

Egg-laying by the Cuckoo

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INTRODUCTION

The purpose of this paper is to summarise three aspects of egg-laying by the Cuckoo *Cuculus canorus*, namely the interval between the laying of successive eggs, the time of day of laying each egg, and the duration of laying. The data were collected by E. P. Chance in the years 1920-25 in Worcestershire, Shropshire and Radnorshire, and in 1939 in Surrey, and were mostly published in a dispersed form in his two books *The Cuckoo's Secret* (1922) and *The Truth about the Cuckoo* (1940); I have obtained some additional information from his egg collection and accompanying papers, now held in the Sub-department of Ornithology, British Museum (Natural History). The sources are given in detail in the appendix on pages 534-535. I have also examined copies of the ciné-films 'The Cuckoo's Secret' (made under Chance's direction in 1921 by the Regent Film Company Limited) and 'The Story of the Cuckoo' (made in 1922 by O. G. Pike), both of which were filmed while Chance was making some of the observations described in this paper.

CHANCE'S FIELD METHODS

The data I have used were believed by Chance to have involved seven female Cuckoos. Five of these were named by him as follows: *Cuckoo A*, *Successor to A* (both watched on Pound Green Common, near Upper Arley, Worcestershire), *Cuckoo S**, *Cuckoo L* (both watched on Sturt Common, Shropshire, 4 km WSW of Pound Green Common) and *Yellow Bunting-Cuckoo* (watched in fields immediately adjacent to Pound Green Common); the other two I have called *Bird no. 6* (watched on Bowdler Common, Knighton, Radnorshire) and *Bird no. 7* (watched at Witley, Surrey). Chance did not mention Pound Green Common or Bowdler Common by name in either of his books, but gave them on the data cards with his egg collection; Sturt Common was so named on these data cards but was called 'Sturt Fields' in Chance 1940.

Pound Green Common was an undulating piece of land about 500 by 400 metres in size, bordered by the Wyre Forest, fields and orchards; it supported mostly gorse, heather and bracken, with isolated deciduous trees and several small orchards (see plate 2 in

* Labelled *Mary Pickford* in Chance 1922 and in his papers in the British Museum, *Cuckoo J*/*Mary Pickford* in the egg collection, and *Cuckoo S*/*Mary Pickford* in Chance 1940.

Chance 1922, and plates 4-6 in Chance 1940). Sturt Common had a dense growth of heather.

Through intensive field-work by himself and several assistants, Chance was able to record the activities of these seven Cuckoos. With one minor exception—*Successor to A*, caught at a nest and ringed on 31st May 1925 and seen again prior to laying in a near-by nest two days later—the birds were unmarked throughout his observations; from their behaviour and the appearance of their eggs, however, he believed them to have been the same individuals under observation from day to day and from year to year. His intentions were principally to collect as many eggs of Cuckoos as possible, particularly from a known female, and to record their manner of deposition in the nest. With the former aim in mind, he deliberately removed the clutches of the host species, mostly Meadow Pipit *Anthus pratensis*, together with each Cuckoo egg as soon as it had been added, and he also made so-called 'decoy' nests in which the Cuckoos sometimes laid. Unparasitised nests were also removed to stimulate the host species to build again, and the total effect was to provide a succession of potential host nests in which the Cuckoos might lay as often as possible.

Having examined Chance's published papers (1919a, 1919b, 1921) and books, his egg collection and the notes in the British Museum, the two films, and the principal site of his observations (Pound Green Common), I believe that he was a good observer and was careful in his writings to distinguish his records from his opinions. Hence, although few of the people involved are now living and there are few written accounts available to support his observations, I have accepted them as reliable.

EGG-LAYING BY THE CUCKOO

The female Cuckoo first watches, from vantage points such as branches of trees, the nesting activities of potential host pairs. Occasionally she flies down to their nests, presumably to find them; eventually, after a period of watching which may last as long as several hours, she descends finally to lay her own egg in the host's nest. Thereafter she seems to take no further interest in that nest (Chance 1940).

In the vast majority of all the recorded instances, the female Cuckoo laid her eggs at intervals of two days (table 1). In a few cases, laying occurred apparently at greater intervals, the maximum recorded being five days. Although considerable effort was expended by Chance and his helpers in maintaining watch, complete continuity was not always achieved and the possibility that the birds sometimes laid undetected cannot be ruled out. In no recorded instance, however, was an interval of less than two days found.

