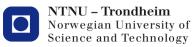


Risk of brood parasitism and predation in relation to human activity in Jahangirnagar University campus, Bangladesh

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Abstract

Brood parasitism and nest predation are two important causes affecting avian breeding success. Human disturbance is furthermore a serious problem in avian conservation and is increasing at a steady rate globally. The main aim of the present study is to examine how human activity influences risk of nest predation and brood parasitism at Jahangirnagar University campus outside Dhaka in Bangladesh. A total of five cuckoo species was recorded in the study area which parasitized six passerine species nests. This study is the first to confirm that plaintive cuckoos use common tailorbirds as hosts in Bangladesh. Two hypotheses were tested. First, as cuckoos assess human activity as a source of disturbance; there should be a negative relationship between parasitism rates and distance from human settlements. Second, as predation mainly depends on predator species and predators are found in all types of habitats; there should be no relationship between predation and distance to human settlements. The results supported both hypotheses. Finally, there was a significant relationship between nest predation and brood parasitism. Parasitized nests had lower success rates than unparasitized nests. The results of the present study showed the importance of natural habitat in cuckoo conservation and the negative effects of human habitat encroachment. Large areas with little human disturbance should be established. Some cuckoo species may be driven to extinction if the human habitat encroachment continues.

Key words: Brood parasitism, cuckoo, nest predation, human disturbance, human habitat.

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1. Introduction

1.1. General background

Avian brood parasitism is a reproductive strategy where parasitic birds do not build their own nests but lay their eggs in the nest of another bird and transfer the costs of rearing their offspring onto another individual, the host (Davies 2000, Johnsgard 1997, Ortega 1998, Payne 2005, Rothstein and Robinson 1998). Brood parasitism is therefore a breeding strategy that involves an escape from the chief duties of parental care (nest building, incubation and rearing the chicks). Two types of brood parasitism have been recognised intraspecific and interspecific brood parasitism. In interspecific brood parasitism, a parasite lay its egg in the nest of different species, e.g. - honeyguides (Indicator), cowbirds (Molothrus) and cuckoos (Cuculus) (Davies 2000). Interspecific brood parasitism is rarer, occurring in about 100 (ca. 1%) of the 9672 species and only found in four orders -Cuculiformes, Piciformes, Passeriformes and Anseriformes (Davies 2000, Sibley and Monroe 1990). Successful parasitism is very costly to the hosts since parasitism reduces their reproductive success (Rothstein 1990). Parasitized hosts usually suffer egg loss, overcrowding and misdirected parental care (Stokke et al. 2005). Female parasitic birds remove one or more host eggs before laying their own egg (Moskát 2005). Most of the cuckoo chicks are good ejectors; it ejects all the host eggs and nestlings from the nest which make severe cost to the host (Moksnes et al. 2013, Rothstein 1990). Cowbirds and some cuckoo chicks grow up together with the host chicks but the host chicks do not compete with the cuckoo chick since the cuckoo hatch earlier and has a higher body growth (Moskát 2005, Stokke *et al.* 2005). Rearing of the cuckoo chick is also costly as the cuckoo chick accelerates host provisioning rate and makes the hosts exhausted (Moskát 2005). Parasitism forces the host to lay more eggs in a single breeding season by inducing renesting which reduces host future fitness (Nager et al. 2001, Stokke et al. 2005, Visser and Lessells 2001).

There is also a relationship between brood parasitism and human activity (Burhans and Thompson 2006, Chace and Walsh 2006, Liang *et al.* 2013, Robinson *et al.* 1995, Tewksbury *et al.* 1998, 2006). Cuckoos usually assess human habitat as a source of disturbance (Liang *et al.* 2013), so cuckoos avoid such areas (Møller 2010). "The habitat



structure hypothesis" proposed by Røskaft *et al.* (2002), states that cuckoos select some special habitat characteristics when choosing a host nest. As cuckoos tend to avoid human-dominated areas, the hosts can benefit by building their nests close to humans (Liang *et al.* 2013). Parasitized and unparasitized nests differ in many variables like height above ground, distance to fruit tree, nest volume, distance to neighbor and host clutch size (Begum *et al.* 2011a, 2011b). On the other hand, cowbird shows the opposite pattern in relation to brood parasitism and human habitat. Cowbird parasitism rate is very high close to human inhabited areas (Burhans and Thompsons 2006, Chace and Walsh 2006, Robinson *et al.* 1995, Tewksbury *et al.* 1998, 2006).

Nest predation is the main cause of nest failure in most bird species (Martin 1993, Remeš *et al.* 2012, Ricklefs 1969, Thompson 2007) and has been recognized as a key correlate of a suite of life-history traits across species (Martin 1995, Remeš and Martin 2002). Nest predation rate mainly varies with nesting pattern (Martin and Li 1992, Wesołowski and Tomiałojć 2005), nest height or plant covers (Martin 1993), environment (Tewksbury *et al.* 2006), topography (Thompson 2007) and altitude (Boyle 2008). It is possibly the main cause of egg loss and nestling death, and affect bird population density (George 1987, Lahti 2001) as well as bird community structure (Martin 1988, Söderström 1999). Moreover, nest predation may become a threat to bird populations if the predation pressures increase too rapidly (Crooks and Soulé 1999).

Several studies have identified nest predation as one of the main regulators in forest bird populations in both tropical and temperate forests (Cooper and Francis 1998, Telleria and Diaz 1995). Predator composition varies across habitats (Pietz and Granfors 2000, Thompson *et al.* 1999). Every area have a typical combination of reptilian, avian and mammalian predators (Cavitt and Martin 2002, Thompson *et al.* 1999) and these predators will either predate nests randomly (Vickery *et al.* 1992) or search for specific species (Sonerud and Fjeld 1987).

Predation rate is positively correlated with agricultural landscapes as predation increases with increasing agricultural activities (Andrén 1992, Rodewald and Yahner 2001). Predator species associated with agricultural habitats are considered generalist predators, such as – raccoons (*Procyon lotor*) and magpies (*Pica pica*) (Andrén 1992, Chalfoun *et al.* 2002,



Kurki *et al.* 2000). Predators connected to forest habitats are considered intrinsic predators and have greater habitat preference than generalist agricultural predators (Tewksbury *et al.* 2006). Recognized intrinsic predators are for example squirrels, chipmunks, and other small mammals (Chalfoun *et al.* 2002, Hannon and Cotterill 1998, Tewksbury *et al.* 1998).

