INTRODUCTION

The Pied Crested Cuckoo (Clamator jacobinus Boddaert) occurs throughout the Indian sub-continent, from the plains up to an altitude of 2600 m in the Himalayas (Ali & Ripley 1969). Within this range it parasitizes a number of host species, in the plains mainly of the genus Turdoides, and in the hills laughing thrushes (Garrulax spp.).

Two sub-species of Pied Crested Cuckoo are found in India: Clamator j. jacobinus (Boddaert) in the southern part of the peninsular, where it is a local migrant, and Clamator jacobinus serratus (Sparrman) which is a summer visitor to the north, wintering apparently in Africa (Whistler 1928). The present paper describes studies carried out on the northern sub-species around Delhi, in the North Indian plains, concentrating on the effects of parasitism on the host species, and the adaptations of the parasite for its particular breeding strategy. The hosts involved were the Jungle Babbler (Turdoides striatus (Dumont), the Common Babbler (T. caudatus (Dumont)), and the Large Grey Babbler (T. malcolmi (Sykes)). All these species live in groups of three to twenty individuals, of which only one pair breed at a time, and all adult members of the group assist in incubation and feeding the nestlings.

One other species of brood parasite, the Hawk-cuckoo (Cuculus varius Vahl) was also found in the study area, but only two eggs were found in babbler's nests. Elsewhere in India this species parasitizes the nests of all the above-mentioned hosts (Baker 1942).

This study on Pied Crested Cuckoos and their effect on the breeding of Turdoides species was carried out as part of a general study on the ecology of Turdoides, and experimental work on cuckoo problems was limited by the necessity to cause as little disturbance as possible to the babblers. Avian nomenclature follows Ali & Ripley (1969, 1971).

METHODS

Observations were carried out from 1 August 1971 to 15 October 1973, and hence covered two complete breeding seasons and part of a third. The area selected for the study formed part of the reserved forest near Delhi, known as the Ridge. It consisted of mixed Acacia/Prosopis woodland, intermingled with low scrub dominated by Zizyphus nummularia White & Walker-Arnold, with scattered Butea monosperma (Lamark) trees.

Ten groups of Jungle Babblers, totalling about seventy-five birds, were selected for intensive study, and all nests of these groups were found. An attempt was made to find all nests of Common Babblers in the same area, but this was unsuccessful. Observations of fledged young and trapping of birds in juvenile plumage, suggested that about 70% of nests were found in 1972, and perhaps 80% in 1973. Only a few nests of the Large Grey Babbler were found, as this was less common than the other two species in the study area.
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Not all nests were located at the same stage. Only a few were found during building and laying, during the period when cuckoos were present, and most were found during incubation or the early nestling period. Sample sizes vary for different statistics because not all nests yielded the same kind of information.

Dates of laying were calculated for nests found with incomplete clutches (one or two eggs), or nests in which the young were seen and aged by weight. In the latter case the date was calculated by estimating the incubation period as fifteen days from the laying of the first egg for the babblers, and twelve days for the Pied Crested Cuckoos (twelve days in four cases, eleven or twelve in another). Jungle Babblers began incubation from the laying of the first egg, whereas in Common Babblers incubation was only intermittent until the third egg. Hatching of the first chick was about the fifteenth day for both species, however. A nest found containing a cuckoo nestling and one or more babbler nestlings was used to calculate the date of laying for both the babblers and the cuckoo, but not for recording the clutch size, as some babblers might have died and been removed.

Nests found during building were checked daily in order to record the laying of the first egg, and each egg was individually marked with a felt-tipped pen as soon as possible after laying, which took place generally 2–4 h after sunrise. Cuckoos’ eggs were also marked to check whether they were sometimes removed. Nests were again checked daily about the time of hatching, but were otherwise checked every two days.

During the nestling period the young in some nests were weighed at two-day intervals, beginning on day two (hatching of the first egg = day one), in order to measure the growth rate of young cuckoos, and to compare the growth rates of babblers with and without cuckoos. In cases where nests were difficult to climb up to, checks were made only as often as was necessary to determine the dates of laying and hatching, and the subsequent success, and no weighings were made.

Close observations were made from a hide at a number of nests during the incubation and nestling periods, in order to observe the behaviour of the parent babblers and of other group members. This was always done between dawn and midday.

Many young cuckoos were removed from the nest ten days after hatching so that their gizzard contents could be examined as part of a study on the food of the babblers. These birds were already capable of scrambling out of the nest, and they were counted as having fledged. They were not removed in cases where the cuckoo was the only surviving nestling, as this would have released the babblers to nest again immediately, and hence upset the concurrent study of babbler population dynamics. In some other cases nestling cuckoos were allowed to fledge in order to observe the date of fledging, and behaviour of the babblers towards the cuckoo after fledging, and the period of post-fledging dependence.

Pied Crested Cuckoos’ eggs closely resemble those of their hosts in colour and size, although the eggs of the Common Babbler are somewhat smaller. Baker (1942) gives the mean weight of 167 North Indian Pied Crested Cuckoos’ eggs as 4·58 g, measurements 23·9 × 18·6 mm, and the measurements of 100 Jungle Babblers’ eggs averaged 25·2 × 19·6 mm (Ali & Ripley 1971). In the present study Jungle Babblers’ eggs were found to average slightly smaller than those of the cuckoo, but there was no significant difference in weight. Common Babblers’ eggs average 21·1 × 16·1 mm (Baker 1932). All are turquoise blue.

Intact cuckoos’ eggs could be identified from those of their host by their less glossy texture, as mentioned by Whistler (1935). When broken they were easily identified by the thick chalky shell, much thicker than a babbler’s shell. Both Hume (1890) and Ali & Ripley (1969) mention that the cuckoos’ eggs can be identified from those of their host by
their more rounded oval shape, but this criterion was not found to be satisfactory in all cases because babbler's eggs varied considerably between different females, and more than one female may occasionally lay in the same nest. Babblers eat the shells of their own eggs completely after the young have hatched, but apparently find the cuckoos' eggs too difficult to cope with, because on several occasions these were found on the ground 20–60 m from the nest.

