International Journal of Fauna and Biological Studies
Available online at www.faunajournal.com

ISSN 2347-2677
IJFBS 2017; 4(3): 48-56
Received: 09-03-2017
Accepted: 10-04-2017

Sajeda Begum
Department of Zoology,
Jahangirnagar University,
Savar, Dhaka, Bangladesh

Correspondence
Sajeda Begum
Department of Zoology,
Jahangirnagar University,
Savar, Dhaka, Bangladesh

Host use by four sympatric species of Cuckoos in Bangladesh

Sajeda Begum

Abstract
The study on host selection by four sympatric cuckoos has been conducted in Bangladesh. Sympatric parasites should show niche segregation through variation in host use. Asian koel (*Eudynamys scolopacea*) parasitized Common myna (*Acridotheres tristis*), Long-tailed shrike (*Lanius schach*) and House crow (*Corvus splendens*); Indian cuckoo (*Cuculus micropterus*) parasitized Black drongo (*Dicrurus macrocercus*). Jungle babbler (*Turdoides striata*) was parasitized by Jacobin cuckoo (*Clamator jacobinus*) and Common hawk cuckoo (*Cuculus varius*), but the breeding season of these two cuckoo species did not overlap. Parasitism rates by cuckoo species in three habitats; human habitations, mixed scrub forests and monotypic plantations showed a significant difference for most host species between habitats, which explains that cuckoos preferred specific habitats even if their favourite host also occurred elsewhere. Indian cuckoo, Common hawk cuckoo and Jacobin cuckoo showed excellent egg mimicry with their hosts while Asian koel showed good mimicry to one of three host species.

Keywords: Asian koel, Common hawk cuckoo, Jacobin cuckoo, Indian cuckoo, sympatric, host selection

1. Introduction

Most studies of avian brood parasites deal with their interactions with hosts, which has been presented as a model system for coevolution [25, 51, 66, 62]. Since it is costly for hosts to be parasitized, natural selection has favoured host defences, like aggression against parasites near their nests [51, 63, 74] and recognition and rejection of parasitic eggs [24, 26, 49, 51]. In most cases these adaptations have been studied in systems where one parasite species utilize one or a few host species [4, 31]. Systems where several parasite species occur in sympatry have been far less studied [15, 19, 20, 33, 40]. Related species living in sympatry should be expected to have segregated into different ecological niches to avoid interspecific competition. This is known as the “Gause’s principle” [34]. There exists substantial support for this hypothesis in birds [27, 30, 53, 68]. Friedmann (1928) [32] was the first to adopt the principle to brood parasites because he concluded that such niche segregation also must occur among sympatric cuckoo species in Africa. It is logical to assume that niche differences as a consequence of interspecific competition between sympatric brood parasites could be manifested in the preference for different host species [45]. This was in fact supported by Baker (1942) [7] who recorded 15 sympatric cuckoo species in Assam, India, which parasitized different host species or bred at different times, thus avoiding competition with each other [71]. Later, such prevention of same host use through interspecific competition was shown by Brooker and Brooker (1989) [15] and Higuchi (1998) [41] who investigated host selection among sympatric cuckoo species in Australia and Japan, respectively. Furthermore, Yom-Tov and Geffen (2005) [77] found that among cuckoos, the number of host species increase with latitude, which is indicative of competitive release and niche expansion. Co-existing brood parasitic species of cowbirds may also reduce potential interspecific competition for nests through differential host use [20]. A very preliminary study on cuckoos in Bangladesh mostly focused on the basic biology and natural history by describing parasite and host interaction has revealed [10-12].

Taking these studies into consideration the picture is, however, still that the knowledge of niche segregation in avian brood parasites is scarce and incomplete. Host selection among sympatric brood parasites is driven, in part, by their breeding habitat preferences as parasitism may be strongly influenced by habitat characteristics as reported for Brown-headed cowbirds (*Molothrus ater*) [8, 13, 67] and Common cuckoo (*Cuculus canorus*) hosts [17]. Habitat preference is closely related to food availability in most bird species. Food requirements of nestlings may, however, differ from those of adults [37]. Brood parasites may therefore disconnect the aspects of their breeding and foraging requirements and rather select habitats with high quality hosts for proper parental care, irrespective of food availability for themselves [67, 73]. In addition, it is well-known that characteristics like perch availability or proximity for observing host behaviour and locate host nests are important aspects of habitat quality [3, 8, 22, 52, 57]. Furthermore, host breeding season, nest accessibility, host abundance, and vulnerability to nest predation are all factors that may influence the choice of hosts in brood parasites [5, 16, 24, 38, 41, 70, 72]. In addition to varying habitat preference, sympatric brood parasite species may be of different size [15], and therefore, as a consequence, they may be segregated by ecological niche separation [32]. In addition to the spatial aspect, brood parasite species or tribes may also be separated in timing of breeding [29, 54, 55], which may reduce the interspecific competition among cuckoo species in sympatry. Egg morphology and mimicry are important factors for selection of suitable hosts as the cuckoo egg must be incubated in the presence of a host clutch for proper incubation and hatching [25, 44, 58]. Therefore, selection for egg mimicry and egg crypsis also drives the sympatric competitive cuckoo species into host partitioning [15, 41].

In the present study the aim was to investigate interactions between four parasitic cuckoo species viz. the Asian koel (*Eudynamys scolopacea*), Common hawk cuckoo (*Hierococcyx varius*), Jacobin cuckoo (*Clamator jacobinus*) and Indian cuckoo (*Cuculus micropterus*) living in sympatry in Bangladesh, at the south-eastern part of the Indian subcontinent. These cuckoos are known to parasitize different host species [2, 7, 9], but very little is known about their host use and possible competition in areas where they occur in sympatry. From the "Gause's principle" the hypothesis that there is potential for interspecific competition between the co-occurring cuckoo species, which should have led to niche segregation. The main prediction following this hypothesis is that these cuckoo species should parasitize different host species in different habitats [10]. Otherwise, if more than one species parasitize the same host they should be likely to differ in other basic ways, e.g. either different breeding seasons or different arrival dates in the breeding habitat, or parasitizing the same host in different habitats [56].

