

Brood parasitic cuckoos and their hosts in Jahangirnagar University campus

Mominul Islam Nahid, Sajeda Begum & Mohammed Mostafa Feeroz

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 Mominul Islam Nahid, Department of Zoology, Jahangirnagar University, Savar, Dhaka. E-mail: nahid_1511@yahoo.com [Corresponding author].
 Sajeda Begum, Department of Zoology, Jahangirnagar University, Savar, Dhaka.
 Mohammed Mostafa Feeroz, Department of Zoology, Jahangirnagar University, Savar, Dhaka.
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Abstract

Brood parasitic cuckoos lay their eggs in a host's nest and thereafter rely completely on their hosts to do their parental care for them. We studied the interactions between four different species of parasitic cuckoos and their three respective hosts in Bangladesh: The Indian Cuckoo *Cuculus micropterus* parasitised the Black Drongo *Dicrurus macrocercus*, The Asian Koel *Eudynamys scolopaceus*, the Long-tailed Shrike *Lanius schach*, and the Common Hawk Cuckoo *Hierococcyx varius*, and Pied Cuckoo *Clamator jacobinus*, the Jungle Babbler *Turdoides striata*. The breeding seasons of the Black Drongo, and Long-tailed Shrike, started in late March and ended in July, which coincided with those of the Indian Cuckoo (late April–early June), and Asian Koel (March–July), respectively. The Jungle Babbler started breeding in late February, continuing up to June. Competition between its two brood parasites appeared minimal because of their non-overlapping breeding seasons: March–May for the Common Hawk Cuckoo, and June–July for the Pied Cuckoo. The eggs of the Indian Cuckoo, Common Hawk Cuckoo, and Pied Cuckoo show excellent egg mimicry, but the Asian Koel's eggs are highly non-mimetic. The nest's height above ground was an important predictor of brood parasitism in Long-tailed Shrike with an increased risk of brood parasitism in low nests. All the host species suffered the costs of brood parasitism, showing reduced breeding success.

Introduction

Avian brood parasitism is a rather rare breeding strategy. Altogether, about 100 species of such brood parasites exist, making up roughly 1% of all bird species (Davies 2000). However, only a few of these parasites and their associated hosts' interactions have been investigated in detail. In Europe, a substantial effort has been put into studying host–parasite interactions in two brood parasites: the Common Cuckoo *Cuculus canorus*, and the Great Spotted Cuckoo *Clamator glandarius*. In North America, the same can be said about interactions between the Brown-headed Cowbird *Molothrus ater* and its hosts (Davies 2000). In Australia, extensive work has been done on the interactions of cuckoo species and their hosts. A total of 11 species of cuckoos, including the world's smallest cuckoo, the Little Bronze Cuckoo *Chalcites minutillus*, and the world's largest cuckoo, the Channel-billed Cuckoo *Scythrops novaehollandiae*, are found in Australia (Brooker & Brooker 1989; Langmore 2013). However, despite the existence of a great diversity of different brood parasite–host systems, few have been thoroughly investigated, and a substantial number of brood parasites have never been studied at all. Recently, a preliminary study on Asian cuckoos, which focused mostly on their basic biology and natural history, by describing parasite- and host-interaction, was carried out (Begum *et al.* 2011a,b; Begum *et al.* 2012).

Parasitic birds lay their eggs in other species' nests, relying on the foster parents to provide all parental care; potential host species may vary significantly, in quality, as hosts (Strausberger & Ashley 1997; Kleven *et al.* 1999; Sackmann & Reboreda 2003; Grim 2006). Reproductive success in many parasitic cuckoos is strongly influenced by the number, and quality, of potential hosts present (Stokke *et al.* 2007), and the parasites are often detrimental to host fitness (Davies 2000). Host adults that accept parasitic clutches can have smaller clutches (Hill & Sealy 1994),

and reduced hatching success (Petit 1991; McMaster & Sealy 1999). Host reproductive success depends on the probability of parasitism by evictor-, and non-evictor cuckoos. Most parasitic cuckoos are evictors, in which the newly hatched cuckoo chick evicts all the host eggs, and nestlings from the nest, thereby imposing a severe cost to the host (Moksnes *et al.* 2013; Rothstein 1990). Non-evicting brood parasites include cowbirds, and some cuckoos. Here, the parasite chicks grow up together with the host chicks. In such cases, the parasite chick, by virtue of hatching earlier (Moskát 2005; Stokke *et al.* 2005), often monopolise parental feeding, thereby lowering the survival of the host's chicks (Zanette *et al.* 2005). In extreme cases, these losses may contribute to host population declines (Brittingham & Temple 1983).