The adult size of the cuckoo falls in the middle of the range of its hosts. The weights of two trapped at Delhi, and of four given by Ali & Ripley (1969) fall between 61–74 g, exactly the same range of weights as are found in the Jungle Babbler, Common Babblers trapped in the Delhi area weighed 28–43 g and Large Grey Babblers 72–82 g.

**Behaviour of the Pied Crested Cuckoo**

Immediately after their arrival in the breeding area Pied Crested Cuckoos perform noisy courtship chases, often involving several birds, and carrying them over long distances. Individuals also call loudly, either perched prominently in the top of a tree, or in flight. The intensity of the chases, and the amount of vocalization, falls sharply after the end of July, and the birds are rather silent in the second half of the season. Apart from the courtship chases they are usually seen alone or in pairs. The chases and vocalizations are presumably concerned with pairing, and perhaps with the establishment of territories.

While feeding or resting the cuckoos are not generally molested by babblers, although Pied Crested Cuckoos flying over usually elicited an alarm call. If they approached within 20 m of a babbler's nest, however, they were vigorously chased off. The Hawk-cuckoo, on the other hand, perhaps because of its close resemblance to an Accipiter hawk, elicits an immediate mobbing response from babblers wherever it is encountered.

Pied Crested Cuckoos were seen feeding mainly in open scrub, taking large hairy caterpillars from on or near the ground, and sometimes feeding on fruit. Single birds were regularly found perching in the woodland canopy, and although sexes are indistinguishable in the field, it seems likely that these birds were females searching for nests of the Jungle Babbler. One bird, followed for an hour, perched frequently for periods of up to 5 min, before shifting 20–50 m. At one point it examined the unused nest of a Jungle Babbler, perching beside it for a minute before moving on.

During observations at babblers' nests Pied Crested Cuckoos were seen to approach on a number of occasions. Usually a non-incubating bird perched nearby would chase off the cuckoo, but when no other bird was present the incubating bird would give chase as soon as the cuckoo approached within 3–4 m.

In the course of one continuous watch from dawn on the eighth day of incubation a cuckoo approached the nest at 07.30 hours and the incubating bird (the female) took off in pursuit. Because of the restricted view from the hide, the two birds were immediately lost from sight. About 30 s later the cuckoo, or another, re-appeared, perched briefly in the thorny twigs which curved over the nest, and then flew off. The time spent above the nest was not more than 5 s and the cuckoo did not settle into the cup, but remained perched at least 15 cm above it. The babbler returned about a minute later and settled onto the eggs.

At 10.00 hours I inspected the nest, which at dusk the previous day had contained four babbler's eggs, and found that it now contained four babbler's eggs and one cuckoo's egg. One of the babbler's eggs showed a circular depressed crack on the upper side, which was probably caused by the impact of the cuckoo's egg falling on it. The depression was similar to several that had previously been observed on babbler's eggs in nests.
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parasitized by cuckoos. Most eggs cracked in this way did not hatch, but at least one did, although the crack was sustained on the third day after laying.

If this observation reveals the habitual laying technique of the Pied Crested Cuckoo then it would explain not only the number of depressed circular cracks, but also the ability of the cuckoos to lay in apparently inaccessible nests of the Common Babbler, built in dense thorn bushes. As Lack (1968) has suggested, the function of the very thick egg shell is probably to protect the egg when falling into the nest. In three cases cuckoos’ eggs were found, after hatching, to have double shells, the inner being separated from the outer by a duplicate egg membrane. The occurrence of this abnormality may be encouraged by the necessity for very strong shells. Liversidge (1971) found that the eggs of Clamator jacobinus serratus sometimes escaped predation when those of their host were eaten, and this might also be due to the greater thickness of their shells.

No evidence of egg removal by the female cuckoo was recorded, although this occurs in the Great Spotted Cuckoo (C. glandarius (Linnaeus)) (Mountfort & Ferguson-Lees 1961), and Ali & Ripley (1969) suggest that it also occurs in the Red-winged Crested Cuckoo (C. coronandus (Linnaeus)). A comparison of babbler clutch size in nests with and without cuckoos’ eggs showed that clutches without tended to average larger than those with (see below, Table 5), in the case of the Jungle Babbler, but this was not observed in the Common Babbler.

In nests where eggs were marked immediately after they had been laid none subsequently disappeared simultaneously with the arrival of a cuckoo’s egg. It is possible that some or all of the difference in observed clutch sizes is due to the removal by babbler of eggs cracked in the course of egg laying by the cuckoos, which was recorded once, but the difference is not statistically significant, and may be due to chance.

Ali & Ripley (1969) also suggest, very tentatively, that young Pied Crested Cuckoos may remove the eggs or young of their host from the nest, in the same way that young European Cuckoos (Cuculus canorus Linnaeus), do, but no evidence of this habit was found, either in the present study, or in Liversidge’s observations on the same species in South Africa. In eight out of the twenty-seven nests from which cuckoos fledged successfully at least one babbler was also fledged, and this was also true for two of the four cases in which two cuckoos were fledged from the same nest. Young babbler disappeared only in cases where the cuckoo hatched two or three days before the first babbler, and was large enough to monopolize the food supply. Dead babbler chicks, clearly starved, were found in several nests containing young cuckoos.

Pied Crested Cuckoos continued to be fed for two to three weeks after leaving the nest. When fledged from a nest without young babbler the cuckoo followed its foster group, uttering continual begging calls. These seem to have had only a weak attraction for Jungle Babblers, however, because birds rarely flew more than a few metres to feed a young cuckoo. Instead the cuckoo flew down, begging loudly, as soon as it saw a babbler find an attractive food item. Young babbler generally remained perched inside dense vegetation during the first week after fledging, the adults bringing food to them from surrounding areas. When they were present the cuckoo remained perched nearby, begging from the adults as they arrived.

There was some suggestion, from the relatively poor condition of cuckoo nestlings in nests where no babbler nestling survived, that the adult babbler began to lose interest in the young cuckoo in the last few days before it left the nest, by which time the black and white plumage of the adult was becoming conspicuous. Sanjeeva Raj (1964) mentions an instance in which a young cuckoo was ignored by its foster group (of Turdoides affinis
(Jerdon)) after fledging, and disappeared within two days, although in this instance one young babbler was also fledged.