During field work in Bangladesh investigations have been carried out to test these predictions. Data on host choice, parasitism rates and the degree of mimicry between cuckoo and host eggs were collected. Cuckoo arrival date, breeding period and habitat preference of hosts and parasites were also collected.

2. Materials and methods

2.1 Study Area

The study was conducted in Jahangirnagar University Campus, central part of Bangladesh (23°52′ N, 90°16′ E), 32 km north of Dhaka city (Fig.1). The size of the entire campus area is approximately 200 hectares consisting of diverse vegetation in and around human settlements. Three distinct habitat types in the study area were classified based on type of vegetation and presence of buildings; a) Human habitations with orchards and gardens, which includes buildings and tin shed houses used for residential, academic and administrative purposes. Various types of fruit trees like *Artocarpus heterophyllus, Mangifera indica,* and *Cocos nucifera* together with ornamental trees, (*Mimusops elengi*, *Livistona chinensis*, *Murraya paniculata*, *Polyalthia longifolia* and *Swietenia mahagoni*) are present as plantations in and around human settlements [10, 11]. b) Mixed scrub forests with plantations and isolated marsh patches. This habitat has a scattered distribution and is characterized by naturally-grown tree species like *Ficus bengalensis*, *Syzygium cumini*, *Zizyphus* sp. *Dalbergia sissoo*, *Albizia* spp. etc. and some planted tree species like *Acacia auriculiformis*, *Shorea robusta*, *Swietenia mahagony*, *Artocarpus heterophyllus* and *Mangifera indica*. Bushes like *Chrysopogon* sp., *Cassia sophera*, *Cassia tora*, *Mymosa pudica*, etc. are also present in this habitat. The low-lying areas remain dry during winter and summer and are used as agricultural lands. During the monsoon season these areas are filled with water and become marshy. c) Monotypic plantations including *Terminalia arjuna*, *Gmelina arborea* and *Lagerstroemia speciosa* which have medicinal value for the local people. Some fruit yielding plants like *Syzygium cumini*, *Artocarpus heterophyllus* and *Cocos nucifera* are also planted around such monotypic plantations by the local people. This habitat also includes a few number of banyan tree, *Ficus bengalensis* at the periphery of the plantations [10, 11].

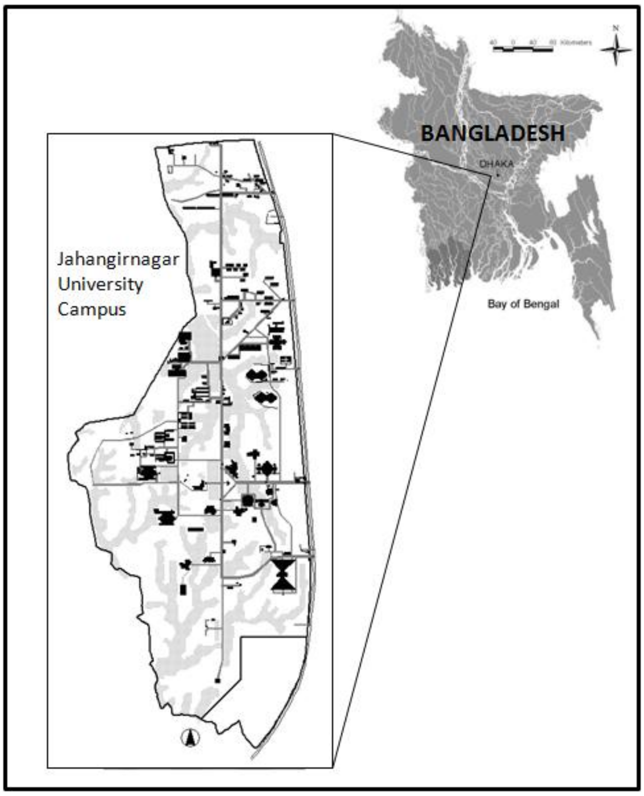

Fig 1: Map of the Jahangirnagar University campus (Source: Begum, 2011)

Some basic data on the four cuckoo species are given in Table 3. Since, however, their biology is relatively poorly known though some additional information about them are described in more detail by [10, 11, 56].

2.2 Field procedures

Nests of all passerines breeding in the study area were searched during the breeding seasons. Breeding data on different cuckoos and hosts were collected during the breeding seasons of 2008 and 2009 (January to August in each year). The different habitats in the study area were systematically explored almost daily during the breeding season. Measurement of eggs (breadth, length) of both host and parasite were made by use of electronic callipers while monitoring the nests regularly (each or every second day). Clutch initiation date (i.e., the date when the first egg was laid) was estimated by the method of Hays and Lecroy (1971) [39] if the nest was found during incubation, but also estimated by backdating from the hatching date, using published information on length of incubation period [2]. Mimicry of the parasitic egg with the host eggs was scored as described by Begum *et al*. (2011b) [11] using the scale of Moksnes and Røskaft (1995) [50] from 1 (perfect mimicry) to 5 (no mimicry). All cuckoo eggs were given the same mimicry score (always the worst) in multiple parasitized nests (which occurred only in the hosts of Asian koel). In case of excellent mimicry between the cuckoo egg and its host eggs (e.g. Jungle babbler-Common hawk cuckoo, Jungle babbler-Jacobin cuckoo and Black drongo-Indian cuckoo), which was almost impossible to detect by the human eye, parasitism was determined after hatching and identification of a cuckoo nestling. The frequency of parasitism was recorded as number of parasitized nests in relation to total number of nests found with eggs or nestlings. The arrival and departure date of cuckoos were also recorded.

