*; from one to five in *Chrysococcyx caprius* and *Cuculus clamosus*; and from one to six in *Clamator jacobinus*. Mean clutch sizes for all species appeared to be between two and four. In the two species represented by the most complete data, the mean number of eggs laid in a series was 2.71 in *Chrysococcyx caprius* and 3.46 in *Clamator jacobinus*.

The number of eggs laid during a typical week was determined for each species by (1) counting the proportion of birds with hard eggs in the oviduct (cuckoos carry hard eggs for a day before laying the egg), and (2) counting the postovulatory follicles and ovulating follicles in each ovary. Estimates of of 1.2–2.5 eggs per week were found for all species sampled. The average number of eggs laid by a female during a breeding season was estimated as the product of the mean number of layings in a week and the number of weeks in the laying seasons of the populations sampled. Most southern African cuckoos appear to have breeding seasons within these restricted, local populations of about 10 weeks. Results for all cuckoo species indicate average laying efforts of 16–26 eggs in a season.

Comparison of laying histories of individual cuckoos in normal summers with rain and in unusually dry summers shows that fewer eggs are laid in droughts. *Chrysococcyx caprius* and *Clamator glandarius* had decreased laying rates in dry situations, and the number of their local hosts that were nesting appeared smaller in the 2 dry years. On the other hand, the hosts of *Clamator jacobinus* appear to nest independently of such seasonal changes in weather, and in these cuckoos, as in *Cuculus clamosus*, no differences in reproductive effort were detected between drought times and times of normal rainfall in the breeding seasons. The correlation of laying by cuckoos in proportion to the availability of host nests suggested here is in agreement with the high rate of laying that occurred when nests were provided artificially in experiments with wild *Cuculus canorus* (Chance 1922; Scholey 1921) and captive *Clamator glandarius* (von Frisch 1969).

The laying biology of the African cuckoo species is similar to the European Cuckoo *Cuculus canorus* measured in terms of laying intervals and in the occurrence of clutch size variation in response to local environmental conditions. The different estimates of number of eggs laid per female *C. canorus* in Europe that were reported by recent field workers and by the older egg-collectors are probably due in part to the more recent studies having overlooked as many as half of the parasitized nests.

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LITERATURE CITED

Ali, S., and S. D. Ripley. 1969. Handbook of the birds of India and Pakistan. Volume 3. Oxford Univ. Press, Bombay.

Baker, E. C. Stuart. 1942. Cuckoo problems. Witherby, London.

Benson, C. W., R. K. Brooke, and C. J. Vernon. 1964. Bird breeding data for the Rhodesias and Nyasaland. Occ. Pap. Natl. Mus. S. Rhodesia 27B:30–105.

Benson, C. W., R. K. Brooke, R. J. Dowsett, and M. P. S. Irwin. 1971. The birds of Zambia. Collins, London.

Bent, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. U.S. Natl. Mus. Bull. 176.

Blaise, M. 1965. Contribution a l'etude de la reproduction du coucou gris *Cuculus canorus* dans le nord-est de la France. L'Oiseau et R. F. O. 35:87–116.

Brockway, B. F. 1968. Budgerigars are not determinate egg-layers. Wilson Bull. 80:106–107.

Buss, T. O., R. K. Meyer, and C. Kabat. 1951. Wisconsin pheasant reproduction studies based on ovulated follicle technique. J. Wildl. Mgmt. 15:32–46.

Čapek, V. 1896. Beiträge zur Fortpflanzungsgeschichte des Kuckucks. Ornithol. Jahrb. 7:41–72, 102–117, 146–157, 165–183.

Chance, E. P. 1922. The Cuckoo's secret. Sidgwick and Jackson, London.

Chance, E. P. 1939. The Cuckoo (*Cuculus canorus*). Simpkin Marshall, no loc., 12 p.

Chance, E. P. 1940. The truth about the Cuckoo. Country Life, London.

Cuthbert, N. L. 1945. The ovarian cycle of the Ring Dove (*Streptopelia risoria*). J. Morphol. 77:351–377.

