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Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh

Thesis for the degree of Philosophiae Doctor

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Norwegian University of Science and Technology
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Common hawk cuckoo (*Cuculus varius*) fed by its host, a jungle babbler (*Turdoids striatus)*. Photo: MK Hasan

Indian cuckoo (*Cuculus micropterus*) fed by its host, a black drongo (*Dicrurus macrocercus*). Photo: MH Khan

Preface

When I was doing my fieldwork for my M.Sc. in Zoology at Jahangirnagar University, I noticed a common myna feeding an Asian koel chick. Feeroz, my beloved husband, captured this amazing picture as a novice researcher. Professor Md. Anwarul Islam, my M.Sc. Supervisor, was teaching 'Conservation Biology' as a Masters Course and first introduced me to the wonderful kingdom of animal behaviour. From this beginning, I became very interested in and was inspired to learn more about the fascinating and exceptional phenomenon of parental care in brood parasitism. Several years later, as I was completing my M.Sc. research, I received a wonderful opportunity to do my PhD research on this topic at the Norwegian University of Science and Technology, far away from my home country, although my study site was at Jahangirnagar University in central Bangladesh.

I am most grateful to my supervisors Professor Eivin Røskaft, Professor Arne Moksnes and Dr. Bård G. Stokke, who have been supportive and inspirational and provided me with helpful advice and feedback about my ideas, results and statistics throughout this research. I express my sincere respect and gratitude to all of them, as this research would not be possible without their kind support. I would also like to thank the 'Cuculus group', which helped me gain many ideas about brood parasitism during my early days of research at NTNU. I give special thanks to Flora Magige, Lester Rocha, Dr. Anton Antonov (who also prepared the model eggs for my field work) and Dr. Lenka Polacikova for fruitful discussions and advice related to my research. I want to thank the staffs at the Department of Biology at NTNU, especially Tove Tronvold who assisted me in official work during my study. My sincere thanks are due to Professor Md. Anisul Islam, Professor Md. Abdul Gafur Khan, Professor M. Farid Ahsan and Professor Baharul Hoque of the University of Chittagong for their cooperation.

I would like to recognise the effort of those who assisted me in the field. I give special thanks to Sayad Mahmudur Rahman, Delip Kumar Das, and Mominul Islam Nahid, all of whom spent many hours in the field looking for nests. In addition, a special thank you goes to Monoronjon for carrying the ladder and Yousuf, who climbed up trees to collect eggs during the hot, humid summer. I would also like to thank my high school and university friends Nagari, Shelly, Neela, Tanuka, Jabed, Kohinoor and Shajjad; my family friends from Bangladesh, Dr. Seema Hoque, Dr. Mozammel Hoque, Dr. Shamsul Alom Selim, Halima, Dr. Atiq Rahman, Masuma, Dr. Merajuddin Ahmed, Mohua; and those who were staying in Trondheim, Raihan, Dr. Aminul Islam, Nimmi, Hossain, Orpana and Shila (my apologies, if I have forgotten anyone). All of these people have been incredibly supportive through hard times. Many thanks are also due to Berit and Aud for sharing nice moments during my stay in Trondheim.

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I want to express my deepest thanks to my brother Aman, sisters Jolly and Nazia and extended family members, Nazma, Faruk and Fuad for their care and moral support throughout my study. My much-loved Amma (Mother) and Baba (Father-in-law) deserve heartfelt gratitude for the precious steadfast support they have always given me. Their endless caring for my family during my absence was incredible even at their old stage of life! This made my work possible. In fact, my work was a dream of my belated beloved father and mother-in-law.

My family, including my treasured sons Adnan and Irfan, has uncomplainingly endured my continuing diversion from ‘the real world’ and has whole-heartedly supported my choices, even when I put miles and miles between us. I cannot say how much I am grateful for this. Lastly, I must extend special thanks to my beloved husband, Mohammed Mostafa Feeroz, who provided ideas and thoughtful opinions and was always ready to help whenever and whatever he could, academic or personal. His presence contributed greatly to the success of this study and I could not have done it without him and above all, to Allah, to whom I grant the supreme authorship of this work.

This research was supported by a grant through a ‘Quota Scheme’ at the Norwegian University of Science and Technology (NTNU) connected to a research grant from The Norwegian Programme for Development, Research and Education (NUFU).

Finally, I am grateful to my Evaluation Committee Dr. Brian D Peer, Dr. Ingunn Tombre, and Dr. Thor Harald Ringsby for the positive evaluation of my thesis.

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List of papers

I. Begum, S., Moksnes, A., Røskaft, E. & Stokke, B.G. 2011a. Interactions between the Asian koel (*Eudynamys scolopacea)* and its hosts. *Behaviour* 148: 325-340.

II. Begum, S., Moksnes, A., Røskaft, E. & Stokke, B.G. 2011b. Factors influencing host nest use by the brood parasitic Asian Koel (*Eudynamys scolopacea*). *Journal of Ornithology* 152: 793-800.