Because of concentration on only recording the parasitism rates were no cuckoo species were captured for collecting morphological data. Data on body weight of both cuckoo and host species was therefore taken from literature [2], where in some cases, no mean values were described except the maximum and minimum ones. For statistical analyses, the median value of body weight was calculated in these cases (Table 3). Statistical analyses were performed using SPSS 16.0.

3. Results

3.1 Host selection

During the study period a total of 567 nests of 14 potential host species were recorded (Table 1). Among these, five were parasitized, while nine species were not. The Asian koel parasitized three different host species (Long-tailed shrike, House crow and Common myna), while Jungle babbler nests were parasitized by both the Common hawk cuckoo and the Jacobin cuckoo (Table 1). Finally the Indian cuckoo parasitized the Black drongo.

Overall parasitism rates by the sympatric cuckoos varied significantly for different host species ($\chi^2 = 34.0$, df = 4, $P < 0.001$). The nests of Common mynas were situated both in open places and in cavities (Begum *et al*. 2011b) [11] and the latter were not parasitized at all. If we consider only the open nests the parasitism rate was 68.3% ($n = 63$). This rate was significantly higher than that for the Black drongo (3.7% ($n = 82$); $\chi^2 = 68.6$, df = 1, $P < 0.001$), Long-tailed Shrike (35.7% ($n = 42$); $\chi^2 = 10.8$, df = 1, $P < 0.001$), House crow (10.8% ($n = 74$); $\chi^2 = 48.1$, df = 1, $P < 0.001$) and Jungle babbler (25.9% ($n = 58$); $\chi^2 = 20.0$, df = 1, $P < 0.0001$) (Table 1). The parasitism rates of the Long-tailed shrike, the House crow and the Jungle babbler were significantly higher than that of the Black drongo ($\chi^2 = 23.0$, df = 1, $P < 0.001$; $\chi^2 = 3.03$, df = 1, $P < 0.081$ and $\chi^2 = 16.6$, df = 1, $P < 0.001$ respectively). The parasitism rate did not differ significantly between the Long-tailed shrike and the Jungle babbler ($\chi^2 = 0.75$, df = 1, $P = 0.400$), however, the parasitism rate of the Long-tailed shrike was significantly higher than that of the House crow ($\chi^2 = 10.5$, df = 1, $P < 0.001$). Finally, the parasitism rate of the Jungle babbler was significantly higher than that of the House crow ($\chi^2 = 6.15$, df = 1, $P = 0.013$).

Table 1: Parasitism rates (in %) of different hosts by different cuckoo species

		Parasitic	species		
Host species	**Asian koel % par**	**Common hawk cuckoo % par**	**Jacobin cuckoo % par**	**Indian cuckoo % par**	**Total number of nest (N)**
Common myna (*Acridotheres tristis*)	31.2	0	0	0	138
Long-tailed shrike (*Lanius schach*)	35.7	0	0	0	42
House crow (*Corvus splendens*)	10.8	0	0	0	74
Black drongo (*Dicrurus macrocercus*)	0	0	0	3.7	82
Jungle babbler (*Turdoides striatus*)	0	25.9	1.7	0	58
Jungle crow (*Corvus macrorhynchos*)	0	0	0	0	21
Asian pied starling (*Gracupica contra*)	0	0	0	0	75
Black-hooded oriole (*Oriolus xanthornus*)	0	0	0	0	21
Red-vented bulbul (*Pycnonotus cafer*)	0	0	0	0	27
Oriental magpie robin (*Copsychus saularis*)	0	0	0	0	22
Orange-headed thrush (*Zoothera citrina*)	0	0	0	0	2
Purple-rumped sunbird (*Leptocoma zeylonica*)	0	0	0	0	1
Rufous tree pie (*Dendrocitta vagabunda*)	0	0	0	0	3
Large cuckoo shrike (*Coracina macei*)	0	0	0	0	1

3.2 Parasitism rates in different habitats

Common mynas were parasitized at a significantly higher rate by Asian koels in human habitations than in mixed scrub forests ($\chi^2 = 4.9$, df = 1, $P = 0.020$) (Table 2). Long-tailed shrikes were never parasitized in the mixed scrub forests while the parasitism rate was almost 100% in both human habitations as well as monotypic plantations, a difference that is statistically significant ($\chi^2 = 38.0$, df = 2, $P < 0.0001$). Finally House crows experienced a significantly higher parasitism rate in monotypic plantations than in human habitations and mixed scrub forests, where parasitism never occurred ($\chi^2 = 51.4$, df = 2, $P < 0.0001$). Thus the Asian koel never parasitized a potential host in the mixed scrub forests while the parasitism rates in the other two habitats were significantly higher ($\chi^2 = 54.2$, df = 2, $P < 0.001$) (Table 2).

Table 2: Parasitism rates (%) in different habitat types by different cuckoo species (Parasitism rates in different habitats tested with pairwise Chi-square tests (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, no indication when not significant).

Cuckoo species	Host species		Habitat types % (N)		
		Human habitation % Par (*n*)	**Mixed scrub forest % Par (*n*)**	**Monotypic plantation % Par (*n*)**	**χ^2- test**
Asian koel	Common myna	33.6 (128)	0 (10)		*
	Long-tailed shrike	100 (5)	0 (26)	90.9 (11)	***
	House crow	0 (59)	0 (4)	72.7 (11)	***
Common hawk cuckoo	Jungle babbler	100 (6)	17.6 (51)	0 (1)	***
Jacobin cuckoo	Jungle babbler	0 (6)	2.0 (51)	0 (1)	
Indian cuckoo	Black drongo	0 (7)	5.3 (57)	0 (18)	

All nests of Long-tailed shrikes in human habitations were parasitized and none of the House crow nests were parasitized in the same habitat. In spite of this the difference in parasitism rate of the two species between human habitations and monotypic plantations was not statistically significant at the 5% level (Kruskal-Wallis ANOVA test, $H = 3.26$, $n_1 = 15$ and $n_2 = 8$, $P = 0.070$).