Nest predation is high in edge habitats across tropical and temperate regions (Andrén and Angelstam 1988, Burkey 1993, Cooper and Francis 1998, Wilcove 1985). In edge areas, predators forage more and exhilarate its predation rate (Gates and Gysel 1978). Recreational trails where there is high human movement can also influence nest predation (Miller *et al.* 1998; Miller and Hobbs 2000). Predation rate is higher near trails than in forested habitats because trails split forests and cause edge areas (Miller *et al.* 1998). Predator composition also varies in trails areas; avian predators are relatively more common in trail areas than mammalian predators (Miller and Hobbs 2000). Nest type and nest position are also linked to predation. Cavity nests suffer less predation than open nests while ground nests suffer higher predation than nests found above ground (Isaksson *et al.* 2007, Martin 1987, Wilcove 1985).

Human disturbance can be a serious problem in conservation issues (Carney and Sydeman 1999). Disturbance can affect breeding success (Giese 1996), drive out animals from feeding areas (Sutherland and Crockford 1993) and sometimes be the cause of direct mortality (Wauters et al. 1997). Animals consider humans as a potential predator and respond consequently (Frid and Dill 2002). Different species respond to human disturbance in different ways (Andrén 1992, Kurki et al. 2000). Human habitat use may change vegetation structure, fragmentation and introduce exotic plants and animals (Chace and Walch 2006). Human disturbed areas reduce bird richness and species' diversity (Clergeau et al. 1998, Jokimäki 1999). Birds mainly face high egg loss and chick mortality in human disturbed areas (Madsen and Fox 1995). Many researchers have found a positive relationship between nest predation and human settlement (Kluza et al. 2000, Liebezeit et al. 2009, Nilon et al. 1995, Smith and Wachob 2006). Human-influenced habitats provide environments which are good for predators (Soh et al. 2002). The number of nests is low in human dominated areas because of fewer nesting trees. Sometimes humans also introduce animals, e.g. pet animals like cats, dogs etc. which also increase nest predation (Chace and walsh 2006, Kristan et al. 2003). Urban areas or human-disturbed habitats also provide



good feeding grounds for raptors, which also act as nest predators (Cringan and Horak 1989).

Brood parasitism and nest predation are the principal causes of nest failure for most bird species (Schmidt and Whelan 1999) and both are heavily inclined by habitat structure and composition (Kurki et al. 2000, Robinson et al. 1995, Tewksbury et al. 1998). As brood parasitism and nest predation both reduce host breeding success, there is also a relationship between the two factors (Arcese et al. 1996, Burhans et al. 2010, Dearborn 1999, Hannon et al. 2009, Heath et al. 2010, Ibáñez-Álamo et al. 2012, Kosciuch and Sandercock 2008, McLaren and Sealy 2000, Ortega and Ortega, 2003). Arcese et al. (1996) proposed "The cowbird predation hypothesis" to explain the link between parasitism and predation. This hypothesis states that parasitized nests survive better than unparasitized nest when cowbirds are territorial. Cowbirds destroy the unparasitized nests, which force the host to re-nest and the cowbird might get a second chance to parasitize it. But when there are more cowbirds in the same breeding area, parasitized nests might suffer from high nest loss or multiple parasitism. "The mafia hypothesis" proposed by Zahavi (1979) also explain the connection of brood parasitism and nest predation - cuckoos and cowbirds destroy the host's nest as a punishment if the host rejects the parasitic egg. But other studies found that parasitized nests faced higher nest predation than unparasitized nests (Burhans et al. 2010, Dearborn 1999, Hannon et al. 2009, Heath et al. 2010, Ibáñez-Álamo et al. 2012, Kosciuch and Sandercock 2008, McLaren and Sealy 2000, Ortega and Ortega, 2003).

Bangladesh, a small tropical country situated in south Asia, has high biodiversity richness. A total of 18 cuckoo species are found breeding in the country (Khan 2008). But this country also has a high human population density, nearly 150 million people (Bangladesh population census 2011, http://www.sid.gov.bd/statistics/bangladesh-at-a-glance-census-2011/). The forested area is continuously decreasing and it has introduced the contact of humans with animals. In this condition, an animal will face extinction unless it changes its behavior to coexist with human disturbance. Some animals benefit by staying close to humans whereas cuckoos consider human habitat as a disturbance and try to avoid it.



1.2. Aims of the study

The main aim of the present study is to examine how human activity influences risk of nest predation and brood parasitism. The following hypotheses were tested:

1. As cuckoos assess human activity as a source of disturbance; there should be a negative relationship between parasitism rates and distance from human settlements.

2. As predation mainly depends on predator species and predators are found in all types of habitats; there should be no relationship between predation and distance to human settlements.

2. Materials and methods

2.1 Study area

The study was carried out in Jahangirnagar University campus (Figure 1), which is located 32 km north of Dhaka city, the capital of Bangladesh. The study site comprises an area of about 200 hectares; geographically it is located at 23°52' N and 90°16' E. Jahangirnagar University campus is situated in a degraded semi-deciduous forest area which has a moderate and humid climate. The climate of the campus can be characterized by hot, rainy, humid summers and dry and cool winter. November to February is winter, March to May is summer and June to October is monsoon. Temperature is high during summer. According to the seasonality, temperature varies 10-15°C in the dry season, 35-38°C in extreme dry and 28-32°C in wet season. The total annual rainfall is about 1,800 mm and mean relative humidity is 86%. The study area in the distant past was a corrosive tract of deciduous Sal forest (Nishat et al. 2002). The existing plant species of this area are of secondary nature. The campus has diverse ecological habitats and vegetation types. It consists of wetlands, grasslands and cultivated lands, bushes, woodlands and human settlements, i.e. houses, academic and administrative buildings and shops which are made with tins, woods and bamboos at different sites of the campus. A total of 230 plant species have been recorded from this area belonging to 159 genera and 62 families (Hossain et al. 1995). The most dominating vegetation including bushes, grasses, woody and fruits trees of the campus area



are described by Begum (2011). Monotypic plant area is dominated by *Acacia moniliformes, Acacia auriculiformes, Lagerstroemia speciosa,* and *Gmelina arborea*. Rice is the most frequently used crop in cultivated land area. A total of 180 species of birds belonging to 43 families have been recorded out of which 74 species are recorded as breeding residents, 41 non-breeding residents and 65 migrants (Mohsanin and Khan 2009).

2.2 Parasite and host community

A total of five cuckoo species have been recorded in the study area; Indian cuckoo (*Cuculus micropterus*), common hawk-cuckoo (*Hierococcyx varius*), pied cuckoo (*Clamator jacobinus*), plaintive cuckoo (*Cacomantis merulinus*) and Asian koel (*Eudynamys scolopacea*). Six passerine species are known to be used as hosts in the area; house crow (*Corvus splendens*), common myna (*Acridotheres tristis*), long-tailed shrike (*Lanius schach*), black drongo (*Dicrurus macrocercus*), common tailorbird (*Orthotomus sutorius*) and jungle babbler (*Turdoides striatus*). Asian koels use house crows, common mynas and long tailed shrikes as hosts, whereas Indian cuckoos use black drongos. Common hawk-cuckoos and pied cuckoos both use jungle babblers as hosts (Begum 2011, Begum *et al* 2011a, 2011b, 2012). This study is the first to confirm that plaintive cuckoos use common tailorbirds as hosts in Bangladesh. During the present study period, no house crow nests were parasitized by the Asian koel.