III. Begum, S., Moksnes, A., Røskaft, E. & Stokke, B.G. 2011. Host use by four sympatric species of cuckoos in Bangladesh. Submitted *The Condor*

IV. Begum, S., Moksnes, A., Røskaft, E. & Stokke, B.G. 2011. Asian cuckoo host responses against experimental parasitism. Submitted *Ibis*

Declaration of Contribution

This thesis is a presentation of my original research work. This thesis includes original papers published in peer reviewed journals and unpublished publications. My supervisors Professor Eivin Røskaft, Professor Arne Moksnes and Dr. Bård Gunnar Stokke provided me with ideas and assisted in the planning and development of this research work as well as helped with the data analyses and manuscript preparation.

Summary

The interaction between brood parasitic cuckoos and their hosts represents a traditional example of coevolution, whereby obligate interspecific brood parasitic cuckoos completely rely on their hosts to do their parental care for them by laying their eggs in the host's nest. This thesis brings together a great deal of information documenting and clarifying the interactions between different species of hosts and their respective parasitic cuckoos in Bangladesh. I recorded parasitism rates to determine the extent of brood parasitism and to identify the host species that were parasitised by sympatric cuckoos. Four parasitic cuckoos were documented: the Asian koel (*Eudynamys scolopacea*), the common hawk cuckoo (*Cuculus varius*; previously known as *Hierococcyx varius*), the pied cuckoo (*Clamator jacobinus*) and the Indian cuckoo (*Cuculus micropterus*). These cuckoos were sympatric and parasitised different host species, including the house crow (*Corvus splendens*), the long-tailed shrike (*Lanius schach*), the common myna (*Acridotheres tristis*), the jungle babbler (*Turdoides striatus*) and the black drongo (*Dicrurus macrocercus*). All of these cuckoo species are obligate brood parasites. The Asian koel utilised the following three hosts: the house crow, the common myna and the long-tailed shrike. The latter was recorded for the first time as a host for the Asian koel in Bangladesh. We found that koel eggs were highly non-mimetic to those of common myna and long-tailed shrike, but showed good mimicry to house crow eggs. Indian cuckoos showed excellent egg mimicry with the eggs of their black drongo hosts, as did common hawk cuckoos and pied cuckoos with their jungle babbler host. The hosts accepted the eggs of all four cuckoo species. However, the common myna was more likely to abandon nests parasitised by the koel than unparasitised ones. All of the host species suffered the costs of koel parasitism, showing reduced breeding success. Proximity to fruit trees was an important predictor of the probability of parasitism in the three koel host species studied. There was a significant positive relationship between nest volume and probability of parasitism by Asian koels. Furthermore, the colonial breeding house crows suffered comparatively less parasitism than the other two koel host species. Long-tailed shrike nests close to conspecific neighbours were less likely to be parasitised, and the risk of parasitism was increased in nests lower to the ground. The risk of parasitism increased during the breeding season for house crows and common mynas. All three Asian koel hosts tolerated multiple parasitism. We investigated whether there was any interspecific

competition among the sympatric cuckoos. In theory, sympatric parasites should show niche segregation through variation in host use. As predicted, each cuckoo species parasitised different host species; however, host use overlapped in common hawk cuckoos and pied cuckoos, but interspecific competition was reduced because these two cuckoo species have different breeding seasons. Furthermore, there was a significant difference in parasitism rate among the three main habitats: human habitations, mixed scrub forests and monoculture plantations. This indicated that different cuckoos favour specific habitats, even if their favourite host also occurs elsewhere. Finally, I tested responses against foreign eggs by the cuckoo hosts as well as by potential cuckoo hosts in the study area. For this purpose, I used differently sized and coloured model eggs. Common mynas and jungle babblers accepted all non-mimetic eggs, as did most of the house crows (91 %). Long-tailed shrikes rejected 75 % of the non-mimetic model eggs. Finally, black drongos turned out to be strong rejectors and could do so without damaging any of their own eggs, most likely because they grasped and ejected the non-mimetic model egg. This result indicates that the black drongo has been in a coevolutionary arms race with the Indian cuckoo since drongos accepted mimetic cuckoo eggs. Species such as the Oriental magpie robin (*Copsychus saularis*), red-vented bulbul (*Pycnonotus cafer*) and Asian pied starling (*Gracupica contra*), which likely have no history of interaction with cuckoos, accepted 100 % of the non-mimetic model eggs.

In conclusion, our findings describe host nest use cues used by the Asian koel, which may provide background for further studies in other sympatric brood parasites. In spite of the high degree of acceptance of parasitic eggs, the breeding success of both cuckoos and hosts should be more closely studied to obtain a better understanding of the costs of parasitism. Future experimental studies are highly recommended to achieve a better understanding of host responses to Asian cuckoo species.

Introduction

Background

Studies on avian brood parasitism have become increasingly specialised and are a fascinating subject in the field of ornithology. Brood parasitic birds do not build their own nests, but lay their eggs in the nests of other birds and leave the parental care to the foster parents (Johnsgard 1997, Rothstein and Robinson 1998, Davies 2000, Payne 2005).