At night the babbler group roost in contact with one another, side by side along the branch of a tree. The juvenile cuckoo does not attempt to join the huddle, perching alone a few metres away, and flying to join the group again when it sets out the next morning.

**Timing of breeding in host and parasite**

Figure 1 shows the distribution of egg laying dates among the three species of babblers during 1972 and 1973. The length of the breeding season is variable, and apparently depends on the rainfall. In 1972, a relatively dry year, only one Jungle Babbler clutch was laid in October, whereas in 1973, after a prolonged rainy season, there were five October nests.

Rainfall in Delhi occurs mainly in the months July–September, as a result of the south-west monsoon, but some also falls during the winter, and this produces a flush of vegetation and insect life in spring (March). The two breeding peaks shown in Fig. 1 will be referred to respectively as the spring and the rainy season peaks, the second beginning quite abruptly with the arrival of the first heavy monsoon showers.

The first Pied Crested Cuckoos arrived in Delhi about the end of the first week of June, a date roughly coinciding with the arrival of the south-west monsoon front on the west coast of India. The rain does not usually reach Delhi until almost a month later. Whistler (1928) gives the first dates of arrival for Pied Crested Cuckoos all over North India. The
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earest is 15 May, but for most places the date is in the last week of May or the first of June.

The airstream over the Arabian Sea during May is generally west-north-west, but in June it changes to west-south-west, making it favourable for migration from the coast of East Africa. The onset of this change is controlled by the northward movement of the inter-tropical front (Ramakrishnan, Sreenivasaiah & Venkiteshwaran 1958). The absence of isolated early records of Pied Crested Cuckoos suggests that birds may await the onset of the favourable west-south-west winds before undertaking the crossing of the Arabian Sea.

Table 1. Comparison of numbers of cuckoos’ eggs laid, and intensity of parasitism in three breeding seasons, June–September only; for Jungle and Large Grey Babblers all nests were found; figures for Common Babblers are estimated on the assumption that 70% of nests were found in 1972 and 80% in 1973; figures in brackets are numbers of nests

<table>
<thead>
<tr>
<th></th>
<th>Jungle Babbler</th>
<th>Common Babbler</th>
<th>Large Grey Babbler</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1971 Observed no. of cuckoos’ eggs/nest</td>
<td>2-0(5)</td>
<td>-</td>
<td>0-5(4)</td>
<td></td>
</tr>
<tr>
<td>1972 Nests available (A)</td>
<td>24</td>
<td>21-5</td>
<td>5</td>
<td>50-5</td>
</tr>
<tr>
<td>Cuckoos’ eggs/nest (B)</td>
<td>0-85(20)</td>
<td>0-31(13)</td>
<td>0-2(5)</td>
<td></td>
</tr>
<tr>
<td>Total cuckoos’ eggs (A x B)</td>
<td>20-4</td>
<td>6-7</td>
<td>1-0</td>
<td>28-1</td>
</tr>
<tr>
<td>1973 Nests available (A)</td>
<td>19</td>
<td>28-8</td>
<td>5</td>
<td>52-8</td>
</tr>
<tr>
<td>Cuckoos’ eggs/nest (B)</td>
<td>1-31(13)</td>
<td>0-5(18)</td>
<td>0-2(5)</td>
<td></td>
</tr>
<tr>
<td>Total cuckoos’ eggs (A x B)</td>
<td>24-8</td>
<td>14-4</td>
<td>1-0</td>
<td>40-2</td>
</tr>
</tbody>
</table>

Table 2. Numbers of babblers’ nests available in each month, and numbers of cuckoos’ eggs laid per nest for 1972 and 1973 seasons only; estimates of Common Babbler nests calculated as for Table 1; figures in brackets are numbers of nests

<table>
<thead>
<tr>
<th></th>
<th>Jungle Babbler</th>
<th>Common Babbler</th>
<th>Large Grey Babbler</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>June Nests available</td>
<td>7</td>
<td>2-5</td>
<td>0</td>
<td>9-5</td>
</tr>
<tr>
<td>Cuckoos’ eggs/nest</td>
<td>1-2(5)</td>
<td>0(2)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Total cuckoos’ eggs</td>
<td>8-4</td>
<td>0</td>
<td>-</td>
<td>8-4</td>
</tr>
<tr>
<td>July Nests available</td>
<td>18</td>
<td>11-8</td>
<td>3</td>
<td>32-8</td>
</tr>
<tr>
<td>Cuckoos’ eggs/nest</td>
<td>1-06(17)</td>
<td>0-6(5)</td>
<td>0(3)</td>
<td></td>
</tr>
<tr>
<td>Total cuckoos’ eggs</td>
<td>19-1</td>
<td>7-1</td>
<td>0</td>
<td>26-2</td>
</tr>
<tr>
<td>August Nests available</td>
<td>8</td>
<td>14-4</td>
<td>2</td>
<td>24-4</td>
</tr>
<tr>
<td>Cuckoos’ eggs/nest</td>
<td>0-5(4)</td>
<td>0-6(10)</td>
<td>0(2)</td>
<td></td>
</tr>
<tr>
<td>Total cuckoos’ eggs</td>
<td>4-0</td>
<td>8-6</td>
<td>0</td>
<td>12-6</td>
</tr>
<tr>
<td>September Nests available</td>
<td>10</td>
<td>21-4</td>
<td>5</td>
<td>36-4</td>
</tr>
<tr>
<td>Cuckoos’ eggs/nest</td>
<td>1-14(7)</td>
<td>0-29(14)</td>
<td>0-4(5)</td>
<td></td>
</tr>
<tr>
<td>Total cuckoos’ eggs</td>
<td>11-4</td>
<td>6-2</td>
<td>2-0</td>
<td>19-6</td>
</tr>
<tr>
<td>Estimate of total cuckoos’ eggs laid</td>
<td>42-9(64-2%)</td>
<td>21-9(32-8%)</td>
<td>2-0(3-0%)</td>
<td>66-8</td>
</tr>
</tbody>
</table>
Adult Pied Crested Cuckoos disappeared from the study area by the end of September. No cuckoo's egg was recorded being laid later than 14 September, which means that the latest that a young cuckoo might become independent would be about the end of October. The departure of the cuckoos again coincides with a change in the direction of the airstream over the Arabian Sea, which switches to easterly in October.