The Common hawk cuckoo parasitized all Jungle babbler nests found near human habitations, close to 18% of those found in mixed scrub forests and none in monotypic plantations, a difference that was statistically significant ($\chi^2 = 18.8$, df = 1, $P < 0.0001$) (Table 2). Only one babbler nest was found in monotypic plantations, therefore, this habitat was excluded from the analysis. The Indian and Jacobin cuckoos parasitized nests only in mixed scrub forests and avoided the two other habitats. Unparasitized Jungle babblers started egg-laying significantly earlier (30 March, SD = 24.4, $n = 42$) than did the parasitized ones (19 April, SD = 37.7, $n = 15$), and a significant difference in start of egg-laying between parasitized and unparasitized nests was found in Jungle babblers (t-test, $P = 0.030$). Only one nest of the Jungle babbler was parasitized by the Jacobin cuckoo, where the host egg laying date was 8 June. No significant difference was found between the mean egg-laying date of parasitized (28 April, SD = 22.9, $n = 3$) and unparasitized nests of Black drongos (21 April, SD = 15.0, $n = 79$, $p = 0.44$). There was no significant differences in mean egg laying date between different species of cuckoos ($F = 0.88$, df = 3 and 76, $P = 0.45$, Table 3).

3.3 Size and color pattern of host and parasite egg

Asian koel eggs are highly non-mimetic both in color, pattern and size when compared to the eggs of the Common myna (turquoise blue) and the Long-tailed shrike (pale creamy with small brown or reddish brown specks and blotches at the broader end) (Table 3). They are, however, moderate, sometimes good mimics of House crow eggs (Table 3, see also Begum *et al*. 2011b). Indian cuckoo eggs are white with reddish brown markings and are very good mimics of those of the Black drongo (Fig.2, Table 3). Common hawk cuckoo and Jacobin cuckoo eggs are highly mimetic to the eggs of the Jungle babbler in both colour pattern and size (Fig.2). The mimicry score differed significantly between different hosts ($F = 689.1$, df = 70 and 4, $P < 0.0001$, Table 3).

Fig 2: Host clutches containing cuckoo and host eggs (left to right); Row1 Jungle babbler (3) eggs and Jacobin cuckoo (1), Row 2: Jungle babbler (3) eggs and Common hawk cuckoo (1), Row3: Black drongo (3) eggs and Indian cuckoo (1). All cuckoo eggs confirmed to be cuckoos by hatching chick.

It has been found in most cases that non-mimetic or poorly mimetic eggs of the Asian koel were accepted by the three hosts. However, Common mynas deserted significantly more parasitized than non-parasitized nests (Begum *et al*., 2011b). Jungle babblers also accepted all eggs of Jacobin and Common hawk cuckoos, which were perfectly good mimics of the host eggs. Furthermore, all Black drongo hosts accepted the Indian cuckoo egg which also showed good mimicry with the host eggs. The Asian koel laid significantly larger eggs than two of its hosts, the Common myna and the

Long-tailed shrike (*t* = -5.69, df = 36, *P* < 0.001; *t* = -30.45, df = 12, *P* < 0.001; respectively, Table 3), however koels laid comparatively smaller eggs than the House crow (*t* = 2.87, df = 4, *P* = 0.045). Common hawk cuckoos laid significantly larger eggs than those of Jungle Babblers (*t* = -2.65, df = 13, *P* = 0.020), while the Indian cuckoo laid smaller eggs than its host, although the volume did not differ significantly (*t* = -1.48, df = 2, *P* = 0.275; Table 3).

Table 3: Characteristics of four sympatric cuckoo species in Bangladesh. *Values of mean body mass are taken from [2, 59].

	Cuckoo				**Host**			
Cuckoo species	**body weight in gm Median (N)**	**egg volume in cm³ Mean ±SD (N)**	**Arrival date/ Departure date**	**Laying date (day1=Jan1) Mean ± SD (N)**		**egg volume in cm³ Mean ±SD (N)**	**body weight in gm Median (N)**	**Mimicry** Mean (N)**
Asian koel	167 (10) ♂♀	7.92 ± 0.94 (142)	Late February/Late November	117 ±28.4 (61)	HC	13.90 ±2.35 (201)	288 (7)	2.4 (7)
					CM	6.29±0.77 (402)	110 (17)	4.9 (35)
					LTS	3.79±0.30 (134)	37 (11)	5.0 (11)
Common hawk cuckoo	104 (1) ♀	5.60 ± 1.22 (13)	Early March/ Late November	111 ± 38.2 ; (15)	JB	4.63 ± 0.76 (182)	61 (8)	1.1 (7)
Jacobin cuckoo	67 (4)	4.8 (1)	Early June/Late July	161 (1)	JB	4.63 ± 0.76 (182)	61 (8)	1. 0 (1)
Indian cuckoo	128 (1)	4.40 ±0.10 (3)	Early April/Late June	120 ± 23.1; (3)	BD	4.88 ±0.47 (258)	46 (15)	1.7 (3)

CM = Common Myna; LTS = Long-tailed Shrike; HC = House Crow; JB = Jungle Babbler; BD = Black Drongo. * *Cuckoo egg mimicry referred by (Moksnes and Røskaft 1995)

3.4 Mutilple parasitism by Asian Koel

A relatively high frequency of multiple parasitism (more than one cuckoo egg in the nest) was observed about 68% of the parasitized nests (45/66) of different hosts received more than one cuckoo egg (2-6), hence suffering multiple parasitism by Asian koels (Table 4). The Common myna (23.2%) and Long-tailed shrike (21.4%) nests were commonly multiply parasitized, while House crow had a similar frequency of multiple parasitized as single parasitized nests (5.4%) (Table 4). Multiple parasitized nests contained from two to six cuckoo eggs (Table 4). No multiple parasitism occurred in the Jungle babbler and the Black drongo, as each parasitized nest of these species contained only one parasitic egg.