Hosts that accept parasitic eggs invest significantly more time and energy provisioning their brood because parasitic nestlings beg more frequently, and more intensely, than the host's nestlings (Dearborn *et al.* 1998; Grim & Honza 2001; Hoover & Reetz 2006). Hosts that reject brood parasitism, by abandoning or burying parasitic clutches, incur time and energy costs in laying new clutches and building more new nests (Sedgwick & Iko 1999).

In the present study our aim was to investigate interactions between three host species, namely, Long-tailed Shrike *Lanius schach*, Black Drongo *Dicrurus macrocercus*, and Jungle Babbler *Turdoides striata*, and their parasitic cuckoo species, namely Asian Koel *Eudynamys scolopaceus*, Indian Cuckoo *Cuculus micropterus*, and Common Hawk Cuckoo *Hierococcyx varius*, and Pied Cuckoo *Clamator jacobinus*, respectively—living sympatrically in the natural habitat of Jahangirnagar University campus, Bangladesh. These cuckoos are known to parasitise different host species (Baker 1942; Ali & Ripley 1987), but very little is known about the host-use pattern by the cuckoos,

wherein one cuckoo species uses different species of hosts, and different species of cuckoos compete to parasitise the same host, in areas where they are sympatric. The main prediction is that these cuckoo species would parasitise different host species at different heights of nesting trees (Begum *et al.* 2011a). A nest's height above the ground plays an important role in nest parasitism. Nests placed at lower heights, with sparse foliage to hide them, are easier to detect by a cuckoo than nests at a higher height, inside dense foliage (Begum *et al.* 2011a). Alternatively, if two or more species parasitise the same host they would be expected to differ in other fundamental ways, e.g., they would either have different breeding periods, or different dates of arrival to the breeding habitat, or parasitising the same host in different habitats. During fieldwork, we carried out investigations to test these predictions in two successive breeding seasons in Jahangirnagar University.

Study area

This study was conducted in Jahangirnagar University campus, central Bangladesh (23°52' N, 90°16' E), 32 km north of Dhaka city. The campus is c. 200 ha, consisting of diverse vegetation in and around human settlements (Begum *et al.* 2011a, b). Hot, rainy, humid summers, and dry and cool winters characterize the climate here. The campus has diverse ecological habitats and vegetation types.

All the hosts bred at high densities in different habitats in the study area. Human settlements, with orchards and gardens, are dominated by various types of fruit trees like jackfruit *Artocarpus heterophyllus*, mango *Mangifera indica*, and coconut *Cocos nucifera*, together with ornamental trees: *Mimusops elengi*, *Livistona chinensis*, *Murraya paniculata*, *Polyalthia longifolia*, *Azadirachta indica*, etc. Mixed scrub forest is characterised by the natural growth of species like banyan *Ficus benghalensis*, *Dalbergia sissoo*, and *Albizia lebbbeck*, as well as planted tree species like *Acacia auriculiformis*, *Shorea robusta*, and *Swietenia mahagoni*. The monotypic plantation area is dominated by *Terminalia arjuna*, *Gmelina arborea*, and *Lagerstroemia speciosa*. There are 230 plant species recorded in the campus, belonging to 159 genera, and 62 families (Hossain *et al.* 1995). A total of 180 species of birds, belonging to 43 families, have been found, out of which 74 are breeding residents, 41 non-breeding residents, and 65 migrants (Mohsanin & Khan 2009).

Study species

Some basic information on the parasitic cuckoos, and their hosts, is given below.