2.3 General methodology

The study was conducted in four successive breeding seasons of 2010 to 2013, from January to August, which comprises the breeding season of most of the passerine birds and cuckoos in the area. Nests were systematically searched in different types of vegetation almost daily from morning to evening during the breeding season. Each nest position was plotted using a hand held Garmin GPS. After the first observation, each nest was visited regularly to record breeding variables including progress in building, egg laying, number of host and parasite eggs, number of host and cuckoo eggs hatched, number of host and cuckoo chicks fledged and final fate of the nest, which was either successful or predated.



To investigate the relationship between human activity to predation and brood parasitism, two more parameters were needed; distance from the nest to the nearest building in the campus area and distance from the nest to the nearest boundary of the campus area. GPS points of all nests were entered into Google earth software to get these two parameters.

Buildings inside the campus and the area outside the boundary were considered as human disturbance. The buildings in the study area consist of departmental, academic offices or living places for students, teachers or other employees, where there is human activity every day. Outside the campus boundary there is a high density of human settlements. The study area has a composition of reptilian, avian and mammalian predators. These predator species are distributed throughout the study area depending on species' suitable site. The common potential predator species in this area are large-billed crow (*Corvus macrorhynchos*), house crow (*Corvus splendens*), rufous treepie (*Dendrocitta vagabunda*), Bengal monitor lizard (*Varanus vengalensis*), Irrawaddy squirrel (*Callosciurus pygerythrus*), small Indian mongoose (*Herpestes auropunctatus*) and different types of snakes (Pers.Obs). Sometimes humans also act as a predator in the area. To test the nest predation, the present study did not allow separating between various predators.

Binary logistic regression models were used to test the influence of distance from the nest to nearest building or boundary on the probability of predation and parasitism. The relation between brood parasitism and nest predation was tested by using Pearson chi-square tests. F-tests were used to test the variation of parasitized and unparasitized and predated and successful nests in relation to the distances of nearest building and boundary. All statistical analyses were performed using IBM SPSS statistics 20.



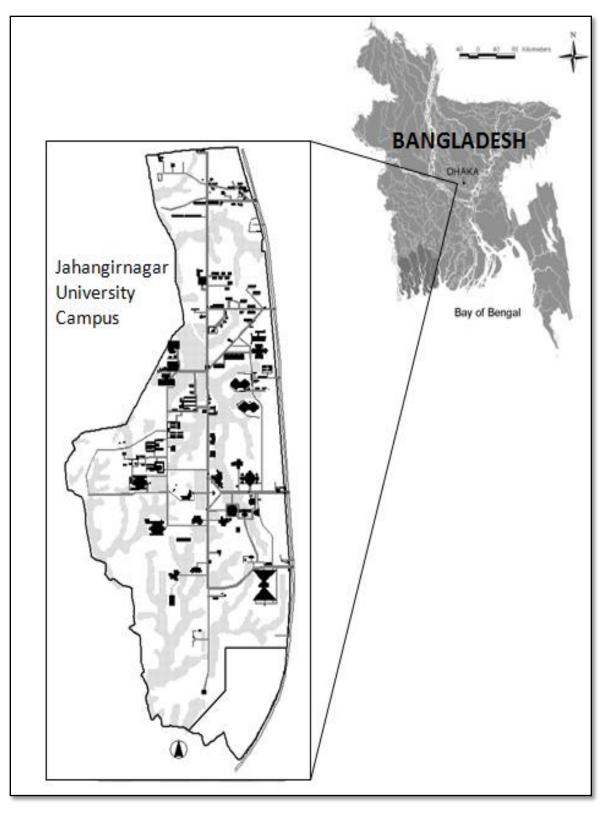


Figure 1: Map of the Jahangirnagar University campus (Source: Begum 2011).



3. Results

A total of 159 nests of five host species were found during the study period (Table 1). Parasitism rate varied statistically significantly between the five host species ($\chi^2 = 38.044$, df = 4, p < 0.001, Table 1). Parasitism rate was highest in the long tailed shrike (77.1%) and lowest in the black drongo (9.3%). In the other three host species, parasitism rates varied between these two extremes (Table 1). Statistically, nest success rate (not predated) also differed significantly between the different host species ($\chi^2 = 55.705$, df = 4, p< 0.001, Table 1). The black drongo had the highest success rate, whereas the common tailorbird had zero success (Table 1).

Table 1: Number of nests found, parasitized and unparasitized nests as well as successfuland predated nests of five host species of cuckoos in the study area.

Host species	Total number of nests	Number of parasitized nests N (%)	Number of unparasitized nests N (%)	Number of successful nests N (%)	Number of predated nests N (%)
Common myna	43	16 (37.2%)	27 (62.8%)	32 (74.4%)	11 (25.6%)
Black drongo	43	4 (9.3%)	39 (90.7%)	41 (95.3%)	2 (4.7%)
Long-tailed shrike	35	27 (77.1%)	8 (22.9%)	15 (42.9%)	20 (57.1%)
Jungle babbler	22	9 (40.9%)	13 (59.1%)	14 (63.6%)	8 (36.4%)
Common tailorbird	16	5 (31.3%)	11 (68.7%)	0 (0%)	16 (100%)

There was no significant interactions between host species and the distance from nest to the nearest building (p = 0.11), nor between host species and the distance from nest to the nearest boundary (p = 0.68). Therefore all species were pooled in the further analyses. Distances between nests and nearest buildings varied statistically significantly between host species (F = 11.709, df = 4, p < 0.001, Table 2). This distance was lowest for common myna and highest for long-tailed shrike (Table 2). There was a tendency for common



tailorbirds to build nests close to human settlement. Distance between nests and nearest boundary also differed significantly between the five host species (F = 4.855, df = 4, p = 0.001, Table 2). This distance was highest in common myna and it was lowest in common tailorbird (Table 2).

Table 2: Distance from nest to the nearest building and the nearest boundary of the five host species of cuckoos in the study area.

Host species	Distance to nearest building (meter ± sd)	Distance to nearest boundary (meter ± sd)
Common myna	38.0 (± 29.7)	309.2 (± 175.4)
Black drongo	88.4 (± 63.4)	191.4 (± 125.7)
Long-tailed shrike	122.9 (± 59.9)	199.9 (± 149.6)
Jungle babbler	90.1 (± 70.6)	274.1 (± 128.3)
Common tailorbird	58.4 (± 68.2)	185.6 (± 159.1)

The total percentages of parasitized nests were 38.4% (Table 3). On the other hand the total percentages of successful nests were 64.2% (Table 3). The success rate of parasitized nests were significantly lower than that of unparasitized nests ($\chi^2 = 4.949$, df = 1, p = 0.037, Table 3).