Charles Darwin (1859) was the first to describe the adaptation of one organism to another and vice versa by the term ‘coadaptation’. However, today this reciprocal evolutionary change among interacting species is defined as ‘coevolution’ (Janzen 1980, Thompson 2005). The interaction between the cuckoo and its hosts represents one of the most remarkable and suitable model systems for the study of coevolution (Rothstein and Robinson 1998). However, there also seems to be a surprising lack of adaptations among many hosts (Davies 1999). In ancient times, Aristotle studied the brood-parasitic interactions between common cuckoos (*Cuculus canorus*) and their hosts (Friedmann 1964, Davies 2000). In modern times, many renowned authors have described different species of brood parasites and provided important contributions to the understanding of the ecology and evolution of avian brood parasitism (e.g., Chance 1922, Friedmann 1929, 1955, 1960, Baker 1942, Wyllie 1981 and Payne 1973, 1977, 1982, 2005).

The evolutionary origin of avian brood parasitism is one of the most interesting and unsolved questions in current ornithology. Darwin (1859) proposed that occasional or accidental laying of eggs by one species in the nest of other species initiated the development of brood parasitism.

Two types of brood parasitism are well recognised. The first, known as conspecific or intraspecific brood parasites, are always non-obligate and involve laying eggs in the nest of others of the same species and are most often found among colonial nesting species, e.g., the African village weaver (*Ploceus cucullatus*). This type of parasitism has been reported in 236 (around 2.4 %) (Rohwer and Freeman 1989) of 9672 species of birds (Sibley and Monroe 1990). It is thought that the cuckoo’s parasitic behaviour evolved from conspecific brood parasitism (Hamilton and Orians 1965). The second type are interspecific brood parasites. These brood parasites lay their eggs in the nests of other bird species and have completely lost the ability to build nests and show any parental care, e.g., honeyguides, viduines, some species of cuckoos in the Cuculinae family and several species of cowbirds, such as the *Molothrus* cowbirds. Interspecific brood parasitism has been documented in approximately 100 species (about 1%) of the 9672 species of birds (Davies 2000) and has evolved independently seven times in birds (Sorenson and Payne 2005): three times in the family Cuculidae, the cuckoos; two times in the family Icteridae, the cowbirds; once in the family Viduidae, the brood parasitic African finches; once in the family Indicatoridae, the honeyguides; and once in the black-headed duck (*Heteronetta atricapilla*).

Brood Parasites and their Hosts: Interactions and Adaptations

Field studies of avian brood parasitism in recent decades have provided a great deal of information on the life histories of brood parasites and their hosts. Their interactions result in a coevolutionary arms races, in which the parasites evolve the abilities to exploit their hosts in more effective ways, while the hosts evolve strategies to mitigate the impact of parasitism (Dawkins and Krebs 1979). Likewise, both parasites and hosts evolve adaptive behavioural traits to maximise their fitness in a conflicting manner (Takasu 2005). For example, hosts have evolved defences, such as aggression, against the parasite and egg rejection in response to parasitism (Davies 2000). Moreover, the degree of defence varies from population to population. Likewise, cuckoos have evolved deceptions such as secretive egg laying and egg mimicry to beat the host's defences. This arms race may proceed to a new stage in which hosts discriminate against odd-looking chicks and parasites counter with chick mimicry (Davies and Brooke 1989b, Langmore et al. 2003, Stokke et al. 2005). The arms race may therefore be an endless process involving escalation and integration of new defence systems on both sides (Davies 2000, Takasu 2005).

Adaptations in Brood Parasites and Hosts: An Overview

Parasitic Adaptations

Many studies have focused on cuckoo-host interactions at the stage before egg laying. Parasitic cuckoos exhibit adaptations that reduce host fitness in several ways. Cuckoos have inconspicuous colours and dull or cryptic hawk-like plumages (Payne 1967), which may facilitate the success of parasitic laying (Kruger et al. 2007). This might be an adaptation to influence host behaviour and hence, reduce the chances of detection by their hosts (Craib 1994, Davies and Welbergen 2008). Brood parasites remove or puncture host eggs (Fraga 1986, Peer and Sealy 1999, Nakamura and Cruz 2000) or sometimes even eat the eggs (Scott et al. 1992). Egg removal enhances host incubation (Davies and Brooke 1988), and it may cause the host to abandon the nest (Peer and Sealy 1999) or, more likely, abandon the clutch if too many eggs are removed (Rothstein 1986). However, parasitic adaptations to hosts' egg removal and egg puncture are the least understood (Peer 2006). Cuckoos have evolved thicker egg shells, which may serve as protection against puncturing attempts by hosts (Swynnerton 1918, Antonov et al. 2006a) and therefore reduce host rejection (Spottiswoode 2010). Adaptation of a shorter incubation period and hence early hatching of cuckoos relative to their hosts' eggs is a competitive advantage for the parasitic young in terms of food acquisition and facilitates the ejection or eviction of host eggs or young (Payne 1977, Davies 2000).