Table 1 shows the number of babblers' nests available to be parasitized during the 1972 and 1973 seasons (figures for the Common Babbler were estimated by assuming that 70% of nests were found in 1972 and 80% in 1973). The observed rate of parasitism in cuckoos' eggs per nest is also shown for all nests which could be examined, and which were available to cuckoos for at least eight days after the laying of the first egg. From these figures it is possible to estimate the total number of cuckoos' eggs laid in the study area as 28.1 in 1972 and 40.2 in 1973.

The intensity of parasitism in cuckoos' eggs per nest was lowest for all three host species in 1972, a year of below average rainfall for North India. General observations suggested that fewer cuckoos were present in the study area in that year, and it is possible that cuckoos were concentrating further south, in areas of adequate rainfall.

Table 2 shows the intensity of cuckoo parasitism for the four months during which the cuckoos were present. Only the 1972 and 1973 seasons are included because the 1971 season was incomplete. In the Jungle Babbler peak intensity of cuckoo parasitism occurred in July and September, the months in which most nests were initiated. In August more
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eggs were laid in Common Babblers' nests than in other months, and it is possible that there is a tendency for cuckoos to switch their attention to this species while there is a hiatus in the initiation of Jungle Babbler nests.

The monthly totals also suggest that the cuckoos reduce their laying rate in August, compared to July and September, and this is even more true when the fact that laying finishes in the middle of September is taken into consideration. Payne (1973) showed that Clamator jacobinus breeding in South Africa lay in clutches of one to four eggs with a pause between each. It is possible that in the Delhi area cuckoos find a prolonged pause in egg laying necessary in mid-season, which may be reflected in the reduced intensity of parasitism in August.

Density of cuckoos in relation to their hosts

It was not possible to make an accurate census of the number of Pied Crested Cuckoos in the study area at any one time. In June, soon after their arrival, parties of three and four birds were seen commonly, but after the beginning of August only pairs or solitary individuals were observed. Sexes were not distinguishable in the field, but parties of two seen after the beginning of July were assumed to be mated pairs. General observations over the whole study area in 1973 suggested that at least three pairs were present throughout the breeding season.

The estimated number of cuckoos eggs laid in the two full seasons seems well within the capabilities of three female cuckoos, since Payne (1973) has shown that female Clamator jacobinus lay at a rate of 1.9–2.5 eggs per week. There were no periods recorded when this rate was being exceeded within the study area, assuming the presence of three female cuckoos.

During the rainy season the study area contained about 115 Jungle Babblers in twenty groups, 120 Common Babblers in fifteen groups, and sixteen Large Grey Babblers in four groups. As only one pair bred at a time in each group the ratio of parasite to hosts in terms of pairs can be estimated as about 1:13, assuming three pairs of cuckoos.

Young cuckoos were easily found by their persistent calls, and probably all those fledged in the study area were noted. Nine were seen in 1972 (32% of eggs laid) and eighteen in 1973 (45% of eggs laid). Assuming the presence of three pairs of cuckoos in 1973, this suggests a reproductive rate of six fledged young per pair.

Availability of nests

For the cuckoos the maximum rate of laying can only be maintained as long as suitable nests are available to parasitize. Some evidence suggests that babbler groups which are particularly affected by cuckoo parasitism tend to synchronize their nesting, a factor which would reduce the chances of a cuckoo's egg being laid in any particular nest.

Figure 2 shows the distribution of egg laying by babblers in ten-day periods during the 1972 and 1973 seasons. Jungle Babbler groups are divided into two categories on the basis of the type of habitat which they occupy (1) holding territories largely within closed canopy woodland, (2 and 3) holding territories partly (2), or wholly (3) outside closed canopy woodland. A study of the breeding success of Jungle Babblers shows that groups with territories outside closed canopy woodland make fewer nesting attempts than those with woodland territories, and that the nesting of non-woodland groups is more concentrated in the season when cuckoos are present, presumably because of lack of suitable food in these territories at other times. Because of this non-woodland groups suffer more drastically from the effects of cuckoo parasitism.
If cuckoo parasitism causes selection for synchronization of nesting the effect should be most noticeable in the host population which is most affected. A comparison of the histograms in Fig. 2 shows that Common Babblers, which suffer less reduction in recruitment due to cuckoos than do Jungle Babblers (see below), have the least tendency to synchronize their nesting, and that the Jungle Babblers nesting in woodland (1) are less synchronized than those outside (2 and 3). The difference between the two categories of Jungle Babbler is statistically significant ($\chi^2 = 6.67$, df = 2, $P = <0.05$), and that between Common Babblers and the woodland Jungle Babbler groups approaches this level ($\chi^2 = 5.93$, df = 2, $P = 0.1-0.05$). The black line in each histogram is calculated from the Poisson distribution having the observed mean, and shows the expected distribution if nests were initiated randomly throughout the season. In comparison with this Common Babblers’ nests appear to be overdispersed in time, though not significantly, woodland Jungle Babblers (1) are more or less randomly dispersed, and non-woodland Jungle Babblers show a tendency to clump their nests.

**Timing of egg laying in relation to the host’s clutch**

Table 3 shows the timing of egg laying by Pied Crested Cuckoos in relation to the laying of their host’s clutch, for the nests of Jungle and Common Babblers. Twenty out of thirty-eight (52.5%) were laid during the host’s laying period, but one was laid as late as the twenty-first day, when the nest contained half grown nestling babblers. Nestling cuckoos hatched from eggs laid later than the eighth day from the laying of the first Jungle Babbler’s egg did not survive to fledging, apparently because the young babblers were able to monopolize the food supply, and selection against late laying is therefore strong.