Table 2. Number of eggs laid during each hour of the day by Cuckoos *Cuculus canorus*

Sources of data summarised here are listed in the appendix on pages 534-535. Times given by Chance were in British Summer Time, but in this table they are shown in Greenwich Mean Time (see page 531)

Individual	Year	08.01- 09.01- 10.01- 11.01- 12.01- 13.00 14.00 15.00 16.00 17.00 18.00 19.00 20.00 19.01- 20.00 TOTAL												
		09.00	09.00	10.00	11.00	12.00	13.00	14.00	15.00	16.00	17.00	18.00	19.00	20.00
<i>Cuckoo A</i>	1920	-	-	-	-	-	1	2	3	1	-	-	-	7
	1921	1	-	-	-	2	2	2	4	4	-	-	-	15
	1922	-	-	1	1	2	2	6	10	-	-	-	-	24
<i>Successor to A</i>	1924	-	-	-	-	-	-	-	-	4	2	1	-	7
	1925	-	-	-	-	-	-	1	2	5	3	3	-	14
<i>Cuckoo S</i>	1921	-	-	-	-	-	-	-	3	2	1	1	-	7
<i>Cuckoo L</i>	1921	-	-	-	-	-	-	-	-	-	-	-	1	1
<i>Yellow Bunting-Cuckoo</i>	1924	-	-	-	-	-	-	-	-	2	1	-	-	3
<i>Bird no. 6</i>	1921	-	-	-	-	-	-	-	1	-	-	-	-	1
<i>Bird no. 7</i>	1939	-	-	-	-	-	-	-	-	-	-	1	-	1
TOTAL		1	0	1	1	1	4	5	6	18	19	11	8	80
Percentage		1%	0%	1%	1%	1%	5%	6%	8%	23%	24%	14%	10%	100%

Table 1. Number of intervals of given length between apparently successive layings by Cuckoos *Cuculus canorus*

Sources of data summarised here are listed in the appendix on pages 534-535

Individual	Year	Length of interval (days)					TOTAL
		1	2	3	4	5	
<i>Cuckoo A</i>	1920	-	10	-	1	12	
	1921	-	12	-	2	14	
	1922	-	23	1	-	24	
<i>Successor to A</i>	1924	-	6	-	-	6	
	1925	-	10	-	-	12	
TOTAL		0	61	1	3	68	
Percentage		0%	90%	1%	4%	100%	

Table 3. Number of visits of given duration to the vicinity of the host's nest for laying by Cuckoos *Cuculus canorus*

Sources of data summarised here are listed in the appendix on pages 534-535

Individual	Year	Duration of visit (minutes)								TOTAL
		One or less	1+ to 5	5+ to 10	10+ to 20	20+ to 30	30+ to 40	40+		
<i>Cuckoo A</i>	1920	1	1	-	-	-	-	1	3	
	1921	10	1	1	1	-	-	-	13	
	1922	5	2	-	-	-	-	-	7	
TOTAL		16	4	1	1	0	1	23		
Percentage		70%	17%	4%	4%	0%	4%	100%		

Nearly all eggs were laid in the afternoon (table 2), mostly during 15.01-19.00 hours GMT. (Times in Chance's books are in British Summer Time—see, for example, Chance 1921, page 221, first egg.) In some cases (noted in the appendix) it is clear that, in their endeavour to obtain the laying of a Cuckoo egg in a particular host nest or to photograph the event, the observers accidentally or deliberately disturbed the female and possibly delayed her time of deposition; in one extreme situation a female was kept under a trap over a nest for an hour before she laid her egg. Nonetheless, the broad effect on the times of laying was probably not large and the general pattern of laying in the afternoon not altered. The data suggest that there was some individual variation between the females involved: thus *Cuckoo A* laid mostly during 12.01-17.00, while *Successor to A* did so during 17.01-20.00, each bird keeping to the same period from year to year. Although most of the eggs were laid in the nests of Meadow Pipits, a possible relationship between the time of laying and the behaviour of the host species cannot be excluded.