At the egg stage, there are several studies that have focused on egg mimicry by parasitic cuckoos (Baker 1913, Swynnerton 1918). In general, parasitic cuckoo eggs are highly variable both in colour and size relative to the size of the bird laying the eggs, which is regarded as a brood parasitic adaptation (Wyllie 1981). Egg mimicry among different races of the common cuckoo evolves in relation to the strength of host rejection. The stronger the host egg discrimination, the better the egg colour and pattern are mimicked by the cuckoo eggs (Brooke and Davies 1988, Stoddard and Stevens 2010, 2011). Therefore, cuckoo egg mimicry evolves in response to host egg rejection (Davies 2011). Egg crypsis, the laying of dark eggs, is also regarded as another counter-adaptation by some cuckoo species against host rejection (Brooker and Brooker 1990, Langmore et al. 2009, Davies 2011). The parasitic chicks may mimic the gape patterns of the host's young or their begging calls (Redondo and Arias de Reyna 1988) to elicit increased parental care (Davies et al. 1998, Kilner et al. 1999). Therefore, the cuckoo's parasitic adaptations are of two kinds, the well-studied adaptation 'trickery' (Rothstein and Robinson 1998, Davies 2000, Kilner and Langmore 2011) and another adaptation called 'tuning', which together may explain the existence of obligate brood parasitic cuckoos (Davies 2011).

Host Adaptations

Many hosts respond insistently toward a parasitic cowbird or cuckoo near the nest by trying to chase or divert it away. Therefore, selection that favours hosts that are aware of parasitic birds as a risk and respond aggressively whenever doing so prevents or reduces parasitism (Robertson and Norman 1976). Aggression toward the parasitic bird is regarded as key adaptation of hosts (Moksnes et al. 1990, Røskaft et al. 2002a) against parasitic egg laying.

Host populations do not all show strong defences against parasitism; some may show only intermediate levels of rejection of non-mimetic foreign eggs (Rothstein 1975b, 1990, Davies and Brooke 1989a, Moksnes et al. 1990, Takasu 1998, Brooke et al. 1998, Stokke et al. 2005). Host species can normally be classified into two categories as either 'acceptor' species or 'rejector' species, as described by Rothstein (1975b). Acceptor species rarely respond to non-mimetic eggs, while rejector species do not accept foreign eggs and reject them. A generalised host adaptation against brood parasites is the recognition and rejection of parasite eggs from their nests, which can lead to the selection for egg mimicry by cuckoos. Furthermore, comparative analyses show that passerine species commonly parasitised by the cuckoo have evolved lower intraclutch variation in egg appearance. This reduced variation would facilitate the discrimination of parasite eggs from host eggs when cuckoo egg mimicry is very accurate (Victoria 1972, Davies and Brooke 1989b). These hosts also show higher interclutch variation than those that have not been parasitised (Øien et al. 1995, Soler and Møller 1996, Stokke et al. 2002). Therefore, rejector individuals have less intraclutch variation in egg appearance than do Acceptor individuals (Stokke et al. 1999, Soler et al. 2000). High interclutch variation and low intraclutch variation allows effective egg discrimination (Øien et al. 1995, Honza et al. 2004), which is an effective mechanism against brood parasitism (Stokke et al. 2002).

Finally, the coevolutionary arms race between parasitic cuckoos and their hosts has extended to the stage of cuckoo chick discrimination (Langmore et al. 2003), in which hosts may preferentially rely on non-phenotypic recognition cues (Sherman et al. 1997, Anderson and Hauber 2007) to discriminate cuckoo chicks.

Kruger (2007) argued that the outcome of cuckoo-host interactions can be classified into three categories: 1) continued exploitation of hosts with no host defences [the common cuckoo-dunnock (*Prunella modularis*) system would be an example]; 2) oscillatory systems, where brood parasitism frequency and host defence levels fluctuate around an evolutionary equilibrium, an example of which would be the common cuckoo-reed warbler (*Acrocephalus scirpaceus*) system, where egg rejection behaviour declines with declining levels of brood parasitism (Brooke et al., 1998); and 3) systems where the evolution of counter adaptations by the hosts prevents successful parasitism (Davies 2000, Rothstein 2001). There are many examples of this final system, such as blackcaps, (*Sylvia atricapilla*) which react aggressively towards cuckoos (Røskaft et al. 2002a) throughout Europe with almost a 100 % rejection of parasitic eggs. If these situations continue, the cuckoo gens either become extinct or successfully switch to another host species.