Table 3: Predation and success rate of parasitized and unparasitized nests.

	Predated nests	Successful nests	Total nests		
	N (%)	N (%)	N (%)		
Parasitized nests	28 (45.9%)	33 (54.1%)	61 (38.4%)		
Unparasitized nests	29 (29.6%)	69 (70.4%)	98 (61.6%)		
Total	57 (35.8%)	102 (64.2%)	159		

The distance from nests to nearest boundary differed significantly between parasitized and unparasitized nests whereas this difference was not significant for predated and successful nests (Table 4). The distance form nests to the nearest building were not significant neither between parasitized and unparasitized nests nor between predated and successful nests (Table 4). Nesting position of parasitized and unparasitized nests are presented in figure 2, whereas, nesting position of predated and successful nest are presented in figure 3.

Table 4: Relationships between distance from nest to nearest boundary and building against different nest categories (parasitized, unparasitized, successful, predated; F-tests).

Parameter	Category	Distance (meter ± sd)	F	df	р
	Mean	235.98 (± 156.6)			
Distance from nest	Parasitized nest	267.8 (± 175.8)	4.158	1	0.043 0.309
to nearest	Unparasitized nest	216.2 (± 140.8)			
boundary	Predated nest	219.02 (± 143.8)	1.042		
	Successful nest	245.5 (± 163.3)	1.042		
	Mean	79.6 (± 67.4)			
Distance	Parasitized nest	81.8 (± 63.3)	0.120	1	0.730
from nest to nearest building	Unparasitized nest	78.2 (± 65.4)	0.120	1	0.750
	Predated nest	84.7 (± 72.9)	0.562	1	0.455
	Successful nest	76.7 (± 59.4)	0.002	1	0.100

A logistic regression analysis was carried out to test the risk of parasitism in relation to human activity, where parasitized or unparasitized nests was used as a dependent variable and the distance from nest to the nearest building, distance from nest to the nearest boundary and host species used as independent variables. The result showed that only the distance from nest to the nearest boundary had a significant effect and there was no effect of distance from nest to the nearest building and host species (Table 5). Furthermore, in a logistic regression analysis where risk of predation was tested, it showed that there was no significant effect of distance from nest to the nearest building and distance from nest to nearest building and distance from nest to here was no significant effect of distance from nest to the nearest building and a significant effect (Table 6).

Table 5: Logistic regression of the relative importance of distance to nearest building, distance to nearest boundary and host species on the risk of parasitism (Nagelkerke $R^2 = 0.045$).

Variable	Estimate	SE	Wald statistic	df	р
Host species	0.22	0.049	0.204	1	0.65
Distance to nearest building	0.003	0.003	1.047	1	0.31
Distance to nearest boundary	0.003	0.001	5.008	1	0.025
Constant	-1.383	0.486	8.103	1	0.004

Table 6: Logistic regression of the relative importance of distance to nearest building, distance to nearest boundary, host species and parasitism on the risk of predation (Nagelkerke $R^2 = 0.337$).

Variable	Estimate	SE	Wald statistic	df	р
Host species	-0.394	0.092	18.170	1	<0.001
Distance to nearest building	-0.001	0.003	0.146	1	0.70
Distance to nearest boundary	0.001	0.001	0.249	1	0.62
Parasitism	-0.846	0.390	4.693	1	0.030
Constant	2.210	0.578	14.599	1	< 0.001



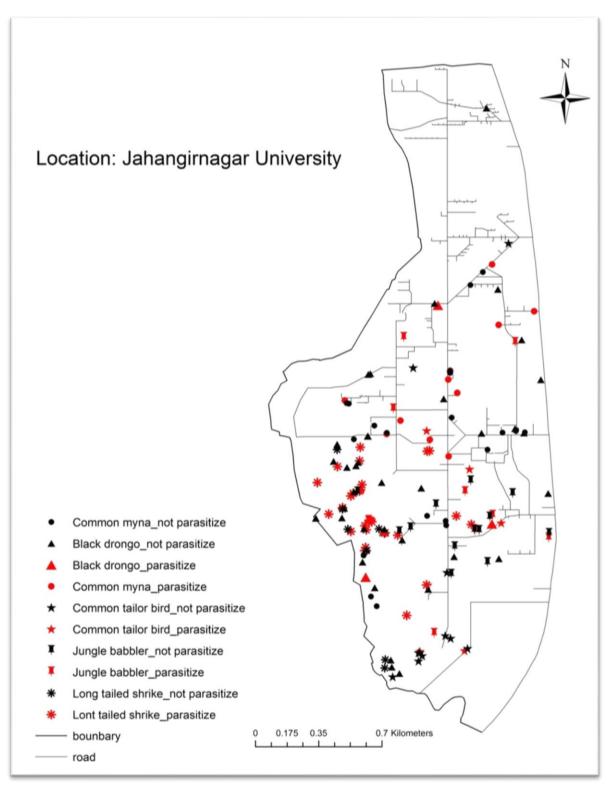


Figure 2: Nesting sites of parasitized and unparasitized nests (see legends for different categories).



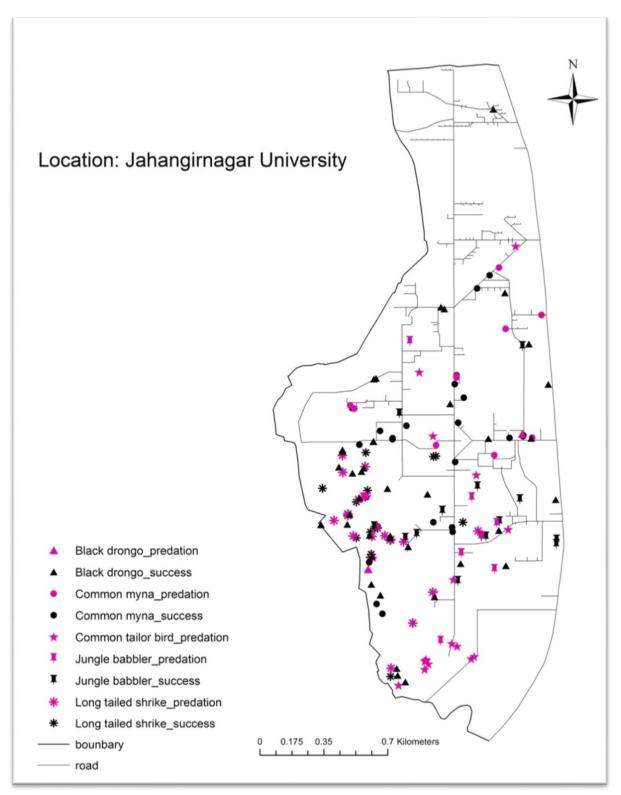


Figure 3: Nesting sites of predated and successful nests (legends indicate different host species).