Indian Cuckoo

This is a common local resident in Bangladesh (Becking 1981; Grimmett *et al.* 1999). In northern China, its breeding season lasts from May to July (Payne 2005), and in India, eggs have been recorded in May, and June (Baker 1934; Ali 1996). It feeds on insects, mainly hairy caterpillars, grasshoppers and crickets, but fruits are also reported as part of their diet (Ali 1996; Payne 2005; Erritzøe *et al.* 2012). Several passerines have been reported, from different areas, as hosts of the Indian Cuckoo (Table 1). Their eggs are variable in colour, varying locally, but are similar to those of their hosts (Payne 2005). Cuckoo nestlings evict both, host's eggs, and their nestlings (Payne 2005).

Common Hawk Cuckoo

The Common Hawk Cuckoo's breeding season lasts from April to June (Whistler 1949), but varies locally (Grimmett *et al.* 1999). Its diet mainly consists of insects, mostly caterpillars and cutworms; sometimes it also eats figs and berries (Ali 1996; Payne 2005). In India, its hosts are normally *Turdoides* (Gaston & Zacharias 2000), and *Garrulax* species (Baker 1934) (Table 1), with the Jungle Babbler being reported as a common host (Gaston 1976; Davidson 1886). Common Hawk Cuckoo eggs are not easily distinguishable from those of their hosts because of their very similar colour and size (Baker 1942; Whistler *et al.* 1949). The cuckoo nestling has been reported to evict young of the host from the nest (Ali 1996; Gaston & Zacharias 2000); however, there is very little information about incubation and nestling periods.

Pied Cuckoo

The Pied Cuckoo breeds in the Indian Subcontinent, arriving on its breeding grounds during the onset of the seasonal rain (Payne 2005). In Bangladesh, Pied Cuckoos are local summer visitors (Grimmett *et al.* 1999); their breeding season coincides with the rainy season locally, usually during the monsoon, from June to September (Gaston 1976). They feed on insects, mainly caterpillars (Payne 2005), as well as berries and fruits (Gaston 1981; Robert 1991). The common hosts of the Pied Cuckoo are listed in Table 1. This cuckoo's nestlings are non-evictors of host eggs, but often monopolise parental care at the expense of host young (Payne 2005).

Asian Koel

Several factors influence the Asian Koel to use different host's nests (Begum *et al.* 2011a). The interaction of Asian Koel with

Table 1. List of the four cuckoo species, and their host species

Parasitic cuckoo species	Host species
Asian Koel	House Crow (Robert 1991; Begum <i>et al.</i> 2011a,b); Large-billed Crow <i>Corvus macrorhynchos</i> (Lamba 1976); Common Myna (Medway & Wells 1976; Wells 1999; Begum <i>et al.</i> 2011a,b); Long-tailed Shrike (Begum <i>et al.</i> 2011a,b); Black Drongo (Smith 1950); Red-billed Blue Magpie <i>Urocyssa erythroryncha</i> (Lewthwaite 1996).
Common Hawk Cuckoo	<i>Turdoides</i> spp. (Gaston & Zacharias 2000); <i>Garrulax</i> spp. (Baker 1934); Jungle Babbler (Gaston 1976, Davidson 1886, Payne 2005, Erritzøe <i>et al.</i> 2012); Large Grey Babbler <i>Argya malcolmi</i> (Erritzøe <i>et al.</i> 2012).
Pied Cuckoo	Common Babbler <i>Argya caudata</i> (Gaston 1976); Jungle Babbler (Gaston 1976); Large Grey Babbler (Gaston 1976); Yellow-billed Babblers <i>Turdoides affinis</i> (Payne 2005); Fiscal-flycatcher <i>Sigelus silens</i> (Erritzøe <i>et al.</i> 2012); Rufous Babbler <i>Argya subrufa</i> (Sashikumar <i>et al.</i> 2011); Laughingthrushes spp. (Futehally 2009).
Indian Cuckoo	Black Drongo (Neelakantan 1952, Becking 1981, Ali & Ripley 1983); Ashy Drongo <i>Dicrurus leucophaeus</i> (Lowther 2010); Azure-winged Magpie <i>Cyanopica cyana</i> (Payne 2005); Streaked Laughingthrush <i>Trochalopteron lineatum</i> (Baker 1942); Tickell's Thrush <i>Turdus unicolor</i> (Erritzøe <i>et al.</i> 2012); Black-hooded Oriole <i>Oriolus xanthornus</i> (Eldhose 2000).