Single Cuckoo-host Use vs. Multiple Cuckoo-host Use Systems

The great diversity in the pattern of host species utilisation by the cuckoo over its vast distribution area is fascinating (Davies 2000). However, host use by the cuckoo in any one region has rarely been properly sampled because most researchers have tended to concentrate their effort on one or a few common hosts (Moksnes and Røskaft 1995). In most cases, studies have examined single cuckoo-host systems where a single parasite species utilises one or several host species. Despite the overall variability in host use, a cuckoo frequently parasitises several distinct sympatric hosts while ignoring many other passerine species that are potentially suitable as hosts (Friedmann 1967, Brooker and Brooker 1989, Higuchi 1989, Davies and Brooke 1989a, b, Moksnes et al. 1990). Therefore, cuckoos choose hosts with a particular size, diet and nest type to ensure that the cuckoo egg and chick development are well matched with the host's life history (Davies 2011). Moreover, common cuckoo gentes with different egg phenotypes parasitise different species of warblers and buntings breeding in sympatry in partially overlapping habitat types (Antonov et al. 2010). In Japan, sympatric host species are parasitised by different common cuckoo gentes, which may explain the expansion of host use range as well as the evolution of cuckoo egg mimicry (Takasu et al. 2009).

Host selection rules remain unclear in some parts of the world. Cuckoos are narrow with regard to their host choice, and the ultimate mechanisms of host selection are still a matter of debate. The widespread evidence is that individuals within and among host populations are not evenly parasitised (Kruger 2007). However, systems where several parasite species occur in sympatry have been far less studied (see e.g., Friedmann 1967, Brooker and Brooker 1989, Higuchi 1989, Chace 2004, 2005). Sympatric brood parasitic cuckoos (*Cuculus*, *Chrysococcyx*, *Clamator*, *Eudynamys*, *Oxylophus*, *Scythrops*) in Africa, Australia and Japan partition their primary hosts. This may reduce the potential costs of interference competition among them for host nests (Friedmann 1967, Payne and Payne 1967, Brooker and Brooker 1989, 1992, Higuchi 1998). Where parasitic cuckoo species overlap in host use, slight differences in habitat use may lead to segregation (Southern 1954). Differential habitat selection by sympatric brood parasites has been observed among cuckoos (Friedmann 1967, Brooker and Brooker 1992) and cowbirds (Peer and Sealy 1999, Chace 2004). In Africa, three sympatric *Cuculus* spp. exhibit a high degree of host specificity as well as habitat specificity (Friedmann 1967). Bronze- (*Molothrus aeneus*) and brown-headed cowbirds occupy the same four riparian and pine-oak forests types, but at broader spatial scales, these cowbirds may reduce or avoid competition for host nests through divergent habitat use (Chace 2004). However, sympatric cuckoos and cowbirds may also overlap extensively in diet, habitat requirements and use of hosts (Payne and Payne 1967, Brooker and Brooker 1992). Competition for suitable hosts by parasitic sympatric cuckoos may influence the evolutionary development and the exploitation of new areas for suitable hosts (Wyllie 1981). In Bangladesh, several cuckoo species breed in sympatry and parasitise different host species in diverse habitats, representing a real multiple cuckoo-host system, which may explain the segregation of multiple cuckoos into multiple host use patterns. This reduces interspecific competition.

The co-evolutionary arms race (Dawkins and Krebs 1979, Thomson 1994, Davies 2000) is a basic theory in cuckoo research (Moskát 2005) and has primarily been conducted on cuckoos in Europe and Australia and cowbirds in North America. The common cuckoo, great spotted cuckoo (*Clamator glandarius*) and some cowbirds have been the focus for quite a lot of studies. However, very few and poor studies have been conducted on the Indian sub-continent.

Details regarding coevolutionary interactions of sympatric parasitic cuckoos and their hosts are still unravelled in many parts of the world, such as in Bangladesh at the southeastern part of the Indian subcontinent. Here, several sympatric cuckoo species, viz. the Asian koel (*Eudynamys scolopacea*), common hawk cuckoo (*Cuculus varius*), pied cuckoo (*Clamator jacobinus*) and Indian cuckoo (*Cuculus micropterus*) live in sympatry. These cuckoos parasitise different host species, such as house crows (*Corvus splendens*), long-tailed shrikes (*Lanius schach*), common mynas (*Acridotheres tristis*), black drongos (*Dicrurus macrocercus*), jungle babblers (*Turdoides striatus*) and others. All of the sympatric cuckoo species throughout the Indian subcontinent are obligate brood parasites.

Aims of the Study

To my knowledge, this is the first study on cuckoo-host interactions in Bangladesh. The aim of my thesis is to learn more about geographic variation in cuckoos' breeding behaviour, to uncover cuckoos' lifestyles and to search for any effect cuckoos might have on their host communities and hosts' cognitive abilities throughout the many different habitats utilised by these sympatric cuckoos. The most important objective of the thesis was to learn about the interactions between different species of Asian cuckoos and their different hosts.

Specifically, I examined the following: 1) interactions between the Asian koel and its different hosts, with a special focus on host selection factors (Paper I and Paper II); 2) host choice by sympatric cuckoo species in different habitats (Paper III); and 3) host recognition and rejection abilities of parasitic eggs using experiments with artificial model eggs in host nests (Paper IV).