4. Discussion

4.1 Brood parasitism and human disturbance

The distance from a nest to nearest boundary differed significantly between parasitized and unparasitized nests but the distance from nest to nearest building did not vary significantly between the two groups. In this study, buildings inside the campus and the area outside the boundary were considered as a source of human disturbance. But the result indicates that only boundary had an effect on parasitism. Most of the buildings inside the campus area are departmental and administrative offices or living places for students, teachers or other employees. Except for the living places, human activity occurs mainly during the weekdays from morning to afternoon, after which those areas are closed. Also, there is no human activity in those areas during weekends and other vacation times. On the other hand, outside the campus boundary, there is high permanent human settlements and the total human activity is also very high at any time. Therefore, the results support the first hypothesis which states that parasitism rates are higher away from human settlements, indicating that brood parasites avoid human disturbance.

Liang *et al.* (2013) also found similar results, because barn swallows (*Hirundo rustica*) avoid common cuckoo (*Cuculus canorus*) parasitism by breeding in close associations with humans. Many passerine birds build nests in villages, towns and cities where cuckoos are rarely present (Cramp and Perrins 1986). Some birds build nests in building areas, and face low risk of parasitism (Møller 2010). Moskát *et al.* (2003) also found that egg rejection behavior is comparatively higher in woodland areas than urban areas.

Opposite results were found in the study of cowbird parasitism. Cowbird parasitism is often more pronounced in areas with high human density (Burhans and Thompsons 2006, Chace and Walsh 2006, Robinson *et al.* 1995, Tewksbury *et al.* 1998, 2006). With increasing human-influenced habitat, cowbird parasitism also increases. Cowbirds usually feed in farm and agricultural areas, which is close to humans.

The result of the present study also showed that nest parasitism varied significantly between host species. The long-tailed shrike suffered the highest parasitism rate and was parasitized by Asian koel. In the study area long-tailed shrike nests were easy to find and it



might help Asian koel to detect the nest. Begum *et al.* (2011b) also found high parasitism rate in long-tailed shrike. Long-tailed shrike accepts Asian koel eggs and it might lack strong defense against koel as well as it might not be able to grasp eject the koel egg (Begum *et al.* 2012). The jungle babbler suffered the second highest parasitism rate. In the study area, the jungle babbler nests were parasitized by two different cuckoo species – the common hawk cuckoo and the pied cuckoo. The egg rejection behavior has not evolved yet in jungle babbler as it accepts all experimental eggs (Begum *et al.* 2012). The common myna also suffered high parasitism rates in the common myna and it has not evolved rejection behavior yet in the study area. Parasitism rate was high in common tailorbird and it was parasitized by plaintive cuckoo. In the study area, plaintive cuckoo laid mimetic eggs which might be a cause to accept cuckoo eggs by common tailorbird. The black drongo suffered the lowest parasitism rate during the study. It accepts the mimetic Indian cuckoo egg whereas it rejects all the experimental eggs (Begum *et al.* 2012).

4.2 Nest predation

The result showed that distance from each nest to nearest building and boundary had no significant influence on risk of predation. Also, there was no significant difference between distances from predated and successful nests to nearest building and boundary. This result supports the second hypothesis which states that predation is more evenly distributed and related to predator species. Several other studies also support that predation is mainly dependent on predator species as well as nest site (Tewksbury *et al.* 2006, Thompson *et al.* 1999).

Identification of the pattern of nest predation is very difficult because predation is intrinsically complex. Nest predation is often related to nesting position, visibility, nest altitude, topography (Boyle 2008, Martin and Li 1992, Tewksbury *et al.* 2006). In the present study, the result showed that nest predation also varied significantly between the host species. The study area is composed of human habitat, agriculture, fragmented plant area and monoculture plant area and the predation pressure is common in each place



depending on the predator species of each habitat. Nesting sites and nest types are also differed between host species and it attracts different types of nest predators.

During the study, the black drongo faced the lowest rate of nest predation. It is a very aggressive bird and builds its nest in the top branches of the trees. The nest predation rate decreases with increasing nest height (Burhans and Thompson 2006). The common myna suffered the second lowest nest predation. In this area, common myna nests were found in both cavity and as well as in the open. Nests in cavity experienced lower predation rates than open nests (Auer *et al.* 2007, Brawn *et al.* 2011, Remeš *et al.* 2012). Common myna also built nests close to human areas where only predators which coexist with humans are found. Large and mammalian predators are absent in human habitat areas whereas only avian predators are common (Soh *et al.* 2002). The jungle babbler nests were very camouflaged in this study area and it help to face less predation rate and camouflage nest experienced low predation rate. The cooperative breeding bird suffered less nest predation because helpers exhilarate nest defense which increase the nesting success (Innes and Johnston 1996). As the jungle babbler is a cooperative breeding bird, helpers also helped to decrease nest predation.

The long-tailed shrike suffered second highest nest predation in this study. Most of the long-tailed shrike nests were in the middle canopy of tree and it was less camouflaged. Predators could easily identify the nest. During the study, many of the long-tailed shrike nests were found in places close to agricultural fields. Generalist predators are common in paddy field areas (Chalfoun *et al.* 2002, Tewksbury *et al.* 2006). Such predators might be significant in high nest predation in long-tailed shrikes. Common tailorbirds suffered the highest nest predation in the present study since it builds its nest very close to the ground. Ground nests are more prone to predation (Isaksson *et al.* 2007, Martin 1987, Wilcove 1985) and rodents, squirrels and monitor lizards play a very important role in nest predation (Pangau-Adam *et al.* 2006). The most important ground nest predators in the study area are Bengal monitor lizards (*Varanus vengalensis*), small Indian mongooses (*Herpestes auropunctatus*), jungle cats (*Felis chaus*), Indian hares (*Lepus nigricollis*), house rats (*Rattus rattus*), Bengal foxes (*Vulpes bengalensis*) and Irrawaddy squirrels (*Callosciurus pygerythrus*) which affect the breeding success of common tailorbirds.



In the study area, there are many human movement trails. These trails also affected the nest predation rate of the host species. Nest predation is higher near trails than others areas (Miller *et al.* 1998). Humans also played a predator role in nest predation in the study area. Some local children collected eggs and chicks from the nests, whereas some people cut the nesting branches of trees to collect fuel wood.