Chance emphasised repeatedly in his books that deposition was usually a brief event. The two films include several sequences which confirm this, though one cannot actually see that the female was in the nest of the host and one must accept Chance's word in this respect. Table 3 summarises the available information on the duration of the visit by the female to the immediate vicinity of the host's nest for the purpose of laying; since the majority of the hosts parasitised were Meadow Pipits, this usually means the time spent on the ground. In most cases the Cuckoo spent not more than a minute on the ground, and frequently rather less. During this time the bird alternately stood to look about herself and moved short distances through the herbage, apparently to find the nest, each activity normally lasting only a few seconds. On reaching the nest she apparently removed an egg of the host and then laid her own egg in the nest. Chance gave the following examples of the length of time spent by *Cuckoo A* on the nest for the purpose of egg deposition: 9, 7, 10, 16, 6, 4, 10 and 8 seconds* (mean 8.8 seconds). Having laid her own egg, she then departed from the nest and its vicinity more or less immediately.

DISCUSSION

In its passage through the oviduct, the egg enters in succession the infundibulum (where it is probably fertilised), the magnum (where the albumen is secreted), the isthmus (where the shell membranes are added), the uterus (where the shell is formed) and the vagina;

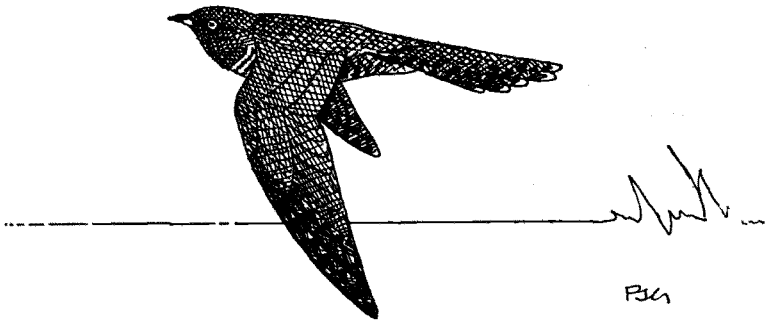
* From eggs 9, 11 and 14 of 1921, and eggs 7, 9, 10, 18 and 21 of 1922, respectively.

in the domestic hen *Gallus gallus* the proportions of the total time taken by the egg to pass through the oviduct are, respectively, about 1%, 13%, 5%, 81% and (presumably) nil in each of these regions (Olsen and Neher 1948, Romanoff and Romanoff 1949, Bell and Freeman 1971). Cell division commences before the egg is laid (Thomson 1964). In birds generally, successive eggs are laid either daily or at longer intervals; it has been suggested that the latter situation may be causally related to difficulties in the procurement of sufficient food to form the eggs (Lack 1968). While this may be true also of the Cuckoo, there is a little evidence that in this species embryonic development at the time of laying may be more advanced than in other birds, implying an unusually long period of retention of the eggs (Perrins 1967, Lack 1968), which might otherwise be laid at shorter intervals than every second day. However, egg retention is not necessarily an adaptation to parasitism, though it may be of potential advantage to a parasitic species (Perrins 1967).

Some species lay only at a particular time of day, many passerines (probably including at least some of those parasitised by Cuckoos) doing so around sunrise (Thomson 1964). Cuckoos, however, lay mostly in the afternoon. The long periods spent by the female apparently observing the nesting activities of potential host pairs around their time of laying, and her closer inspections on the ground prior to her visit for egg-laying, presumably enable her to synchronise her own laying with that of the host; laying later on the same day (rather than in the morning of the following day) would enable this synchronisation to occur with the least delay. While the Cuckoo may resemble other birds in ovulating shortly after the time of laying of the previous egg (Romanoff and Romanoff 1949), the probability that the nesting activities of potential host pairs are a proximate factor in her ovulation seems high for three reasons. First, she is absolutely dependent on the nesting of the host species for the rearing of her own egg. Second, synchronisation of laying is important in order that the host shall rear her egg, and that her young shall not hatch out much later than the host's own offspring and thereby be unable to eject them from the nest. Third, nests of the host species at a suitable stage for receiving Cuckoo eggs would be most readily available during the former's peak laying period, and several pairs of potential hosts could be kept under observation: at this time there would presumably be the least difficulty for the female Cuckoo in finding a nest at the right stage, and laying could occur as fast as ova are released. On the other hand, outside the host's peak laying period and in years and localities where even at the best of times host nests are scarce, the female may have difficulty in locating enough suitable nests to allow her to deposit her own eggs every second day. In these circumstances, egg deposition

would have to be curtailed. While copulation in the Cuckoo may possibly occur daily or almost daily, it may not necessarily be required as often as this, since spermatozoa may remain viable in the oviduct for a considerable period—for example, up to ten days in the domestic hen (Marshall 1961)—being released gradually from the vaginal glands where they are stored (Bell and Freeman 1971). However, once an ovum has been released and fertilised, it seems unlikely that its development could be reversed and laying prevented. Consequently, a mechanism to regulate the release of the ovum would presumably be required.