Study Area, Study Species and General Methods

Study Area

This study was carried out on the Jahangirnagar University campus, which is located in the central region of Bangladesh ($30^{0}16^{\prime}$ N, $90^{0}52^{\prime}$ E), 32 km north of Dhaka (Fig. 1). The entire university study site is about 200 ha. The Jahangirnagar University campus has isolated patches of 'sal' (*Shorea robusta*) forest, which originated from an earlier tropical deciduous 'sal' forest community (Nishat et al. 2002). The campus has many different vegetation types, forming a mixture of diverse habitats. These vegetation types include fruit trees dominated by *Artocarpus heterophyllus*, *Mangifera indica*, *Mimusops elengi*, *Ficus bengalensis*, *Murraya paniculata* and *Livistona chinensis*, grasslands, open woodlands dominated by tree species such as *Tectona grandis*, *Acacia auriculiformis*, *Swietenia mahagoni*, *Shorea robusta*, *Dalbergia sissoo*, *Albizia* spp. and bushes such as *Chrysopogon* sp., *Cassia sophera* and *Cassia tora* and monotypic plantations including *Acacia auriculiformis*, *Gmelina arborea* and *Lagerstroemia speciosa* (Fig. 2).

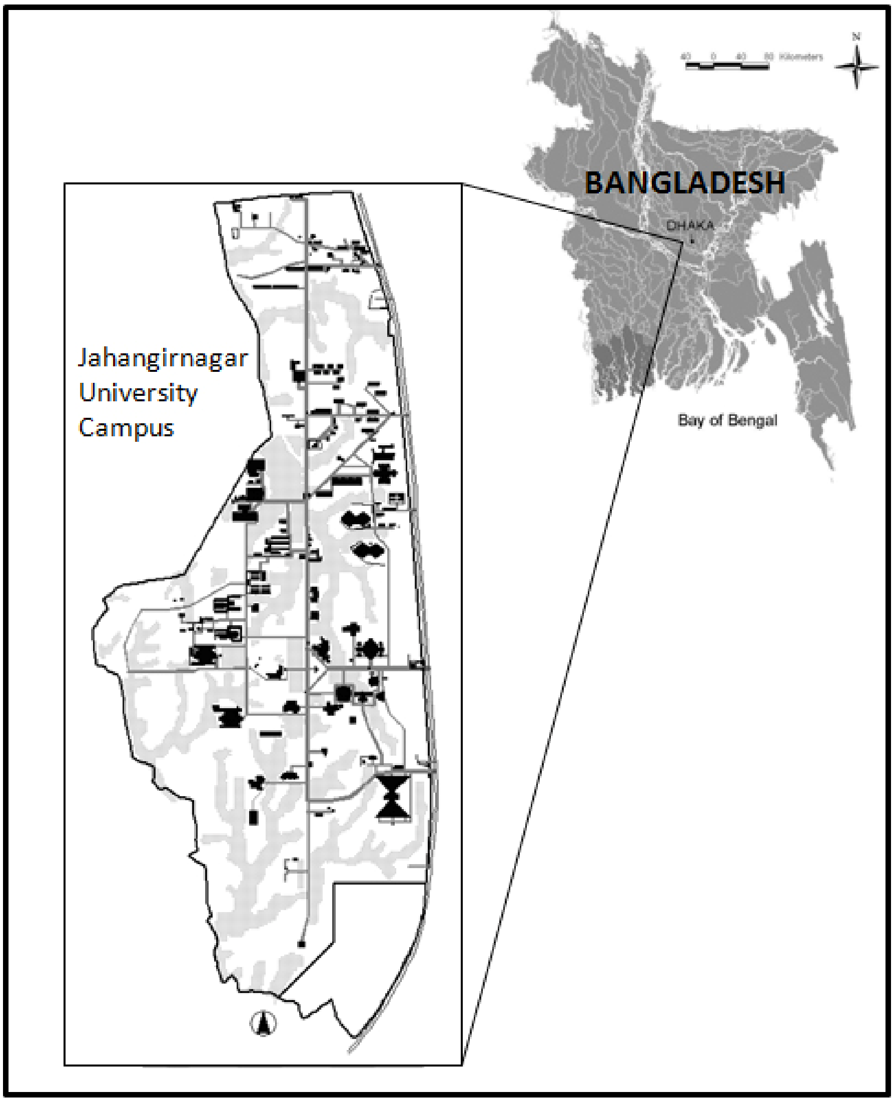

Fig. 1. Map of study area

Fig. 2. Different cuckoo habitats in the study area; a. Human habitations, b. Mixed scrub forests, c. Monotypic plantations.

In addition, the area consists of agricultural lands, orchards and botanical gardens in and around human settlements. A total of 180 bird species, including 76 passerines and 104 non-passerines, have been recorded in the area. In total, 34 passerine species have been found to be breeding residents (Mohsanin and Khan 2009).