Table 3. *Timing of cuckoos’ eggs in babblers’ nests*

<table>
<thead>
<tr>
<th>No. of days from laying of first babbler’s egg (day 1)</th>
<th>1–4</th>
<th>5–8</th>
<th>9–12</th>
<th>13–16</th>
<th>17–20</th>
<th>21–24</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jungle Babbler</td>
<td>16</td>
<td>7</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Common Babbler</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td>20</td>
<td>10</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Chance (1922, 1940) has shown that European Cuckoo females locate the nests of their hosts during the building stage. This enables them, almost invariably, to lay their eggs during the host’s laying period. The large proportion of Pied Crested Cuckoos’ eggs laid after the end of their host’s laying period suggests that they may not be able to find enough nests during the building stage. Jungle Babblers tend to be rather inconspicuous while nest building, much of the work being done in poor light just before going to roost, and this may cause difficulty for the cuckoo.

Resistance from the babblers may also prevent cuckoos from depositing their eggs at the optimum time, although this implies that the cuckoo is capable of retaining an egg if frustrated. On several occasions Jungle Babblers were seen to successfully drive off cuckoos which had approached to within a few metres of their nest, although in these instances it is possible that the cuckoo was merely making an inspection. Several babblers usually combined during these interactions and it seems unlikely that the cuckoo could have succeeded in laying in the face of opposition from a number of birds of its own size.

Liversidge (1961) showed that in one case an egg of *Clamator jacobinus* collected immediately after laying, had developed to a stage equivalent to 17–20 h after the beginning of incubation in the domestic fowl. There was no suggestion that this egg had been
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delayed abnormally, but it indicates that retention can occur. Perrins (1967) suggested that eggs are normally retained up to 24 h by the European Cuckoo, and that this explains, in part, the very short incubation period observed for this species. Two eggs removed in the present study on the day of laying showed no signs of premature development to the naked eye, although both had been laid in unsuitable nests already containing nestling babblers.

Eggs laid well beyond the end of the host's laying period may result from females being frustrated at their first choice nest. Accidental hosts are uncommon for the Pied Crested Cuckoo, and it seems probable that the species prefers to lay in the nest of the correct host at the wrong time, rather than that of the wrong host at the right time, the apparent preference of the European Cuckoo when frustrated (Chance 1922).

Multiple laying by cuckoos in the same nest was quite frequent in the study area. The following intervals were observed between successive eggs laid in the same nest: 1, 2, 2, 3, 3, 4, 4, 7, 7 and 12 days. The preponderance of two- and three-day intervals over nil- and one-day intervals suggests that the same female may often be involved if, as is true for the majority of parasitic cuckoos (Payne 1973), the eggs are laid at two-day intervals. Two young cuckoos were reared successfully from the same nest on four occasions out of the eleven which indicates that there is little disadvantage in laying at least two eggs in the same nest. In two cases, however, two eggs laid in the same nest were sufficiently dissimilar in shape to suggest the presence of two females.

Table 4. Distribution of numbers of cuckoos' eggs per nest, all seasons

<table>
<thead>
<tr>
<th>Number of nests with 0, 1, 2, 3 or 4 eggs</th>
<th>Proportion of nests parasitized</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Jungle Babbler</td>
<td>11</td>
</tr>
<tr>
<td>Common Babbler</td>
<td>19</td>
</tr>
</tbody>
</table>

Table 4 shows the distribution of the number of Pied Crested Cuckoos' eggs per nests for the Jungle and Common Babblers. Out of forty-three eggs laid in Jungle Babblers' nests eighteen were laid in nests already containing one or more cuckoo's eggs, but the same for Common Babblers' nests was 12:1. The fact that, for both species, nests containing only one egg predominated suggests that double laying occurred only when no suitable unparasitized nest was available.

Relative growth rates of babbler and cuckoo nestlings

In addition to having an incubation period three days shorter than that of their hosts, nestling Pied Crested Cuckoos also develop more rapidly after hatching, being ready to leave the nest at eleven to twelve days old compared to fourteen to sixteen days for the Jungle Babbler. The mean maximum rate of growth recorded for eight nestling cuckoos was 6.5 g per day, compared with a mean of 5.2 g per day for Jungle Babblers (n = 21), which have the same sized egg, and 2.7 g per day (n = 5) for Common Babblers. The burden of rearing a cuckoo, therefore, appears to be about twice as great for Common as for Jungle Babblers, and a proportionately higher loss of nestling babblers was noted in the former species.

Figure 3 shows two examples of the growth curves of nestling Pied Crested Cuckoos and those of the Jungle Babbler nestlings in the same nest. Not only do the cuckoos achieve a higher maximum rate of growth, but this rate is reached earlier, and carried on to a higher weight level before slowing down. This is despite the fact that the adult weights
of the two species are the same. The rate of growth during the first few days after hatching was appreciably slower for the cuckoo in nest BLB2, hatching two to three days behind its three babbler nest-mates, than for the other cuckoo which had only one babbler to compete with on hatching. In nest P2 it was the late hatching babbler which was slow to accelerate its growth rate, a pattern seen in late hatching nestlings irrespective of the presence of a cuckoo. All nestlings shown in Fig. 3 fledged successfully.

No difference was found between the rates of growth of babbler nestlings with and without cuckoos. Disappearance of nestlings due to starvation occurred only during the first few days after hatching, usually in the first day, and this applied equally to babbler and cuckoo nestlings. Those which survived beyond this point developed normally, and at the normal rate, regardless of their size in relation to that of other nestlings. The cuckoo nestlings can apparently monopolize the attention of the adult babblers only when the babbler nestlings are very small.

At one nest, containing a six-day-old Common Babbler nestling, and a seven-day-old cuckoo nestling, both were fed with equal frequency, despite the fact that the cuckoo out-weighed the babbler by 41 g to 16 g. The babbler chick had difficulty in accepting some of the larger food items presented, however, and these were then passed on to the cuckoo, which must, in this way, have received a greater weight of food.

The effect of parasitism by the Pied Crested Cuckoo on the reproductive success of its host

Pied Crested Cuckoos were found to affect the rate of increase of their hosts populations in the following ways.

(1) A cuckoo’s egg may crack one of the hosts eggs during laying, so that it fails to hatch.
(2) If the cuckoo hatches early one or more of the host’s nestlings may die of starvation.
Brood parasitism by the pied crested cuckoo

(3) Where a cuckoo is the only fledgling its dependence delays the initiation of another nesting attempt.