Dalke, P. D. 1963. Ecology, productivity, and management of Sage Grouse in Idaho. J. Wildl. Mgmt. 27:811–841.

Davis, D. E. 1942. The regression of the avian postovulatory follicle. Anat. Rec. 82:297–307.

Davis, D. E. 1958. Relation of "clutch-size" to number of ova ovulated by Starlings. Auk 75:60–66.

Dean, W. R. F. 1971. Breeding data for the birds of Natal and Zululand. Durban Mus. Novitates 9:59–91.

Diesselhorst, G. 1955. Eizahl des Kuckucks. Vogelwelt 76:53–58.

Dominic, C. J. 1959. A study of the post-ovulatory follicle in the ovary of the domestic pigeon, *Columba livia*. J. Zool. Soc. India 12:27–33.

Erpino, M. J. 1969. Seasonal cycle of reproductive physiology in the Black-billed Magpie. Condor 71:267–279.

Floquet, A., and G. Grignon. 1964. Etude histologique du follicule post-ovulatoire chez la Poule. Compt. Rend. Soc. Biol. 158:132–135.

Friedmann, H. 1948. The parasitic cuckoos of Africa. Wash. Acad. Sci., Monogr. 1.

Friedmann, H. 1964. Evolutionary trends in the avian genus *Clamator*. Smithsonian Misc. Coll. 146 (4):1–127.

Friedmann, H. 1968. The evolutionary history of the avian genus *Chrysococcyx*. U.S. Natl. Mus. Bull. 265.

Groebbels, F. 1957. Rufe, Revier und Eizahl beim Kuckuck. Vogelwelt 78:89–94.

Hamilton, W. J., and M. E. Hamilton. 1965. Breeding characteristics of Yellow-billed Cuckoos in Arizona. Proc. Calif. Acad. Sci., 4th Ser, 32:405–432.

Hamilton, W. J., and G. H. Orians. 1965. Evolution of brood parasitism in altricial birds. Condor 67:361–382.

Harrison, R. J. 1969. Reproduction and reproductive organs, p. 253–348. *In* H. T. Andersen [ed.] The biology of marine mammals. Academic Press, New York.

Heinroth, O., and M. Heinroth. 1926–28. Die Vögel Mitteleuropas. H. Bermühler Verlag, Berlin.

Hunter, H. C. 1961. Parasitism of the Masked Weaver *Ploceus velatus arundinaceus*. Ostrich 32:55–63.

Jenner, E. 1788. Observations on the natural history of the Cuckoo. Phil. Trans. Roy. Soc. London 78:219–235.

Jensen, R. A. C., and M. K. Jensen. 1969. On the breeding biology of southern African cuckoos. Ostrich 40:163–181.

Jensen, R. A. C., and C. J. Vernon. 1970. On the biology of the Didric Cuckoo in southern Africa. Ostrich 41:237–246.

Kabat, C., I. O. Buss, and R. K. Meyer. 1948. The use of ovulated follicles in determining eggs laid by the Ring-necked Pheasant. J. Wildl. Mgmt. 12:399–416.

Kern, M. D. 1972. Seasonal changes in the reproductive system of the female White-crowned Sparrow, *Zonotrichia leucophrys gambelii*, in captivity and in the field. 1. The ovary. Z. Zellforsch. 126:297–319.

Klomp, H. 1970. The determination of clutch-size in birds, a review. Ardea 58:1–124.

Köster, F. 1971. Zum Nisverhalten des Ani, *Crotophaga ani*. Bonner Zool. Beitr. 22:4–27.

Krüger-Velthusen. 1892. Über einige Beobachtungen hinsichtlich des Fortpflanzungsgeschäftes unseres Kuckucks. J. Ornithol. 1892:449–450.

Labitte, A. 1948. Quelques notes sur le coucou

Cuculus canorus L. en pays drouais. L'Oiseau et R. F. O. 18:78–93.

LABITTE, A. 1954. Questions posées au sujet de la réproduction de *Cuculus canorus* L. L'Oiseau et R. F. O. 24:267–278.