4.3 Brood parasitism and nest predation

This study found a significant positive relationship between nest predation and brood parasitism. Parasitized nest had lower success rate than unparasitized nest. Similar results have been found in some other host nests parasitized by cuckoos (Ibáñez-Álamo *et al.* 2012) and cowbirds (Burhans *et al.* 2010, Dearborn 1999, Hannon *et al.* 2009, Heath *et al.* 2010, Kosciuch and Sandercock 2008, McLaren and Sealy 2000, Ortega and Ortega 2003). Brood parasitic nestling begs frequently and louder than the host nestlings which plays an important role in nest detection by predators (Dearborn 1999, Gochfeld 1979, Hannon *et al.* 2009, Haskell 1994, Kosciuch and Sandercock 2008, Payne 1991, Robinson *et al.* 1995). The great-spotted cuckoo chick begs loudly, and this attracted predators and caused failure of its host, the common blackbird (*Turdus merula*) (Ibáñez-Álamo *et al.* 2012). Dearborn (1999) also found higher predation rate in indigo bunting (*Passerina cyanea*) nests parasitized by brown-headed cowbirds (*Molothrus ater*)

In parasitized nests, host nestlings beg louder than in unparasitized nest (Dearborn *et al.* 1998, Parker *et al.* 2002). But this behavior is found only when the host nest is parasitized by cuckoo which chicks are not evictor. In the present study, common hawk cuckoo, Indian cuckoo and plaintive cuckoo are evictor whereas Asian koel and pied cuckoo are not evictor. So, only the common myna and the long-tailed shrike nests which were parasitized by the Asian koel and the jungle babbler nests which were parasitized by pied cuckoo might be predated for louder host nestlings beg alongside with cuckoo nestling begs. The cowbird chicks feed more frequently and it accelerates the host provisioning rate, which also helps the predator to identify the nest position (Dearborn *et al.* 1998, Hoover and Reetz 2006). Cowbirds frequently eject the host egg before laying its own egg which also attracts predators (Hann 1941, Scott *et al.* 1992, Smith 1981). Brood-parasitic birds use



landscape structure composition and host activity to select host nests (Davies 2000, Norman and Robertson 1975, Øien *et al.* 1996) and it has been suggested that predators also use the same cues to identify nests (Robinson *et al.* 1995, Wilson and Arcese 2006). On the other hand, Canestrari *et al.* (2014) found the opposite results which support the cowbird predation hypothesis. The carrion crow (*Corvus corone*) nest, parasitized by great spotted cuckoo, experienced lower predation rate than unparasitized nests. The cuckoo chicks produce a repellent secretion which forced the predator to avoid contact with this nest. Avilés *et al.* (2006) also found a negative relation between nest predation and brood parasitism. Passerine hosts which suffer high nest predation, experienced lower rate of parasitism by brown-headed cowbirds. This study also suggests that predators played a very important role in coevolution of brood parasite and host species. Parasite species do not select the host which usually suffers high nest predation.

5. Conclusion

In conclusion, the present study has three main findings. First, there is a significant relationship between brood parasitism and human activity. Cuckoos avoid nests which are close to highly utilized human habitats. The host can therefore benefit by building nests close to human areas whereas some hosts avoid this areas also. The second finding is that predation is distributed everywhere, mainly depending on predator species. Different predator species are common in human areas as well as other areas related to suitable habitats. The last finding is that there is a significant positive relationship between nest predation and brood parasitism. Parasitized nests have lower success rates than unparasitized nests. It is easier to find parasitized nests for predators than unparasitized nests.

The results of the present study show the importance of forest habitat in conservation of biodiversity. It also points to the negative effects of human habitat encroachment. Human disturbance is an increasing problem in conservation issues. The present study indicates the importance of natural habitat in cuckoo conservation, and large areas with no human disturbance should be established. If the human habitat encroachment continues, there is a chance that some cuckoos species will become extinct.



References

- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology **73**:794-804.
- Andrén, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands experimental evidence. Ecology **69**:544-547.
- Arcese, P., J. N. M. Smith, and M. I. Hatch. 1996. Nest predation by cowbirds and its consequences for passerine demography. Proceedings of the National Academy of Sciences 93:4608-4611.
- Auer, S. K., R. D. Bassar, J. J. Fontaine, and T. E. Martin. 2007. Breeding biology of passerines in a subtropical Montane forest in northwestern Argentina. Condor 109:321-333.
- Avilés, J. M., B. G. Stokke, and D. Parejo. 2006. Relationship between nest predation suffered by hosts and Brown-headed Cowbird parasitism: a comparative study. Evolutionary Ecology 20:97-111.
- Begum, S. 2011. Brood parasitism in Asian cuckoos: different aspects of interactions between cuckoos and their hosts in Bangladesh. PhD Thesis, Department of Biology, Norwegian University of Science and Technology, Trondheim: NTNU.
- Begum, S., A. Moksnes, E. Røskaft, and B. G. Stokke. 2011a. Factors influencing host nest use by the brood parasitic Asian Koel (*Eudynamys scolopacea*). Journal of Ornithology 152:793-800.
- Begum, S., A. Moksnes, E. Røskaft, and B. G. Stokke. 2011b. Interactions between the Asian koel (*Eudynamys scolopacea*) and its hosts. Behaviour **148**:325-340.
- Begum, S., A. Moksnes, E. Røskaft, and B. G. Stokke. 2012. Responses of potential hosts of Asian cuckoos to experimental parasitism. Ibis **154**:363-371.
- Boyle, W. A. 2008. Can variation in risk of nest predation explain altitudinal migration in tropical birds? Oecologia **155**:397-403.
- Brawn, J. D., G. Angehr, N. Davros, W. D. Robinson, J. N. Styrsky, and C. E. Tarwater. 2011. Sources of variation in the nesting success of understory tropical birds. Journal of Avian Biology 42:61-68.
- Burhans, D. E., B. G. Root, T. L. Shaffer, and D. C. Dey. 2010. Songbird nest survival is invariant to early-successional restoration treatments in a large river floodplain. The Wilson Journal of Ornithology 122:307-317.



- Burhans, D. E., and F. R. Thompson. 2006. Songbird abundance and parasitism differ between urban and rural shrublands. Ecological Applications **16**:394-405.
- Burkey, T. V. 1993. Edge effects in seed and egg predation at 2 neotropical rain-forest sites. Biological Conservation **66**:139-143.
- Canestrari, D., D. Bolopo, T. C. Turlings, G. Röder, J. M. Marcos, and V. Baglione. 2014. From Parasitism to Mutualism: Unexpected Interactions Between a Cuckoo and Its Host. Science 343:1350-1352.
- Carney, K. M., and W. J. Sydeman. 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds **22**:68-79.
- Cavitt, J. F., and T. E. Martin 2002. Effects of forest fragmentation on brood parasitism and nest predation in eastern and western landscapes. Cooper Ornitholigical Society, Camarillo.
- Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and urban planning **74**:46-69.
- Chalfoun, A. D., M. J. Ratnaswamy, and F. R. Thompson. 2002. Songbird nest predators in forest-pasture edge and forest interior in a fragmented landscape. Ecological Applications 12:858-867.
- Clergeau, P., J. P. L. Savard, G. Mennechez, and G. Falardeau. 1998. Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. Condor 100:413-425.
- Cooper, D. S., and C. M. Francis. 1998. Nest predation in a Malaysian lowland rain forest. Biological Conservation **85**:199-202.
- Cramp, S., and C. M. Perrins 1986. The birds of the Western Palearctic, vol 5. Oxford University Press, Oxford.
- Cringan, A. T., and G. C. Horak. 1989. Effects of urbanization on raptors in the western United States. Pages 219-228. Proceedings of the western raptor management symposium and workshop. National Wildlife Federation, Washington DC.
- Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:563-566.
- Davies, N. B. 2000. Cuckoos, Cowbirds other Cheats. T. & AD Poyser, London.
- Dearborn, D. C. 1999. Brown-headed cowbird nestling vocalizations and risk of nest predation. Auk **116**:448-457.