Study Species

Three cuckoo species, the Asian koel, common hawk cuckoo and Indian cuckoo, are widely distributed and are common residents throughout many types of habitats in

Bangladesh, while the pied cuckoo is a summer visitor (Grimmett et al. 1999). All these cuckoo species occur in sympatry and coexist with their current hosts in diverse habitats in the study area.

The Asian koel is the most common resident among the cuckoos in the study area (Fig. 3). Each of the host species of Asian koel is a common resident and is also widely distributed throughout Bangladesh. The house crow and the common myna mostly inhabit areas near humans, as they are highly opportunistic omnivores (Feare and Craig 1999), while the long-tailed shrike more commonly occurs in open mixed forests and bushes with scattered trees. These host species are described in detail in paper I (Fig. 3).

Fig. 3. Asian koel and its hosts; a. female koel, b. male koel, c. common myna, d. house crow, e. long- tailed shrike

The black drongo is one of the most common and widely distributed passerine birds throughout the Indian sub-continent (see Payne 2005) (Fig. 4). They feed on insects (mainly agricultural pests) and breed in trees, usually near the fringe of a branch. Their breeding season lasts from April to August, with a peak in May or June (Ali and Ripley 1987) in different areas. In Bangladesh, their clutch consists of 3–4 eggs. Their incubation period is normally around 15 days, and the nestlings are in the nest for about 19 days (Ali and Ripley 1987).

Fig. 4. Indian cuckoo and its host; a. Indian cuckoo, b. black drongo

Finally, the jungle babbler is one of the most common passerine birds throughout the whole peninsula of India (Whistler 1949). This species serves as host for several cuckoo species (Lowther 2005). It is a common bird found in gardens near human habitations as well as deciduous forests and cultivated areas (Ali and Ripley 1987). They are gregarious, occurring in parties of about 6 to 12 individuals and are commonly known as ‘seven sisters’ due to their social habits (Whistler 1949, Ali and Ripley 1987). Jungle babblers mainly feed on insects, but fruits like figs and berries are also a part of their diet (Ali and Ripley 1987). Their nests are normally built in small thorny trees, and the breeding season lasts from March to September. In Bangladesh, their clutch consists of 3 to 5 eggs, but in India, they occasionally lay up to 7 eggs (Gaston 1977). The incubation period is generally around 14 days. The jungle babbler is parasitised by the common hawk and pied cuckoos (Gaston 1976, Gaston and Zacharias 2000) (Fig. 5).

Fig. 5. a. Common hawk cuckoo b. pied cuckoo c. jungle babbler, a host for both cuckoo species

Methods

This study on natural parasitism was carried out in two successive breeding seasons of 2008 and 2009 (January to August, each year). During these years, I also conducted experiments by introducing artificial model eggs into host nests to test the host responses. These experiments were extended in the following year, 2010. Nests of most host species were systematically searched for in different habitats within the study area. Data were collected on different factors, including the distance between host nests and cuckoo vantage points, the distance to conspecific breeding neighbours, nest size, nest height, egg measurements, and egg mimicry. I also estimated parasitism rates among different hosts, host selection and habitat preferences among the sympatric cuckoos. Experiments with artificial eggs were conducted by following the general procedures of Moksnes et al. (1990). If the model egg remained in the nest and was incubated for at least 5 days, it was classified as accepted. If the model egg disappeared from the nest and the remaining eggs were incubated, the case was classified as a rejection. Detailed descriptions of field procedures and field observations, including the occurrence of cuckoo parasitism, host use and host responses to parasitism, are found in detail in all papers (I, II, III, IV).

Summary of Papers

Paper 1. Interactions between the Asian koel (Eudynamys scolopacea) and its hosts

I explored host-parasite interactions between the parasitic Asian koel and its different host species: the house crow, the long-tailed shrike and the common myna. These three host species are among the most common passerine residents in the study area. Common mynas and long-tailed shrikes experienced significantly higher parasitism rates than did house crows. In terms of degree of mimicry of cuckoo eggs with host eggs, long-tailed shrikes and common mynas were distinct from those of Asian koels, while mimicry was significantly better between koel and house crow eggs. Parasitism rates and multiple parasitism (more than one cuckoo egg) were higher in common mynas and long-tailed shrikes than in house crows. Asian koels did not parasitise any nests of common mynas situated in holes or cavities. For all three host species, the breeding success of the host was significantly reduced in parasitised nests compared with non-parasitised nests. Common mynas were more likely to desert parasitised nests than non-parasitised nests, which could indicate that this host has developed at least a slight defence against parasitism. In this system, host responses were otherwise almost absent or at a very low level, probably due to a much lower virulence behaviour in the parasitic Asian koel chick than, for example, common cuckoo chicks (which evict all host young). Both host and cuckoo young survived in koel-parasitised nests.