LABITTE, A. 1958. Observations sur le coucou. L'Oiseau et R. F. O. 28:153–163.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

LIVERSIDGE, R. 1961. Pre-incubation development of *Clamator jacobinus*. Ibis 103a:624.

LIVERSIDGE, R. 1966. Fluctuations in a breeding population in the eastern Cape. Proc. Second Pan-African Ornithol. Congr., Ostrich Suppl. 6: 419–424.

LIVERSIDGE, R. 1971. The biology of the Jacobin Cuckoo *Clamator jacobinus*. Proc. Third Pan-African Ornithol. Congr., Ostrich Suppl. 8:117–137.

MAKATSCH, W. 1955. Der Brutparasitismus in der Vogelwelt. Neumann Verlag, Radebeul.

MUNDY, P. J., AND A. W. COOK. 1971. Sokoto province. (I)Sokoto town and environs. Nigerian Ornithol. Soc. Bull. 8:21–24.

NALBANDOV, A. V. 1959. Neuroendocrine reflex mechanisms: bird ovulation, p. 161–173. *In* A. Gorbman [ed.] Comparative endocrinology. John Wiley & Sons, New York.

NIETHAMMER, G. 1938. Handbuch der Deutschen Vogelkunde. Band II. Akademische Verlagsgesellschaft, Leipzig.

NIVEN, C. K., AND P. N. F. NIVEN. 1966. The birds of Amanzi, Uitenhage District, C. P. South Afr. Avifauna Ser., No. 34.

OTTOW, J., AND G. DUVE. 1963. Zur Kenntnis der Fortpflanzung von *Chrysococcyx caprius* und *Cuculus canorus gularis* in Süd-Africa. J. Ornithol. 106:431–439.

OWEN, J. H. 1912. Notes on mortality in nestling-cuckoos. Brit. Birds 6:330–333.

OWEN, J. H. 1913. Cuckoos' eggs and nestlings in 1913. Brit. Birds 7:233–234.

OWEN, J. H. 1914. Cuckoos' eggs and nestlings in 1914. Brit. Birds 8:118.

OWEN, J. H. 1915. Cuckoos' eggs and nestlings in 1915. Brit. Birds 9:96–97.

OWEN, J. H. 1916. Cuckoos' eggs and nestlings in 1916. Brit. Birds 10:141–142.

OWEN, J. H. 1917. Cuckoos' eggs and nestlings in 1917. Brit. Birds 11:160–161.

OWEN, J. H. 1918. Cuckoos' eggs and nestlings in 1918. Brit. Birds 12:142.

OWEN, J. H. 1919. Cuckoos' eggs and nestlings in 1919. Brit. Birds 13:109.

OWEN, J. H. 1920. Cuckoos' eggs and nestlings, 1920. Brit. Birds 14:134–135.

OWEN, J. H. 1921. Cuckoo eggs and nestlings, 1921. Brit. Birds 15:209–210.

PALUDAN, K. 1952. Contributions to the breeding biology of *Larus argentatus* and *Larus fuscus*. Videns. Medd. Dansk Naturh. Foren. 114:1–128.

PARMELEE, D. F., AND R. B. PAYNE. 1973. On multiple clutches and the breeding strategy of arctic Sanderlings. Ibis 115:218–226.

PAULUSSEN, W. 1957. Nieuwe gegevens over de eieren, de waarden en de biologie van de koekoek, *Cuculus canorus* L. Gerfaut 47:241–258.

PAYNE, R. B. 1965. Clutch size and numbers of eggs laid by Brown-headed Cowbirds. Condor 67:44–60.

PAYNE, R. B. 1966. The post-ovulatory follicles of blackbirds (*Agelaius*). J. Morphol. 118:331–352.

PAYNE, R. B. 1969a. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Red-winged Blackbirds. Univ. Calif. Publ. Zool. 90.

PAYNE, R. B. 1969b. Overlap of breeding and molting schedules in a collection of African birds. Condor 71:140–145.