its different host species is described in more detail in Begum *et al.* (2011b). In the Indian Subcontinent, its breeding season lasts from March to September, varying locally (see Payne 2005). Its diet consists mainly of fruit (Payne 2005; Begum *et al.* 2011a), but invertebrates, and birds' eggs are also eaten (Payne 2005). Different passerine species, from several areas, have been described as hosts of the Asian Koel (Table 1). It is a generalist in its host choice, and therefore parasitises many sympatric passerines (Payne 2005; Erritzøe *et al.* 2012; Begum *et al.* 2011a, b).

It has been reported that it often lays more than one egg in a host's nest, usually two to three, and that House Crows *Corvus splendens*, and Long-tailed Shrikes accept them, while Common Mynas are more likely to desert parasitised nests (Begum *et al.* 2011b; Payne 2005). The cuckoo nestling may evict host eggs or nestlings, but it may also be raised together with the host's own young (Payne 2005). Asian Koel nestlings, however, reduce the breeding success of their hosts (Payne 2005; Ali *et al.* 2007; Begum *et al.* 2011a).

Materials & methods

We searched for nests of all passerines breeding in the study area during the breeding seasons of 2010 and 2011 (January to August in each year). The different habitats in the study area were systematically explored, almost daily, during the breeding season. We classified the habitat in the study area into three distinct types, based on the type of vegetation, and presence of buildings, namely, human settlements, mixed scrub forest, and monotypic plantation. We collected data on host selection, parasitism rates, height of both, parasitised and un-parasitised nests, and the degree of mimicry between cuckoo and host eggs, as well their breeding success. Clutch initiation date (i.e., the date when the first egg was laid) was estimated by the method used by Hays & LeCroy (1971), and using published information on length of incubation period (Ali & Ripley 1987) if the nest was found during incubation. We tested the status of eggs with the following simple method: When a fresh egg is placed in water, it stays at the bottom, and when incubation starts, it floats increasingly higher as the embryo develops, gradually rising to the surface over a period of days.

The mimetic accuracy of eggs was scored as per Begum *et al.* (2011b), using the Moksnes & Røskaft (1995) scale: 1 (perfect mimicry), to 5 (no mimicry) (Table 2). In case of excellent mimicry between a cuckoo's and its host's eggs (e.g., Jungle Babbler–Common Hawk Cuckoo, Jungle Babbler–Pied Cuckoo, and Black Drongo–Indian Cuckoo), difficult to detect by the naked human eye [78E–F, G–H], parasitism was determined after the eggs hatched, and it was possible to identify the cuckoo nestling. Statistical analyses were performed in SPSS 20.0. All test were considered significant if $p \leq 0.05$ ¹.



78a–h. A comparison of the eggs of host species, and their parasitic cuckoos (left to right).

Table 2. Different egg mimicry scale used by Moksnes & Røskaft (1995)

Sl. No.	Mimicry scale	Description
1	Perfect mimicry	When the cuckoo egg was difficult to distinguish from host egg in colour and pattern except being larger in size
2	Good mimicry	The cuckoo egg is slightly different from host egg in both colour and pattern and it is easy to identify upon close observation of the clutch
3	Moderate mimicry	The cuckoo egg was easy to separate from the host eggs, but the colour and pattern was similar in many respects
4	Poor mimicry	Cuckoo and host eggs were different in colour and pattern
5	Non-mimetic	The cuckoo egg and the host egg did not match in any respect

1. Implies a 95% confidence in the test results.

Table 3. Number of parasitised and un-parasitised as well as successful and unsuccessful nest of three host species used by the four cuckoo species of the study area.