- Dearborn, D. C., A. D. Anders, F. R. Thompson, and J. Faaborg. 1998. Effects of Cowbird parasitism on parental provisioning and nestling food acquisition and growth. Condor **100**:326-334.
- Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology **6**:11.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology **59**:871-883.
- George, T. L. 1987. Greater land bird densities on island vs mainland relation to nest predation level. Ecology **68**:1393-1400.
- Giese, M. 1996. Effects of human activity on adelie penguin Pygoscelis adeliae breeding success. Biological Conservation **75**:157-164.
- Gochfeld, M. 1979. Begging by nestling shiny cowbirds: adaptive or maladaptive. Living Bird **17**:41-50.
- Hann, H. W. 1941. The cowbird at the nest. Wilson Bull 53:211-221.
- Hannon, S. J., and S. E. Cotterill. 1998. Nest predation in aspen woodlots in an agricultural area in Alberta: The enemy from within. Auk **115**:16-25.
- Hannon, S. J., S. Wilson, and C. A. McCallum. 2009. Does cowbird parasitism increase predation risk to American redstart nests? Oikos **118**:1035-1043.
- Haskell, D. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. Proceedings of the Royal Society of London. Series B: Biological Sciences **257**:161-164.
- Heath, S. K., L. A. Culp, and C. A. Howell. 2010. Brood parasitism and nest survival of Brown-headed Cowbird hosts at high-elevation riparian sites in the eastern Sierra Nevada, California. Western North American Naturalist **70**:364-376.
- Hoover, J. P., and M. J. Reetz. 2006. Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates, in a cowbird host. Oecologia 149:165-173.
- Hossain, A. B. M. E., S. A. Khan, and M. A. Islam. 1995. An inventory of plant diversity in relation to ecology and environment of Jahangirnagar University: I. Vegetational composition and their taxonomic identity. Bangladesh Journal of Life Sciences 7:95-108.
- Ibáñez-Álamo, J. D., L. Arco, and M. Soler. 2012. Experimental evidence for a predation cost of begging using active nests and real chicks. Journal of Ornithology 153:801-807.



- Innes, K. E., and R. E. Johnston. 1996. Cooperative breeding in the white-throated magpiejay. How do auxiliaries influence nesting success? Animal Behaviour **51**:519-533.
- Isaksson, D., J. Wallander, and M. Larsson. 2007. Managing predation on ground-nesting birds: The effectiveness of nest exclosures. Biological Conservation **136**:136-142.
- Johnsgard, P. A. 1997. The avian brood parasites: deception at the nest. Oxford University Press, New York.
- Jokimäki, J. 1999. Occurrence of breeding bird species in urban parks: effects of park structure and broad-scale variables. Urban Ecosystems **3**:21-34.
- Khan, M. M. H. 2008. Protected areas of Bangladesh: A guide to wildlife. Nishorgo Program, Wildlife Management and Nature Conservation Circle, Bangladesh Forest Department.
- Kluza, D. A., C. R. Griffin, and R. M. DeGraaf. 2000. Housing developments in rural New England: effects on forest birds. Animal Conservation **3**:15-26.
- Kosciuch, K. L., and B. K. Sandercock. 2008. Cowbird removals unexpectedly increase productivity of a brood parasite and the songbird host. Ecological Applications **18**:537-548.
- Kristan, W. B., A. J. Lynam, M. V. Price, and J. T. Rotenberry. 2003. Alternative causes of edge-abundance relationships in birds and small mammals of California coastal sage scrub. Ecography **26**:29-44.
- Kurki, S., A. Nikula, P. Helle, and H. Lindén. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. Ecology 81:1985-1997.
- Lahti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation **99**:365-374.
- Liang, W., C. Yang, L. Wang, and A. P. Møller. 2013. Avoiding parasitism by breeding indoors: cuckoo parasitism of hirundines and rejection of eggs. Behavioral Ecology and Sociobiology 67:913-918.
- Liebezeit, J. R., S. J. Kendall, S. Brown, C. B. Johnson, P. Martin, T. L. McDonald, D. C. Payer, C. L. Rea, B. Streever, A. M. Wildman, and S. Zack. 2009. Influence of human development and predators on nest survival of tundra birds, Arctic Coastal Plain, Alaska. Ecological Applications 19:1628-1644.
- Madsen, J., and A. D. Fox. 1995. Impacts of hunting disturbance on waterbirds a review. Wildlife Biology **1**:193-207.



- Martin, T. E. 1987. Artificial nest experiments effects of nest appearance and type of predator. Condor **89**:925-928.
- Martin, T. E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? Ecology **69**:74-84.
- Martin, T. E. 1993. Nest predation among vegetation layers and habitat types revising the dogmas. American Naturalist **141**:897-913.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological monographs **65**:101-127.
- Martin, T. E., and P. Li. 1992. Life-history traits of open-nesting vs cavity-nesting birds. Ecology **73**:579-592.
- Matessi, G., and G. Bogliani. 1999. Effects of nest features and surrounding landscape on predation rates of artificial nests. Bird Study **46**:184-194.
- McLaren, C. M., and S. G. Sealy. 2000. Are nest predation and brood parasitism correlated in Yellow Warblers? A test of the cowbird predation hypothesis. The Auk 117:1056-1060.
- Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. Landscape and Urban Planning **50**:227-236.
- Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications 8:162-169.
- Mohsanin, S., and M. M. H. Khan. 2009. Status and seasonal occurrences of the birds in the Jahangirnagar University Campus, Bangladesh. Bangladesh Journal of Life Sciences 21:29-37.
- Moksnes, A., F. Fossøy, E. Røskaft, and B. G. Stokke. 2013. Reviewing 30 years of studies on the Common Cuckoo: accumulated knowledge and future perspectives. Chinese Birds **4**:3-14.
- Møller, A. P. 2010. The fitness benefit of association with humans: elevated success of birds breeding indoors. Behavioral Ecology **21**:913-918.
- Moskát, C. 2005. Common Cuckoo parasitism in Europe: behavioural adaptations, arms race and the role of metapopulations. Ornithological Science **4**:3-15.
- Moskát, C., Z. Karcza, and T. Csorgo. 2003. Egg rejection in European blackbirds (Turdus merula): the effect of mimicry. Ornis Fennica **80**:86-91.