In non-parasitic species, egg deposition may take anything from about three minutes to several hours (Romanoff and Romanoff 1949, Seel 1968); the female Cuckoo, however, lays much more quickly, possibly to prevent disturbing the host to the point of desertion (Thomson 1964), but also perhaps to avoid attracting undue attention from predators to herself or to the host nests.



ACKNOWLEDGEMENTS

I am indebted to the Trustees of the British Museum for giving me access to E. P. Chance's egg collection, to the Royal Society for the Protection of Birds and the National Film Archive for showing me the films 'The Cuckoo's Secret' and 'The Story of the Cuckoo', and to Dr R. W. Arnold for criticising the manuscript of this paper.

SUMMARY

This paper summarises data collected by E. P. Chance on egg-laying by Cuckoos *Cuculus canorus*, mostly in the nests of Meadow Pipits *Anthus pratensis*. As a rule, laying occurred (1) at intervals of two days, (2) in the afternoon, and (3) very quickly: when visiting a nest to lay, the female spent no more than a minute in its immediate vicinity and, on average, only about nine seconds depositing the egg.

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Appendix. Sources of data used in this paper

Although Chance's two books report many of the same events and their accounts are closely similar, the data used here were derived from the following sources:

<i>Cuckoo A</i>	1920-21	Chance 1922
	1922	Chance 1940
<i>Successor to A</i>	1924-25	Chance 1940 and British Museum
<i>Cuckoo S</i>	1921	Chance 1940 and British Museum
<i>Cuckoo L</i>	1921	Chance 1922 (p. 157)
<i>Yellow Bunting-Cuckoo</i>	1924	Chance 1940 (pp. 127-129) and British Museum
<i>Bird no. 6</i>	1921	Chance 1922 (p. 166) and British Museum
<i>Bird no. 7</i>	1939	Chance 1940 (p. 151)

Those used in compiling tables 1-3 were derived from observations on the laying of the following eggs:

TABLE 1

<i>Cuckoo A</i>	1920	5-8, 10-18, 20, 21	Chance (1922) indicated that laying dates of eggs 1-4 were estimated; from his account, I think this true also of 9 and 19
	1921	1-15	—
	1922	1-25	The laying date of egg 3 was estimated, but in view of those of 2 and 4 being five days apart, the interval between those of 2 and 3 must have been either two or three days
<i>Successor to A</i>	1924	1-7	—
	1925	1-12, 14, 15	There was no positive evidence for the laying of 'egg 13'

TABLE 2

<i>Cuckoo A</i>	1920	11, 13, 14, 16-18, 20	—
	1921	1-15	Chance (1922) indicated that human disturbance possibly delayed the laying of eggs 8, 9 and 14
	1922	1, 2, 4-25	Disturbance: eggs 7, 13, 20, 24 and 25
<i>Successor to A</i>	1924	1-7	Disturbance: egg 5
	1925	1-12, 14, 15	Disturbance: egg 10

TABLE 2 (continued)

<i>Cuckoo S</i>	1921	2-4, 10-12, 14	Disturbance: egg 4. According to information in the British Museum, egg 11 was laid at 16.30 hours, not 15.25 as implied on page 163 of Chance 1922
<i>Cuckoo L</i>	1921	3	Disturbance
<i>Yellow Bunting-Cuckoo</i>	1924	7, 9, 13	—
<i>Bird no. 6</i>	1921	(one egg only)	—
<i>Bird no. 7</i>	1939	(one egg only)	—

TABLE 3

<i>Cuckoo A</i>	1920	14, 16, 20	—
	1921	1-6, 8-14	—
	1922	1, 2, 4, 9, 16, 18, 24	—

The European Cuckoo is an obligate parasite with the female always laying eggs in a host nest. However, only 40% of cuckoo species parasitise in this way. The Yellow-billed Cuckoo for example builds its own nest although it will also lay eggs in neighbouring Yellow-billed Cuckoo nests. Laying your eggs in the nest of a neighbour of the same species is recorded in many species including ducks, passerines, seabirds etc. The advantage of laying your eggs in somebody else's nest is that you don't have to take any further interest in the difficult business of rearing your offspring. Interest