(4) Young babblers reared during the period when cuckoos are present have a higher survival during the first three months after leaving the nest than those reared at other times, and hence losses due to cuckoos have a disproportionate effect on numbers surviving the following season.

Table 5 shows the mean number of eggs laid, and young fledged, in nests with and without cuckoo parasitism. The mean number of young babblers fledging from Jungle Babbler nests containing a young cuckoo was 1·14 young per nest, compared with 2·5 young per nest from nests without cuckoos. These represent 32% and 60% respectively of the mean number of eggs laid per nest. In the Common Babbler 33% of eggs laid in nests parasitized by cuckoos were reared to fledging, against 77% in nests without cuckoos.

The relative contribution made by Pied Crested Cuckoos to the decreased breeding

Table 5. Clutch size and fledging success in parasitized and non-parasitized nests, June–September only

<table>
<thead>
<tr>
<th></th>
<th>1971</th>
<th>1972</th>
<th>1973</th>
<th>Together</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Jungle Babbler</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without cuckoo</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean clutch</td>
<td>2·33 (3)</td>
<td>2·8 (10)</td>
<td>2·14 (7)</td>
<td>4·2 (10)</td>
</tr>
<tr>
<td>Mean young fledged</td>
<td></td>
<td></td>
<td></td>
<td>2·5 (20)</td>
</tr>
<tr>
<td>With cuckoo</td>
<td></td>
<td></td>
<td></td>
<td>40·5</td>
</tr>
<tr>
<td>Mean clutch</td>
<td>3·67 (9)</td>
<td>3·5 (6)</td>
<td></td>
<td>3·6 (15)</td>
</tr>
<tr>
<td>Mean young fledged</td>
<td>0·84 (6)</td>
<td>1·0 (5)</td>
<td>1·4 (10)</td>
<td>1·14 (21)</td>
</tr>
<tr>
<td><strong>Common Babbler</strong></td>
<td></td>
<td></td>
<td></td>
<td>68·4</td>
</tr>
<tr>
<td>Without cuckoo</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean clutch</td>
<td>3·28 (7)</td>
<td>3·44 (9)</td>
<td></td>
<td>3·37 (16)</td>
</tr>
<tr>
<td>Mean young fledged</td>
<td>2·75 (8)</td>
<td>2·43 (7)</td>
<td></td>
<td>2·6 (15)</td>
</tr>
<tr>
<td>With cuckoo</td>
<td></td>
<td></td>
<td></td>
<td>23</td>
</tr>
<tr>
<td>Mean clutch</td>
<td>3·33 (3)</td>
<td>3·5 (6)</td>
<td></td>
<td>3·44 (9)</td>
</tr>
<tr>
<td>Mean young fledged</td>
<td>2·0 (3)</td>
<td>0·5 (4)</td>
<td></td>
<td>1·14 (7)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>% loss</th>
<th>% loss</th>
</tr>
</thead>
<tbody>
<tr>
<td>Together</td>
<td></td>
<td>67</td>
</tr>
</tbody>
</table>

Table 6. Ways in which cuckoos affect the reproductive success of babblers

<table>
<thead>
<tr>
<th></th>
<th>Jungle Babbler</th>
<th>Common Babbler</th>
</tr>
</thead>
<tbody>
<tr>
<td>% loss</td>
<td>4·2</td>
<td>3·37</td>
</tr>
<tr>
<td>Mean clutch without cuckoo</td>
<td>3·6</td>
<td>3·44</td>
</tr>
<tr>
<td>Number fledging, assuming normal survival (J. Bab. 62%; C. Bab. 77%)</td>
<td>2·14</td>
<td>2·6</td>
</tr>
<tr>
<td>Observed mean number fledged</td>
<td>1·14</td>
<td>1·14</td>
</tr>
<tr>
<td>Total loss due to cuckoos</td>
<td>38·1</td>
<td>42·5</td>
</tr>
</tbody>
</table>

Table 7. Proportion of babblers nests parasitized by cuckoos

<table>
<thead>
<tr>
<th></th>
<th>1971</th>
<th>1972</th>
<th>1973</th>
<th>Together (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jungle Babbler</td>
<td>5/5</td>
<td>12/20</td>
<td>10/13</td>
<td>27/38 = 71·0</td>
</tr>
<tr>
<td>Common Babbler</td>
<td>4/13</td>
<td>9/18</td>
<td>13/31</td>
<td>27/38 = 71·0</td>
</tr>
<tr>
<td>Large Grey Babbler</td>
<td>2/4</td>
<td>1/5</td>
<td>1/5</td>
<td>4/14 = 28·6</td>
</tr>
</tbody>
</table>
success of Jungle and Common Babblers is estimated in Table 6. In the Jungle Babbler breeding success is reduced 24% by decreased fledging success, while in the Common Babbler this contributes 42.5% to the loss of breeding capacity. This difference is probably due to the fact that Common Babblers nestlings are smaller at hatching than those of the Jungle Babbler, and therefore less able to compete with a young cuckoo.

Table 7 shows the proportion of babblers' nests parasitized by Pied Crested Cuckoos during June–September 1972 and 1973. The effective decrease in the production of the babblers during this period can be calculated from this and Table 5 as 38.6% for Jungle Babblers, and 23.5% for Common Babblers. Out of thirty-nine Jungle Babblers reared during the study and surviving until 1 March in the following year, twenty-nine were from clutches laid during June–September, and this means that the overall decrease in recruitment due to cuckoo parasitism can be calculated at 32% (this calculation is given in the Appendix). For the Common Babbler survival to the following spring is not known, but thirty-seven out of fifty-two nests (71.2%) were begun during June–September, and assuming equal survival for the birds fledging at different seasons, the overall decrease in recruitment due to the cuckoos is 18.1% (see Appendix).