Host species	Total number of nests	Number of parasitised nests N (%)	Number of un-parasitised nests N (%)	Number of successful nests N (%)	Number of unsuccessful nests N (%)
Black Drongo	27	2 (7.4%)	25 (92.6%)	25 (92.6%)	2 (7.4%)
Jungle Babbler	11	6 (54.5%)	5 (45.5%)	7 (63.6%)	4 (36.4%)
Long-tailed Shrike	21	17 (81%)	4 (19%)	9 (42.9%)	12 (57.1%)

Results & observations

During the study period we found a total of 59 nests of the three host species, of which 25 were parasitised by the four cuckoo species (Table 3). Nestlings fledged successfully from 41 of the 59 nests; the remaining nests were assumed as predated, based on physical signs, e.g., a broken nest, or broken eggshells in the nest, or on the ground. Altogether, five, out of 18 species of trees growing in the area were used for nesting by the hosts species.

Black Drongos started breeding after the first shower in late March, and 27 nests were observed on 11 species of plants; two of these nests were predated. Chicks fledged successfully from the remaining 25 nests, including from two parasitised nests, indicating a high breeding success (Table 3). Most of the nests were found in April (n=14). The parasitised nests of Black Drongo were found from April to June. Highest number of nests (n=5) were in shegun trees *Tectona grandis*.

The peak month for nesting of Jungle Babbler was April, when the highest number (n=7) of nests was found. We found 11 nests on nine different species of plants, six of which were parasitised: Common Hawk Cuckoo (five nests), and Pied Cuckoo (one nest). Chicks fledged successfully from seven nests, the rest were predated (Table 3). Nests parasitised by the Common Hawk Cuckoo were found from March to May, whereas the nest parasitised by the Pied Cuckoo was found in June. The highest number of nests (n=2 each) were found in mango *Mangifera indica*, and acacia *Acacia auriculiformis* trees.

We found 21 nests of the Long-tailed Shrike, of which 17 were parasitised by the Asian Koel. Chicks fledged successfully from nine nests, whereas 12 nests were predated (Table 3). April and May were the peak nesting months of the Long-tailed Shrike, with the highest number of their nests being found in April (n=10). The parasitised nests were found in April–July. The Long-tailed Shrike used ten different species of plants to nest in, normally preferring small- to medium-sized trees, but some

nests were found in tall trees. The highest number (n=7) of nests was found in koroi trees *Albizia lebbbeck*.

Overall, the sympatric cuckoos' parasitism rates varied significantly for different

host species ($\chi^2 = 26.986$, $df = 2$, $P < 0.001$)². It was highest in the Long-tailed Shrike (81%), and lowest in the Black Drongo (7.4%), whereas, in Jungle Babbler it was 54.5%.

The nest height, from the ground, was significantly lower for parasitised- than un-parasitised nests of Long-tailed Shrikes, and higher for parasitised- than un-parasitised nest of Black Drongo; no significant difference was found on this parameter for nests of Jungle Babblers (Table 4).

The average clutch size for Long-tailed Shrike was four to five, for Jungle Babblers, three to five, and for Black Drongos, two to four. Clutch size was measured only from un-parasitised nests. More than one koel egg (1–5) was found in the parasitised nests of Long-tailed Shrikes, whereas, only single cuckoo eggs were found in the parasitised nests of Black Drongos (Table 4). In the parasitised nests of Jungle Babblers, a single cuckoo egg was found in each of the three nests parasitised by the Common Hawk Cuckoo, whereas two cuckoo eggs were found in the single nest parasitised by Pied Cuckoo (Table 4). In the parasitised Long-tailed Shrike nests, the host chicks grew up together along with the koel chicks. Though the Asian Koel nestling is a non-ovictor, the female koel removes one or more host eggs before laying, leading to more host young fledging in un-parasitised than in parasitised nests (Table 4). The number of host young fledged was lower in parasitised- than in un-parasitised nests of Black Drongo and Jungle Babbler as the chicks of their brood parasites—Indian Cuckoo, and Common Hawk Cuckoo respectively—are evictors (Table 4). There was only one parasitised nest of a Jungle Babbler that was parasitised by a Pied Cuckoo (where two cuckoo chicks fledged), but we exclude this nest from our analysis of parasitic chicks fledged in Jungle Babbler, as the Pied Cuckoo is a non-ovictor, and this data will affect the result of other nests parasitised by Common Hawk Cuckoo.