Table 4: Multiple parasitism in different hosts by different cuckoos

Number of parasitic eggs	Common myna eggs (%)	Long-tailed shrike eggs (%)	House crow eggs (%)	Jungle babbler eggs (%)	Black drongo eggs (%)
0	95 (68.8%)	27 (64.3%)	66 (89.2%)	42 (72.4%)	79 (96.3%)
1	11 (8.1%)	6 (14.3%)	4 (5.4%)	16 (27.6%)	3 (3.7%)
2	13 (9.4%)	5 (11.9%)	4 (5.4%)	-	-
3	10 (7.2%)	3 (7.1%)	-	-	-
4	5 (3.6%)	1 (2.4%)	-	-	-
5	3 (2.2%)	-	-	-	-
6	1 (0.7%)	-	-	-	-
Total	138	42	74	58	82

4. Discussion

The study provides the preliminary information on host use of different species of cuckoos in Bangladesh. Some cuckoo species appeared to be more generalists in host use, while others were specialized in their host use, thus parasitize a few related host species. Some cuckoos also have overlapping ranges of host species, but the data are inadequate to get dependable approximate of such overlaps and their importance. With several cuckoo species breeding sympatrically, host use segregation as a result of interspecific competition is to be expected as indicated by evidence from Japan [41].

Selection of suitable hosts by different parasitic cuckoo species may differ because of preferences for host size, food, breeding site, egg-laying seasons, and nest accessibility among different hosts [43]. The sympatric parasitic cuckoo species reduce the competition by selecting different hosts with different breeding strategies, their habitat preferences or breeding sites, food habit and laying seasons. If two or more cuckoos parasitize the same host species, the prediction might be that they should show other fundamental differences in their breeding ecology [56]. Common hawk cuckoo parasitism was highest which coincides with the host Jungle babbler breeding season while Jacobin cuckoo parasitism was lowest as it started at the beginning of June when the host Jungle babbler nearly seized its breeding. Jungle babblers started breeding in mid-February. Early breeding could thus be a strategy to avoid parasitism [10, 35].

Cuckoos usually select hosts smaller than themselves because of the abundance of smaller passerine hosts [58]. However, the Asian koel selected different sized hosts; both larger (House crow) and smaller (Common myna and Long-tailed shrike) than themselves. House crows experienced the lowest parasitism rate which might be explained by the fact that larger hosts are capable of defending their nests successfully against predators as well as brood parasites [48, 65]. Colonial nesting and roosting may be other possible factors where vigilance behavior of the neighbouring individuals may have reduced the Asian koels' opportunity to lay their eggs in the nests of House crows [10, 18]. The Jungle babbler is a smaller host than the Common hawk cuckoo, but of similar size as the Jacobin cuckoo. These two parasitic cuckoos seem to be specialized on this specific host because of very good egg mimicry.

The Asian koel arrived earlier than any of the other cuckoo species and parasitized three hosts among which Common mynas and House crows are early breeders while Long-tailed shrikes started breeding later **[10, 56]**. The Asian koel breeds in habitats where there are fruit-bearing trees **[14, 23]** and as a comparatively larger cuckoo it also has a broader niche of potential hosts [15]. The Asian koel seems to be more generalistic in its host choice, thus exploits different hosts such as Black-naped orioles (*Oriolus chinensis*) and Black drongos if crows are not available **[42, 69]** with different breeding habitats, which may reduce intraspecific competition.

4.1 Host preferences in different habitats

The four cuckoo species overlapped in their use of different breeding habitats; human habitations with orchards and gardens, mixed scrub forests and monotypic plantations. They did not stay away from each other through strict habitat separation or any avoidance behavior. However, according to Ali and Ripley (1987) [2] and Payne (2005) [59] they utilize separate ecological niches concerning their food habits.

The number of Common myna nests and parasitism rates by the Asian koel were highest near human habitations. Host nest density may in general play an important role in host selection [72]. Another factor that most probably contributed to the koel's high parasitism rate in human habitations was that this habitat had most fruit trees bearing the main diet of the Asian koel. These trees also serve as vantage points for the cuckoo [10]. The regional composition of habitats can directly influence the density of parasites and therefore also risk of parasitism of different hosts. This has been shown for generalistic brood parasites like the brown-headed cowbird which requires specific habitats for feeding [61]. House crows were, however, not parasitized by the Asian koel in human habitations because of colonial nesting in this habitat **[10]**. Parasitism rates were highest in monotypic plantations where the crows nested solitarily with longer distances between nests of conspecific neighbours. For House crows Begum *et al*. (2011a) [10] showed that distance between conspecific neighbours was a reliable predictor for the risk of being parasitized by the Asian koel, rather than host nest density.