The total effect of cuckoo parasitism on the babblers is certainly more complex than the simple calculations above would suggest. No assessment was possible of factors such as increased predation of fledglings due to the conspicuous calls of the young cuckoo, the long-term effects of nestling deprivation on birds which succeeded in fledging, or of density dependent mechanisms operating on the babbler population. General ecological factors affecting the breeding success of babblers are beyond the scope of this paper, but as mentioned under ‘availability of nests’, it appears that groups living in optimum habitat (woodland) are large, and make several nesting attempts during the season. Smaller groups, living outside woodland, usually nest only during the rainy season breeding peak, and the effect of cuckoo parasitism will be greatest on these, since they are not capable of rearing young outside the period in which the cuckoos are present.

A comparison of the number of Pied Crested Cuckoos' eggs laid in the nests of groups holding territory inside and outside closed-canopy woodland showed that woodland groups of Jungle Babblers averaged 1.08 cuckoo eggs per nest (n = 25), while the nests of groups living outside woodland averaged 1.2 eggs per nest (n = 18). This suggests that pressure from cuckoos is roughly equal in both habitats.

DISCUSSION

Friedmann (1964) and Liversidge (1971) have compared the adaptations of the genus *Clamator* to brood parasitism with those of the better known genus *Cuculus*. Species of *Clamator* differ chiefly in not possessing sympatric gentes laying eggs adapted to different host species, and in the fact that the nestling *Clamator* does not evict the eggs and young of its host.

The first requirement in becoming a successful parasite is to adopt a successful host. The range and population density of the parasite are inevitably controlled by the distribution and abundance of its hosts. The European Cuckoo maintains a wide distribution by parasitizing a wide range of host species, and this has led to the evolution of distinct gentes with eggs closely mimicking those of their hosts. Southern (1954) has pointed out that a certain degree of habitat isolation is necessary for these gentes to evolve, and in places such as Britain, where this is lacking, mimicry is rather poor, despite the fact that individual cuckoos are faithful to a single host species (Chance 1922).
The evolution of egg mimicry depends on the ability of the host species to discriminate the eggs of the parasite (Baker 1923). Once such behaviour begins there is selection pressure for the parasite to evolve eggs which resemble those of the host and, having done so, to parasitize only that species. New gentes can be initiated only by eggs laid in the nests of species which are not normally parasitized, and the fact that such casual hosts are quite common in the case of the European Cuckoo helps to explain the proliferation of gentes in this species.

No cuckoos' eggs were found in nests other than those of *Turdoides* spp., although nests of *Pycnonotus* spp., hosts of *Clamator jacobinus* in Africa, were common during the period when cuckoos were present. In addition no juvenile cuckoos were seen being fed by other hosts, suggesting that, at least in the Delhi area there is little scope for the initiation of new gentes. Perhaps assisted by the absence of sympatric gentes, the Pied Crested Cuckoo in India has evolved an egg which is virtually indistinguishable from that of its hosts, all of which lay eggs of a similar colour. Conversely the nestling shows no trace of mimicry, being easily distinguishable, even before the feathers develop, by its rather blackish skin, and later by the black-and-white plumage, contrasting strongly with the dull brown of the babbler.

The occurrence of mimicry in the egg, but not in the nestling, probably results from the relatively greater strength of the feeding drive in the parent birds. The evolution of desertion behaviour in response to an alien egg being laid in the nest can occur fairly easily because the loss in time and energy to a bird deserting during egg-laying, or the early incubation period, is quite small, particularly in a species with a long breeding season. The corresponding loss if desertion occurs during the nestling period is much higher, both in terms of energy expended, and in lost opportunity in a species subject to heavy nest predation, so that a mistaken rejection carries a correspondingly heavy penalty. The evolution of rejection behaviour towards a chick is likely to be much slower, therefore, than the evolution of egg-desertion. Both rates of evolution are likely to be slower where some of the hosts own offspring may survive despite the presence of a cuckoo, because in this situation, even if the presence of a cuckoo is correctly detected, the host may reduce its reproductive potential by resorting to desertion.

Eviction behaviour, as manifest in the genus *Cuculus*, may be partly an adaptation to parasitizing hosts much smaller than themselves, for which the rearing of a single nestling cuckoo is equivalent to rearing a whole brood of their own offspring. In the genus *Clamator* most species parasitize hosts similar to, or larger than, themselves in size, and hence eviction is unnecessary, provided that the female cuckoo removes or destroys one of the host's eggs while laying. At the same time, by allowing some of the host's young to be reared the *Clamator* cuckoos are acting as 'prudent parasites' in minimizing the amount of damage that they do.

Owen (1933) records a case where the European Cuckoo apparently brought a local population of Sedge Warblers (*Acrocephalus schoenobaenus* (Linnaeus)) close to extinction. Such an outcome would be unlikely in the case of *Turdoides* species which rear some young outside the period when the cuckoos are present, but for the same reason the cuckoo needs to avoid having too drastic an effect on its hosts. If all cuckoo eggs laid had hatched and evicted their nest mates, only 0-9 Jungle Babblers would have been reared per nest during June–September. Babblers have a high adult survival rate, and under these circumstances the option to breed at all while cuckoos were present might become evolutionarily unprofitable.

Removal of one of the host's eggs at the time of laying is not invariable in *Clamator*; it
was not observed in the present study, and was not recorded in Liversidge's study on South African *C. jacobinus* (1971). In the present study one egg was often damaged when the cuckoo laid, and as these eggs did not usually hatch the result was equivalent to egg removal. In the *Clamator* studies where egg removal was observed (Jensen & Jensen 1969, Mountfort & Ferguson-Lees 1961) the populations involved were ones where multiple laying by the cuckoos was the rule, and under these circumstances it becomes imperative that some eggs are removed to ensure that the brood does not become too large. Mountford & Ferguson-Lees describe Great Spotted Cuckoos (*C. glandarius*) parasitizing Magpies (*Pica pica* (Linnaeus)) and mention that Magpies' eggs in nests where cuckoos' eggs had been laid often appeared 'slightly dented'. They attributed this to careless feet or deliberate pecks, but the damage sounds rather like that caused by the impact of a falling egg.