- Nager, R. G., P. Monaghan, and D. C. Houston. 2001. The cost of egg production: Increased egg production reduces future fitness in gulls. Journal of Avian Biology 32:159-166.
- Nilon, C. H., C. N. Long, and W. C. Zipperer. 1995. Effects of wildland development on forest bird communities. Landscape and Urban Planning **32**:81-92.
- Nishat, A., S. M. I. Huq, S. P. Barua, A. H. M. A. Reza, and A. S. M. Khan 2002. Bioecological zones of Bangladesh. IUCN Bangladesh Country Office, Dhaka, Bangladesh.
- Norman, R. F., and R. J. Robertson. 1975. Nest searching behavior in the brown-headed cowbird. Auk **92**:610-611.
- Øien, I. J., M. Honza, A. Moksnes, and E. Roskaft. 1996. The risk of parasitism in relation to the distance from reed warbler nests to cuckoo perches. Journal of Animal Ecology **65**:147-153.
- Ortega, C. P. 1998. Cowbirds and other brood parasites. University of Arizona Press, Tucson.
- Ortega, C. P., and J. C. Ortega. 2003. Brown-headed Cowbird (*Molothrus ater*) parasitism on Warbling Vireos (*Vireo gilvus*) in southwest Colorado. Auk **120**:759-764.
- Pangau-Adam, M. Z., M. Waltert, and M. Mühlenberg. 2006. Nest predation risk on ground and shrub nests in forest margin areas of Sulawesi, Indonesia. Biodiversity and Conservation 15:4143-4158.
- Parker, G. A., N. J. Royle, and I. R. Hartley. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. Ecology Letters **5**:206-215.
- Payne, R. B. 1991. Indigo Bunting (*Passerins cynea*) in the birds of North America, no. 4. . Academy of Natural Sciences, Philadelphia and American Ornithological Union, Washington D.C.
- Payne, R. B. 2005. Cuckoos, *Cuculidae*. Oxford University Press.
- Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management **64**:71-87.
- Remeŝ, V., and T. E. Martin. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. Evolution **56**:2505-2518.
- Remeš, V., B. Matysioková, and A. Cockburn. 2012. Long-term and large-scale analyses of nest predation patterns in Australian songbirds and a global comparison of nest predation rates. Journal of Avian Biology 43:435-444.



- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology:1-48.
- Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.
- Rodewald, A. D., and R. H. Yahner. 2001. Influence of landscape composition on avian community structure and associated mechanisms. Ecology **82**:3493-3504.
- Røskaft, E., A. Moksnes, B. G. Stokke, C. Moskát, and M. Honza. 2002. The spatial habitat structure of host populations explains the pattern of rejection behavior in hosts and parasitic adaptations in cuckoos. Behavioral Ecology 13:163-168.
- Rothstein, S. I. 1990. A model system for coevolution avian brood parasitism. Annual Review of Ecology and Systematics **21**:481-508.
- Rothstein, S. I., and S. K. Robinson 1998. The evolution and ecology of avian brood parasitism. An overview. In: *Parasitic birds and their hosts: studies in coevolution*. Oxford University Press, New York.
- Schmidt, K. A., and C. J. Whelan. 1999. The relative impacts of nest predation and brood parasitism on seasonal fecundity in songbirds. Conservation Biology **13**:46-57.
- Scott, D. M., P. J. Weatherhead, and C. D. Ankney. 1992. Egg eating by female brownheaded cowbirds. Condor **94**:579-584.
- Sibley, C. G., and B. L. Monroe 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, USA.
- Smith, C. M., and D. G. Wachob. 2006. Trends associated with residential development in riparian breeding bird habitat along the Snake River in Jackson Hole, WY, USA: Implications for conservation planning. Biological Conservation 128:431-446.
- Smith, J. N. M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population. Condor **83**:152-161.
- Söderström, B. 1999. Artificial nest predation rates in tropical and temperate forests: a review of the effects of edge and nest site. Ecography **22**:455-463.
- Soh, M. C. K., N. S. Sodhi, R. K. H. Seoh, and B. W. Brook. 2002. Nest site selection of the house crow (Corvus splendens), an urban invasive bird species in Singapore and implications for its management. Landscape and Urban Planning 59:217-226.
- Sonerud, G. A., and P. E. Fjeld. 1987. Long-term-memory in egg predators an experiment with a hooded crow. Ornis Scandinavica **18**:323-325.



- Stokke, B. G., A. Moksnes, and E. Røskaft. 2005. The enigma of imperfect adaptations in hosts of avian brood parasites. Ornithological Science **4**:17-29.
- Sutherland, W. J., and N. J. Crockford. 1993. Factors affecting the feeding distribution of red-breasted geese branta-ruficollis wintering in romania. Biological Conservation 63:61-65.
- Telleria, J. L., and M. Diaz. 1995. Avian nest predation in a large natural gap of the amazonian rain-forest. Journal of Field Ornithology **66**:343-351.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology **79**:2890-2903.
- Tewksbury, J. J., L. Garner, S. Garner, J. D. Lloyd, V. Saab, and T. E. Martin. 2006. Tests of landscape influence: Nest predation and brood parasitism in fragmented ecosystems. Ecology **87**:759-768.
- Thompson, F. R. 2007. Factors affecting nest predation on forest songbirds in North America. Ibis **149**:98-109.
- Thompson, F. R., W. Dijak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. Auk **116**:259-264.
- Vickery, P. D., M. L. Hunter, and J. V. Wells. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos **63**:281-288.
- Visser, M. E., and C. M. Lessells. 2001. The costs of egg production and incubation in great tits (Parus major). Proceedings of the Royal Society B-Biological Sciences 268:1271-1277.
- Wauters, L. A., L. Somers, and A. A. Dhondt. 1997. Settlement behaviour and population dynamics of reintroduced red squirrels *Sciurus vulgaris* in a park in Antwerp, Belgium. Biological Conservation 82:101-107.
- Wesołowski, T., and L. Tomiałojć. 2005. Nest sites, nest depredation, and productivity of avian broods in a primeval temperate forest: do the generalisations hold? Journal of Avian Biology **36**:361-367.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **66**:1211-1214.
- Wilson, S., and P. Arcese. 2006. Nest depredation, brood parasitism, and reproductive variation in island populations of song sparrows (*Melospiza melodia*). Auk 123:784-794.
- Zahavi, A. 1979. Parasitism and nest predation in parasitic cuckoos. American Naturalist **113**:157-159.