These sympatric cuckoos with similar size may exhibit different habitat preferences [15]. The Common hawk cuckoo occurred in orchards and gardens near human habitation **[36]** as their di*et al*so consists of fruits, berries [75, 59], though edges of light wood forests nearby low lying marshy areas are the preferred habitat and hence prefers to feed mainly on insects from the ground. On the other hand, almost similar sized cuckoo species, the Jacobin cuckoo prefers to feed in trees, low bushes and by hopping on the ground, searching for insects under leaves and in forks of branches [2, 36]. The Indian cuckoos feed in high forest trees and foliage of the canopy [36, 59]. The Asian koel differs from many other cuckoos in that fruit is an important part of their diet **[2]** and therefore, all parasitized nests by Asian koels remained closer to fruit trees **[10]**. Thereby, all these sympatric cuckoos belonging to different genera reduce their competition for food by segregation of ecological niches in the same habitat **[32]**. Mixed scrub forests with both natural shrub vegetations and monoculture plantations, is a preferred habitat for some of the host species like Long-tailed shrikes, Jungle babblers and Black drongos and the parasitism rate was less than 20%. It might be because of better cover and concealment (total foliage hypothesis; [46, 47] in the mixed scrub forest than around human habitations.

Again, some parasitized nests by Common hawk cuckoos and all parasitized nests by Indian and Jacobin cuckoos were found in mixed scrub forests. It is described that Common hawk cuckoo, Jacobin cuckoo and Indian cuckoo prefer woodlands or forests [2, 36, 59] rather than open areas with fruit trees and hence select suitable hosts which are insectivorous and built nests in forests. The Long-tailed shrike was not parasitized in mixed scrub forests. This was probably because Asian koels selected shrike nests in the two other habitats with more fruit-bearing trees which were used as vantage points by the koel [10]. Potential hosts breeding where vantage points are scarce or absent may suffer less parasitism than those breeding where vantage points are abundant **[64]**. This is well known for the hosts of several avian brood parasites, e.g. the common cuckoo [5, 52, 57].

4.2 Cuckoo egg mimicry

Eggs of Asian koels are highly non-mimetic to eggs of both the Common myna and the Long-tailed shrike, but resemble eggs of House crows [2, 6]. Eggs of Common hawk cuckoo and Jacobin cuckoos resembled the eggs of Jungle babblers quite perfectly, and the eggs of Indian cuckoos were also good mimics of those of the Black drongo [56]. Most parasitic eggs were accepted, but Common mynas nests parasitized by the Asian koel were deserted more often than unparasitized ones [11]. In spite of the high degree of host acceptance of parasite eggs, the breeding success of both cuckoo and host species should be studied in more detail.

4.3 Multiple parasitism

Although cuckoo density has not been measured during study period, but high frequency of multiple parasitism reflects high density of cuckoos locally [60, 76]. It may be reflected that because of comparatively high density of Asian koels in the study area forced to synchronize parasitism with different host species laying to maximize egg hatchability and chick survival [28]. Furthermore, female cuckoos can be induced to lay more eggs when more host nests are available [21, 58].

5. Conclusion

Four parasitic cuckoo species were breeding in the study area, one of which is very common. Among the hosts of the most common brood parasitic Asian koel, multiple parasitism was very common. There was no overlap in host choice by the cuckoos in the study area, except for the Common hawk cuckoo and the Jacobin cuckoo; however, there was no overlap in time in the study area. Furthermore, studies are required for a better understanding of evolution of mimetic eggs in the cuckoo species involved in the present study.

These findings provide the baseline data for further investigation regarding co-evolutionary interactions between brood parasites and hosts in this geographical region.

Acknowledgements
I thank Md. Yousuf and Monoronjon for their tremendous help in fieldwork. I am indebted to all members and staffs in the Wildlife Research Group, Department of Zoology, Jahangirnagar University for cooperation during data collection in the field. I am furthermore grateful to all the members of the Brood Parasitism Research Group, Department of Biology, Norwegian University of Science and Technology (NTNU) for valuable suggestions during my field work. The study was supported by a Grant through a 'Quota Scheme' at NTNU.