Although multiple laying in the same nest must be greatly influenced by the relative densities of host and parasite, their relative sizes may also be important. Cases of more than one egg in a nest are quite rare for the European Cuckoo (Baker 1942), which parasitizes hosts between 10 and 20% of its own adult weight. South African *Clamator jacobinus*, parasitizing bulbuls (*Pycnonotus* spp.) which weigh about half their own weight, laid 21·6% of their eggs in nests which already contained one (Liversidge 1971). In the present study seventeen out of forty-four (39%) cuckoos' eggs were laid in Jungle Babblers' nests which already contained one, and for the Great Spotted Cuckoo parasitizing Magpies the proportion was 60% (Friedmann 1964), the Great Spotted Cuckoo being smaller than its host. Multiple laying is also the rule in the Red-winged Crested Cuckoo (*Clamator coromandus*) which parasitizes hosts larger than itself (Ali & Ripley 1969). Thus the genus shows a steady increase in the amount of multiple laying with increase in the relative size of the host.

One feature of the behaviour of the Pied Crested Cuckoo which contrasts with that of most other parasitic cuckoos is the relatively small amount of vocalization. In the genera *Cuculus*, *Cacomantis*, and *Eudynamys* persistent vocalization by the male continues throughout the breeding season, whereas Pied Crested Cuckoos are relatively quiet after the first month in their breeding area. This suggests a difference in social structure between *Clamator* species and the other parasitic cuckoos, and it is possible that pairing is more permanent in this genus. Liversidge (1971) describes how the male *C. jacobinus* distracts the host pair, while the female slips in to lay an egg; von Frisch (1973) observed similar behaviour in captive *C. glandarius* and the same tactics are probably used by *C. levantii* (Swainson) (Steyn 1973). This possibility was also suggested for the Pied Crested Cuckoo by Ali (1930) and fits the observation of laying recorded in the present study. If co-operation by the pair is the normal strategy for egg laying in *Clamator* species, this would explain the need for a durable pair bond.

A number of factors probably contribute to making the genus *Turdoides* particularly suitable as cuckoo hosts.

1. Species of the genus are common everywhere in lowland India, and occupy all types of habitat, from semi-desert to tropical evergreen forest.

2. In Delhi, and probably over most of the drier parts of India, *Turdoides* spp. have comparatively long breeding seasons, spanning the entire period during which the Pied Crested Cuckoos are present.

3. All species lay unmarked eggs, which are probably easier to mimic than marked eggs.

The effect of parasitism by Pied Crested Cuckoos on their babbler hosts cannot be
assessed completely. It varies with the habitat, and with the seasonal rainfall, and probably also geographically, because in some areas the peak of babbler breeding comes before the arrival of the cuckoos (Andrews & Naik 1970). At Delhi the fact that cuckoos are more common in years of heavy rainfall leads to the surprising fact that more young babbler are reared in seasons of low rainfall because of the lower rate of parasitism.

It is unlikely that cuckoo parasitism has much effect on the general level of babbler populations, which are probably limited by food supply at the critical season, but, depressing breeding success, it may affect group size. Young babbler do not begin to leave their natal group until half way through their second year, so that an increase in breeding success should lead to an increase in group size, and a shift in the age structure of the population towards more younger birds. If the population level is fixed by other factors an increase in group size would mean a decrease in the number of groups, and hence the number of breeding pairs per unit area. Cuckoo parasitism, by reducing group size, may actually increase the number of nests available to be parasitized, another factor which might make babbler attractive hosts.

ACKNOWLEDGMENTS

For financial support while carrying out the field work, I should like to thank the Royal Society, the Leverhulme Trustees and the British Ornithologists’ Union, and for assistance while in Delhi, Prof. C. M. Dass of the Department of Zoology, University of Delhi. Dr C. M. Perrins, L. Schifferli, L. Cornwallis and Dr E. K. Dunn, all of the Edward Grey Institute, gave detailed criticisms of this paper in earlier drafts.

SUMMARY

(1) In the course of a study on the ecology and behaviour of babblers (Turdoides spp.) near Delhi, North India, a number of observations on parasitism by the Pied Crested Cuckoo (Clamator jacobinus) were made.

(2) The behaviour of the cuckoo, the timing of its breeding in relation to that of its host species, the relative densities of parasite and hosts, the intensity of parasitism, and its effects on the breeding success of the host species are described. Measurements of the growth rates of cuckoo and host nestlings are compared.

(3) The adaptations of the genus Clamator to brood parasitism are compared with those of the genus Cuculus, and the differences related to the type of hosts selected.

(4) General strategies for brood parasitism are discussed, and reasons advanced to suggest that the genus Turdoides is particularly suited to exploitation by brood parasites in India.

REFERENCES

Calculations for the theoretical reduction in the recruitment rate of babblers, due to parasitism by Pied Crested Cuckoos

Jungle Babbler

Observed decrease in number fledged from parasitized nests 54.4%
Observed proportion of nests parasitized, June–September 71.0%
Observed proportion of entire seasons young surviving on 1 March following, which fledged from clutches laid in June–September 74.4%
Total reduction in numbers fledged, June–September 54.4% × 71.0% = 38.6%
Effect on annual recruitment
Theoretical increase in success in the absence of cuckoos, June–September

\[
\frac{100}{100 - 38.6} - 1 \times 100 = 62.9\%
\]

Theoretical increase in the number of young surviving, following 1 March

\[
\frac{100}{100 - 38.6} - 1 \times 74.4 = 46.8\%
\]

Hence percentage reduction in number surviving due to cuckoo parasitism

\[
\frac{46.8}{100 + 46.8} \times 100 = 31.9\%
\]
Common Babbler

- Observed decrease in number fledged from parasitized nests: 56.0%
- Observed proportion of nests parasitized, June–September: 42.0%
- Proportion of all nests found in which clutches were laid during June–September: 71.2%
- Total reduction in number fledged, June–September: 56.0% \times 42.0\% = 23.5%

Effect on annual recruitment

Theoretical increase in success in the absence of cuckoos, June–September:

\[
\left(\frac{100}{100-23.5} - 1\right) \times 100 = 31.0\%
\]

Theoretical increase in the number reared in the entire season:

\[
\left(\frac{100}{100-23.5} - 1\right) \times 71.2 = 22.05\%
\]

Hence percentage reduction in the number reared during the entire season, due to cuckoo parasitism:

\[
\left(\frac{22.05}{100+22.05}\right) \times 100 = 18.1\%
\]