Asian Koel eggs had a greenish ground colour with numerous brownish spots of varying sizes; these were highly non-mimetic in colour, pattern, and size when compared with the eggs of the Long-tailed Shrike (pale creamy with small brown or reddish brown specks and blotches at the broader end) (Mimicry score 5.0; n=12) (Fig. 1). Indian Cuckoo eggs were white with reddish brown markings and were very good mimics of those of the Black Drongo (white with reddish brown blotches) (Mimicry score 1.7; n=2) (Fig. 1). Common Hawk Cuckoo and Pied Cuckoo eggs were highly mimetic to the eggs of the Jungle Babbler in both colour pattern and size. The mimicry score was 1.1; n=3, and 1.0; n=1 respectively (Fig. 1). The Jungle Babbler eggs were deep turquoise blue and glossy in texture, whereas the Common Hawk Cuckoo eggs were similar in colour but less glossy, and slightly more elongated. The Pied Cuckoo eggs were similar in colour and glossy but slightly smaller and roundish than host eggs (Fig. 1).

Table 4. Different breeding variables in relation to parasitised (PAR) and un-parasitised (UNPAR) nests of three host species. Mean, standard deviations (sd) and N = Number of nests are given. P indicates significant differences of t-tests between parasitised and un-parasitised nests.

Host species	Variables	PAR			UNPAR			p
		Mean	Sd	N	Mean	Sd	N	
Black Drongo	Height above ground (m)	13.0	2.8	2	8.8	2.5	25	0.036
	Parasitic egg	1.0	0	2	-	-	-	-
	Host young fledged	0	0	2	2.5	0.9	25	0.001
	Parasites fledged	1.0	0	2	-	-	-	-
Jungle Babbler	Height above ground (m)	5.8	2.1	6	5.0	3.1	5	0.615
	Parasitic egg*	1.0	0	3	-	-	-	-
	Host young fledged*	0	0	5	2.2	1.8	5	0.001
	Parasites fledged*	0.2	0.4	5	-	-	-	-
Long-tailed Shrike	Height above ground (m)	5.53	1.5	17	7.5	1.0	4	0.026
	Parasitic egg	2.3	1.2	12	-	-	-	-
	Host young fledged	0.2	0.6	17	0.75	1.5	4	0.255
	Parasites fledged	0.9	1.0	17	-	-	-	-

* Only Common Hawk Cuckoo data included in the analysis, since a single nest parasitised by Pied Cuckoo is excluded.

² Higher χ^2 value indicate more dissimilar the pattern between the species.

Discussion

Selection of suitable hosts, by different parasitic cuckoo species, may differ because of preferences for host size, food, breeding site, egg-laying season, and nest accessibility among different hosts (Lack 1963). The four sympatric cuckoo species in the study area were mostly found to parasitise different host species with different breeding aspects, and within host species, certain factors like nest height might influence a cuckoo to select a particular nest. The breeding season of the cuckoo species overlapped with that of the host species. The Black Drongo breeding season was from late March to June and parasitised nests were found in April and early June. The Long-tailed Shrike breeding season lasted from April to July, and the parasitised nests were also found during the same time. However, Jungle Babblers were parasitised by both the Common Hawk Cuckoo, and the Pied Cuckoo. If two or more cuckoos parasitise the same host species we predicted that they would show other fundamental differences in their breeding ecology. In support of this prediction, we found that the Common Hawk Cuckoo, and Pied Cuckoo had different breeding seasons, which might help both the species to minimise competition. During the study, the breeding season of the Jungle Babbler was recorded from late February to June. The nests parasitised by the Common Hawk Cuckoo was found from March to May, whereas those parasitised by the Pied Cuckoo were found in June. The main breeding season of the Common Hawk Cuckoo was much earlier than for the Pied Cuckoo. Similar observations were also found in different areas (Gaston 1981; Ali 1996). The Jungle Babbler was parasitised at a considerably higher rate by Common Hawk Cuckoos, than by Pied Cuckoos. The arrival dates of these two cuckoo species, at the breeding grounds, suggest that the intensity of Common Hawk Cuckoo parasitism was highest from March through May, while that of Pied Cuckoo was at the beginning of June, during the short period this cuckoo occurred in the study area. Gaston (1976) recorded that the overall laying pattern in Jungle Babblers is two-peaked, one in March–April, and the other in July–September, with a reduced laying rate in August. A possible reason for the very low parasitism rate of the Pied Cuckoo could be that the Jungle Babbler nearly ceased its breeding in June. It was not possible to estimate the exact number of Pied Cuckoos, but not more than two to three individual birds were observed at the beginning of June each year (2010–2011). After July they were not seen in the study area, supporting the premise that they are there for a very short period of time. The first Common Hawk Cuckoo egg was laid, in a Jungle Babbler's nest, in the middle of March, while Jungle Babblers started breeding in late February. Early breeding could thus be a strategy to avoid parasitism (Begum *et al.* 2011b).