References

1. Ali H, Hassan SA, Rana SA, Beg M, Mahmood-ul-Hassan M. Brood parasitism of Asian koel *Eudynamys scolopacea* on the house crow Corvus splendens in Pothwar region of Pakistan. Pakistan J. of Agricultural Science. 2007; 44:627-634.
2. Ali S, Ripley SD. Handbook of the birds of India and Pakistan, together with those of Nepal, Sikkim, Bhutan and Ceylon. Oxford University Press, London, UK, 1987.
3. Antonov A, Stokke BG, Moksnes A, Røskaft E. Factors influencing the risk of common cuckoo *Cuculus canorus* parasitism on marsh warblers *Acrocephalus palustris*. J. of Avian Biology. 2007; 38:390-393.
4. Antonov A, Stokke BG, Vikan JR, Fossøy F, Ranke PS, Røskaft E *et al*. Egg phenotype differentiation in sympatric cuckoo *Cuculus canorus* gentes. J. of Evolutionary Biology. 2010; 23:1170-1182.
5. Aviles JM, Stokke BG, Parejo D. Relationship between nest predation suffered by hosts and brown-headed cowbird parasitism: A comparative study. Evolutionary Ecology. 2006; 20:97-111.
6. Baker ECS. Cuckoos. Some theories about the birds and their eggs. Bulletin of the British Ornithological Club. 1922; 42:93-112.
7. Baker ECS. Cuckoo problems. H. F. & G. Witherby, London, UK, 1942.
8. Barber DR, Martin TE. Influence of alternate host densities on brown-headed cowbird parasitism rates in black-capped vireos. Condor. 1997; 99:595-604.
9. Becking JH. Notes on the breeding of Indian cuckoos. J Bomb. Nat. Hist. Soc. 1981; 78:201-231.
10. Begum S, Moksnes A, Røskaft E, Stokke BG. Factors influencing host nest use by the brood parasitic Asian koel (*Eudynamys scolopacea*). J Ornithol. 2011a; 152(3):793-800.
11. Begum S, Moksnes A, Røskaft E, Stokke BG. Interactions between the Asian koel (*Eudynamys scolopacea*) and its hosts. Behaviour. 2011b; 148(3):325-340.
12. Begum S, Moksnes A, Røskaft E, Stokke BG. Responses of potential hosts of Asian cuckoos to experimental parasitism. Ibis. 2012; 154: 363-371.
13. Benson TJ, Anich NM, Brown JD, Bednarz JC. Habitat and landscape effects on brood parasitism, nest survival, and fledging production in Swainson's warblers. J of Wildlife Management. 2010; 74:81-93.
14. Blakers M, Davies SJJF, Reilly PN. The Atlas of Australian birds. Australian Ornithologists Union. Melbourne, Victoria, Australia, 1984.
15. Brooker LC, Brooker MG. Cuckoo hosts in Australia. Australian Zoological Review. 1989; 2:1-67.
16. Brooker LC, Brooker MG. Why are cuckoos host specific? Oikos. 1990; 57:301-309.
17. Campobello D, Sealy SG. Avian brood parasitism in a Mediterranean region: Hosts and habitat preferences of common cuckoos *Cuculus canorus*. Bird Study. 2009; 56:389-400.
18. Canestrari D, Marcos JM, Baglione V. Cooperative breeding in Carrion Crows reduces the rate of brood parasitism by Great Spotted Cuckoos. Animal Behaviour. 2009; 77:1337-1344.
19. Chace JF. Habitat selection by sympatric brood parasites in southeastern Arizona: the influence of landscape, vegetation and species richness. Southwestern Naturalist. 2004; 49:24-32.
20. Chace JF. Host use by sympatric cowbirds in southeastern Arizona. Wilson Bulletin. 2005; 117:375-381.
21. Chance EP. The Truth about the Cuckoo. Country Life Ltd., London, 1940.
22. Clarke AL, Øien IJ, Honza M, Moksnes A, Røskaft E. Factors affecting Reed Warbler risk of brood parasitism by the Common Cuckoo. Auk. 2001; 118:534-538.
23. Coats BJ. The birds of Papua New Guinea. Non-Passerines. Dove, Alderey, Queensland, Australia, 1985, 1.
24. Davies NB. Cuckoos, cowbirds and other cheats. T & A D Poyser, London, UK, 2000.
25. Davies NB, Brooke Mde L. Cuckoos versus reed warblers: adaptations and counter adaptations. Animal Behaviour. 1988; 36:262-284.
26. Davies NB, Brooke Mde L. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J. of Animal Ecology. 1989; 58:207-224.
27. Diamond JM. Niche shifts and the rediscovery of interspecific competition. American Scientist. 1978; 66:322-331.
28. De Marsico MC, Reboreda JC. Differential reproductive success favour strong host preferences in a highly specialized brood parasite. Proc. R. Soc. 2008; 275:2499-2506.
29. Douglas DJT, Newson SE, Leech DI, Noble DG, Robinson RA. How important are climate-induced changes in host availability for population processes in an obligate brood parasite, the European cuckoo? Oikos. 2010; 119:1834-1840.
30. Ehrlich PR, Holm RW. The process of evolution. McGraw & Hill, New York, USA, 1963.
31. Fossoy F, Antonov A, Moksnes A, Roskaft E, Vikan JR, Moller AP *et al*. Genetic differentiation between sympatric cuckoo host races - Males matter. Proceedings of the Royal Society of London Series B, Biological Sciences. 2011; 278:1639-1645.
32. Friedmann H. The origin of host specificity in the parasitic habit in the Cuculidae. Auk. 1928; 45:33-38.
33. Friedmann H. Alloxenia in three sympatric African species of Cuculus. Proceedings of the United States National Museum. 1967; 124:1-14.
34. Gause GF. The struggle for existence. Hafner Press, New