PAYNE, R. B., AND K. PAYNE. 1967. Cuckoo hosts in southern Africa. Ostrich 38:135–143.

PEARL, R., AND A. M. BORING. 1918. Sex studies X. The corpus luteum in the ovary of the domestic fowl. Amer. J. Anat. 23:1–35.

PERRINS, C. M. 1967. The short apparent incubation period of the Cuckoo. Brit. Birds 60:51–52.

PRINGLE, N. L. 1946. Cuckoo eggs. Ostrich 17:368–369.

QUICKELBERGE, C. D. 1967. Winter breeding in Klaas' Cuckoo. Ostrich 38:205.

REED, R. A. 1968. Studies of the Diederik Cuckoo *Chrysococcyx caprius* in the Transvaal. Ibis 110: 321–331.

REY, E. 1892. Altes und Neues aus dem Haushalte des Kuckucks. R. Freese, Leipzig.

REY, E. 1894. Beobachtungen über den Kuckuk bei Leipzig aus dem Jahre 1893. Ornithol. Monatsschrift Deut. Vereins Schutz Vogelwelt 19:159–168.

ROMANOFF, A. L., AND A. J. ROMANOFF. 1949. The avian egg. John Wiley & Sons, New York.

RUTHKE, P. 1951. Die Brutvögel des Mönnegebietes im pommerschen Oderdelta. Ornithol. Abhandl. 11:1–40.

SCHIERMANN, G. 1926. Beitrag zur Schädigung der Wirtsvögel durch *Cuculus canorus*. Beitr. Fortpflanzungsbiologie der Vögel 2:28–30.

SCHOLEY, G. J. 1921. Another Cuckoo record. Brit. Birds 15:180–186.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York.

SKEAD, C. J. 1951–52. Cuckoo studies on a South African farm. Ostrich 22:163–175, 23:2–15.

SKEAD, C. J. 1972. A juvenile Klaas' Cuckoo *Chrysococcyx klaas* with its hosts in late June 1971. Ostrich 43:134.

SKUTCH, A. F. 1959. Life history of the Groove-billed Ani. Auk 76:281–317.

SLEPTSOV, M. M. 1948. [A method for studying the intensity of bird breeding by their ovaries.] SB "Okhrana prirody" 5:119–129.

SPENCER, O. R. 1943. Nesting habits of the Black-billed Cuckoo. Wilson Bull. 55:11–22.

TARBOTON, W. R. 1968. Check list of birds of the south central Transvaal. Witwatersrand Bird Club, Johannesburg.

VALVERDE, J. A. 1971. Notas sobre la biologia de reproduccion del Crialo *Clamator glandarius* (L.). Ardeola No. Especial:591–647.

VAN TIENHOVEN, A. 1968. Reproductive physiology of vertebrates. W. B. Saunders Co., Philadelphia.

VERNON, C. J. 1970. Pre-incubation embryonic development and egg "dumping" by the Jacobin Cuckoo. Ostrich 41:259–260.

VON FRISCH, O. 1969. Die Entwicklung des Häherkuckucks (*Clamator glandarius*) im Nest der Wirtsvögel und seine Nachzucht in Gefangenschaft. Z. Tierpsychol. 26:641–650.

VON HAARTMAN, L. 1971. Population dynamics, p.

391–459. *In* D. S. Farner and J. R. King [eds.] Avian biology. Volume 1. Academic Press, New York.

WARNCKE, K., AND J. WITTENBERG. 1958. Eizahl des Kuckucks. Vogelwelt 79:20–22.

WILLIAMSON, K. 1967. A bird community of accreting sand dunes and salt marsh. Brit. Birds 60:145–157.

WOODS, R. S. 1960. Notes on the nesting of the Roadrunner. Condor 62:483–484.

WYNNE-EDWARDS, V. C. 1939. Intermittent breeding of the Fulmar (*Fulmarus glacialis*) (L.), with some general observations on non-breeding in seabirds. Proc. Zool. Soc. London, A. 109:127–132.

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