In the case of Black Drongo, breeding season overlapped entirely with that of the parasitic Indian Cuckoo. The Asian Koel arrived earlier than any of the other cuckoo species and parasitised three host species: House Crow, Common Myna, and Long-tailed Shrike. Amongst these, the Common Mynas, and House Crows are early breeders while Long-tailed Shrikes started breeding later (Begum *et al.* 2011b) though in this study we have only sampled the nests of Long-tailed Shrikes. The Asian Koel is a generalist in host choice and thus exploits different hosts with different breeding times, and habitats, which may reduce intraspecific competition (Begum *et al.* 2011a, b).

The risk of parasitism on Long-tailed Shrike nests was inversely proportionate to their height above the ground. Nests of this species were constructed in sparse foliage of large or small trees, and bamboo thickets. Most of the parasitised nests

were in small trees or in low bamboo thickets. Nests of Long-tailed Shrike, which are low down on trees where branches and foliage are sparse, may be easier to detect (Øien *et al.* 1996; Moskát & Honza 2000; Clarke *et al.* 2001). Whereas, in Black Drongo the nest height of parasitised nests were higher than that of un-parasitised nest, although we have a low sample size on parasitised nest (n=2). Both parasitised and un-parasitised Jungle Babbler nests were found at similar heights and were constructed on different species of trees.

Eggs of Asian Koel are highly non-mimetic with those of the Long-tailed Shrike, but resemble eggs of House Crows (Baker 1922). Eggs of Common Hawk Cuckoo and Pied Cuckoos resemble the eggs of Jungle Babblers quite perfectly, and the eggs of Indian Cuckoos are also good mimics of those of the Black Drongo. Most parasitic eggs were accepted by the hosts. Long-tailed Shrikes suffered higher parasitism rates. Furthermore, fledging success of the host was reduced in parasitised nests, when compared to un-parasitised ones. In spite of the significant cost of parasitism, Long-tailed Shrikes seem to have a poorly developed rejection instinct, with no observed cases of egg ejection even though the parasite egg appeared to be highly non-mimetic (Begum *et al.* 2011a). This situation is contrary to many hosts of the Common Cuckoo (Davies & Brooke 1989; Moksnes *et al.* 1990). The lack of observations of this species as a host, in literature, may indicate that it is a novel host of the Asian Koel (Begum *et al.* 2011b).

To summarise: The different cuckoo species used three species as hosts, experiencing different parasitism rates. When two cuckoo species parasitised the same host, their non-overlapping breeding seasons helped them to minimize the competition. A nest's height above the ground was an important predictor of parasitism in Long-tailed Shrike nests. The three hosts generally accepted mimetic as well as poorly mimetic cuckoo eggs, leading to a significant reduction in host breeding success. Regarding the high degree of a host's acceptance of parasitic eggs, it is suggested that the breeding successes of both, the cuckoo, and the host species should be studied in more detail. Further experimental studies, to provide a better understanding of the egg recognition ability in these hosts, are recommended.

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