York, USA, 1934.
35. Gill BJ. Behavior and ecology of the shining cowbird Chrysococcyx lucidus. In: Parasitic birds and their hosts; Studies in coevolution (Rothstein, S.I. & Robinson, S.K., eds). Oxford University Press, New York, NY, 1998, 143-151.
36. Grimmett R, Inskipp C, Inskipp T. A guide to the birds of India, Pakistan, Nepal, Bangladesh, Bhutan, Sri Lanka and the Maldives. Princeton University Press, Princeton, 1999.
37. Hamilton GD, Orians GH. Evolution of brood parasitism in altricial birds. Condor. 1965; 67:361-382.
38. Hauber ME. Site selection and repeatability in brown-headed cowbird (*Molothrus ater*) parasitism of eastern phoebe (*Sayornis phoebe*) nests. Canadian J of Zoology. 2001; 79:1518-1523.
39. Hays H, LeCroy M. Field criteria for determining incubation stage in eggs of the Common Tern. Wilson Bull. 1971; 83:425-429.
40. Higuchi H. Responses of the Bush Warbler Cettia diphone to Artificial Eggs of *Cuculus canorus* in Japan. Ibis. 1989; 131:94-98.
41. Higuchi H. Host Use and Egg Color of Japanese Cuckoos. In: Parasitic birds and their hosts; Studies in coevolution (S. I. Rothstein, and S. K. Robinson, eds). Oxford University Press, New York, Oxford. 1998, 80-93.
42. Holmes DA, van Balen S. The birds of Tinjil and Deli Islands, West Java. Kukila. 1996; 8:117-126.
43. Lack D. Cuckoo hosts in England. Bird Study. 1963; 10:185-201.
44. Lack D. Ecological adaptations for breeding in birds. Methuen, London, UK, 1968.
45. Lack D. Ecological isolation in birds. Blackwell, Oxford, UK, 1971.
46. Martin TE. Breeding productivity considerations - what are the appropriate habitat features for management. Washington: Smithsonian Inst Press, 1992.
47. Martin TE. Nest predation among vegetation layers and habitat types - revising the dogmas. Am. Nat. 1993; 141(6):897-913.
48. Mason P. Brood parasitism in a host generalist, the shiny cowbird.1. The quality of different species as hosts. Auk. 1986; 103:52-60.
49. Moksnes A, Røskaft E. Responses of some rare cuckoo hosts to mimetic model cuckoo eggs and to foreign conspecific eggs. Ornis Scandinavica. 1992; 23:17-23.
50. Moksnes A, Røskaft E. Egg morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. J of Zoology, London. 1995; 236:625-648.
51. Moksnes A, Røskaft E, Braa AT, Korsnes L, Lampe HM, Pedersen HC. Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. Behaviour. 1990; 116(1):64-89.
52. Moskát C, Honza M. Effect of nest and nest site characteristics on the risk of Cuckoo *Cuculus canorus* parasitism in the Great Reed Warbler Acrocephalus arundinaceus. Ecography. 2000; 23:335-341.
53. Murray BGJ. The ecological consequences of interspecific territorial behavior in birds. Ecology. 1971; 52:414-423.
54. Møller AP, Antonov A, Stokke BG, Fossøy F, Moksnes A, Røskaft E *et al*. Isolation by time and habitat and coexistence of distinct host races of the common cuckoo. J of Evolutionary Biology. 2011a; 24:676-684.
55. Møller AP, Saino N, Adamik P, Ambrosini R, Antonov A, Campobello D *et al*. Rapid change in host choice of the common cuckoo *Cuculus canorus* linked to climate change. Proceedings of the Royal Society of London Series B, Biological Sciences. 2011b; 278:733-738.
56. Nahid MI, Begum S, Feeroz MM. Brood parasitic cuckoos and their hosts in Jahangirnagar University Campus. Indian BIRDS. 2016; 12(2):43-48.
57. Øien IJ, Honza M, Moksnes A, Røskaft E. The risk of parasitism in relation to the distance from Reed Warbler nests to Cuckoo perches. J of Animal Ecology. 1996; 65:147-153.
58. Payne RB. The evolution of clutch size and reproductive success in parasitic cuckoos. Evolution. 1974; 28:169-181.
59. Payne RB. The cuckoos; with a molecular genetic analysis of cuckoo phylogeny by Michael D Sorenson and Robert B Payne. Oxford University Press, Oxford, UK, 2005.
60. Preston FW. The cowbird (*M. ater*) and the cuckoo (*C. canorus*). Ecology, 1948; 29:115-116.
61. Robinson SK, Brawn JD, Morse SF, Herkert JR. Use of different habitats by breeding brown-headed cowbirds in fragmented midwestern landscapes. Studies in Avian Biology. 1999; 18:52-61.
62. Røskaft E, Moksnes A. Coevolution between brood parasites and their hosts: an optimality theory approach. In: Parasitic birds and their hosts: studies in coevolution. (Rothstein, S.I. and S.K. Robinson, eds.) Oxford University Press, New York. 1998, 236-254.
63. Røskaft E, Moksnes A, Stokke BG, Bicik V, Moskat C. Aggression to dummy cuckoos by potential European cuckoo hosts. Behaviour. 2002a; 139:613-628.
64. Røskaft E, Moksnes A, Stokke BG, Moskat C, Honza M. The spatial habitat structure of host populations explains the pattern of rejection behavior in hosts and parasitic adaptations in cuckoos. Behavioral Ecology. 2002b; 13:163-168.
65. Rothstein SI. Evolutionary Rates and Host Defenses against Avian Brood Parasitism. The American Naturalist. 1975; 109:161-176.
66. Rothstein SI. A model system for coevolution: avian brood parasitism. Annual Review of Ecology, Evolution and Systematics. 1990; 21:481-508.
67. Rothstein SI, Verner J, Stevens E. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic brown-headed cowbird. Ecology. 1984; 65:77-88.
68. Sætre GP, Post E, Kral M. Can environmental fluctuation prevent competitive exclusion in sympatric flycatchers? Proceedings of the Royal Society of London Series B, Biological Sciences. 1999; 266:1247-1251.
69. Smith TEH. Black drongos fostering a koel J. Bombay Nat. Hist. Soc. 1950; 49:304-305.
70. Soler JJ, Martinez JG, Soler M, Møller AP. Host sexual selection and cuckoo parasitism: an analysis of nest size in sympatric and allopatric magpie *Pica pica* populations parasitized by the great spotted cuckoo Clamator glandarius. Proceedings of the Royal Society of London Series B, Biological Sciences. 1999; 266:1765-1771.

71. Southern HN. Mimicry in cuckoos' eggs. In J. Huxley, Hardy, A. C. and F. E. B [eds.], Evolution as a process. G. Allen, 1958, 219-232.
72. Stokke BG, Hafstad I, Rudolfsen G, Bargain B, Beier J, Campàs DB *et al*. Host density predicts presence of cuckoo parasitism in reed warblers. Oikos. 2007; 116(6):913-922.
73. Thompson FR I. Temporal and spatial patterns of breeding brown-headed cowbirds in Midwestern United States. Auk. 1994; 111:979-990.
74. Welbergen JA, Davies NB. Strategic variation in mobbing as a front line of defense against brood parasitism. Current Biology. 2009; 19:235-240.
75. Whistler H. A popular handbook of Indian birds. Oxford University Press, Bombay, India, 1949.
76. Wyllie I. The Cuckoo. Batsford, London, 1981.
77. Yom-Tov Y, Geffen E. Host specialization and latitude among cuckoos. J of Avian Biology. 2005; 36:465-470.