Paper II. Factors influencing host nest use by the brood parasitic Asian koel (Eudynamys scolopacea)

The brood parasitic Asian koel followed different patterns when selecting nests of different hosts. In all three host species, the probability of parasitism increased when the distance between the host nests and potential parasite vantage points (here, fruit yielding trees) decreased, and furthermore, there was a noteworthy positive correlation between nest volume and chances of parasitism. Large nests may indicate a 'high quality host' or 'high quality territory' to cuckoos. I found that comparatively larger nests were poorly camouflaged and thus were more easily visible to the Asian koel. Nests of long-tailed shrikes and house crows close to active conspecific neighbours were less likely to be parasitised than nests further away. Moreover, the risk of parasitism in long-tailed shrikes increased with nest heights lower to the ground. Most of the results of the present study are in accordance with findings from other brood parasite–host systems and indicate that brood parasites use many similar cues when selecting host nests.

Paper III. Host use by four sympatric species of cuckoos in Bangladesh

Sympatric parasite species are expected to have segregated into different ecological niches, and they should prefer different host species to avoid interspecific competition. As predicted, each cuckoo species parasitised different host species. The Asian koel parasitised common mynas, long-tailed shrikes and house crows. The Indian cuckoo parasitised black drongos, while the common hawk cuckoo laid eggs in the nests of jungle babblers. The latter host was also parasitised by the pied cuckoo, but the breeding season of the two last mentioned cuckoo species did not overlap because they have different arrival dates in the study area. As a result, the intensity of parasitism by common hawk cuckoos, which arrived early, was higher than that of pied cuckoos, which arrived later in the season when the jungle babbler had nearly ceased breeding. I also recorded parasitism rates by the cuckoo species in three main habitats in the study area: human habitations, mixed scrub forests and monotypic plantations, which were classified according to vegetation type (Fig. 5). For most host species, there was a significant difference in the parasitism rate between habitats, indicating that cuckoos preferred specific habitats even if their favourite host also occurred in other habitats. Indian cuckoos, common hawk cuckoos and pied cuckoos showed excellent egg mimicry with their hosts, while Asian koels showed good mimicry to only one of their three host species.

Paper IV. Asian cuckoo host responses against experimental parasitism

Host adaptations against parasitism (the acceptance or rejection of non-mimetic eggs) and cuckoo counteractions (egg mimicry) are expected to be favoured by natural selection. I experimentally parasitised nests of ten potential cuckoo host species using differently sized and coloured model eggs (brown, blue and white) to test host responses. Two species were strong rejectors: black drongos and black-hooded orioles, which rejected all (100 %) of the non-mimetic model eggs. Long-tailed shrikes rejected 75 % of the model eggs, while most house crows (90.9 %) accepted the model eggs. Jungle crow pairs accepted 56 %; they deserted their nests in 44 % of the experiments. Finally, common mynas and jungle babblers accepted (100 %) all non-mimetic eggs, although they are very common hosts in the area. As a frequent cavity or hole nester, the common myna has not yet developed rejection behaviour in its breeding range. Further studies are needed to explain why jungle babblers accepted non-mimetic experimental eggs despite the excellent egg mimicry of their brood parasites (common hawk cuckoo and pied cuckoo). Species such as the Oriental magpie robin, the red-vented bulbul and the Asian pied starling, which probably have no or very little history of interaction with cuckoos, accepted 100 % of the non-mimetic model eggs.

Discussion

This thesis provides basic information and findings about Asian brood parasitic cuckoos, their hosts, and their interactions with common hosts. My results and findings have unravelled new information about this cuckoo-host system in the sub-continent.

Sympatric Cuckoos and their Hosts

In coevolutionary interactions between cuckoos and their hosts, the increasing fitness costs of parasitism on hosts select for increased host defences, which in turn may compel parasites to evolve adaptations to overcome host's defences by 'trickery', such as 'egg mimicry' (Davies 2000). However, many host-parasite systems still lack these adaptations (Davies 2000). For example, the dunnock accepts the highly non-mimetic eggs of the common cuckoo (White 1789, Davies 2000). The 'evolutionary lag' (Rothstein 1975a, 1990) and the 'evolutionary equilibrium' (Zahavi 1979, Spaw and Rohwer 1987, Lotem et al. 1992, Lotem and Nakamura 1998, Hauber et al., 2004) hypotheses have been the most common explanations of such "maladaptive" behaviour. However, it is very difficult to discriminate between these two hypotheses (Rothstein 1982).

My study is the first to investigate host-parasite interactions and the effects of parasitism by the obligate brood parasitic Asian koel on the breeding success of three different host species (Paper I). It is also the first study on sympatric cuckoos, such as the common hawk cuckoo, pied cuckoo and Indian cuckoo, and their respective hosts in this region (Paper III). The first prerequisite in becoming a successful parasite is to adopt a successful host. The distribution and population density of the parasites are predictably controlled by the distribution and abundance of their hosts (Stokke et al. 2007). The European common cuckoo maintains a wide distribution by parasitising a wide range of host species, and this has led to the evolution of distinct gentes with eggs closely mimicking those of their hosts (Moksnes and Røskaft 1995, Davies 2000). Although there have been occasional records of Asian koel parasitism in other regions of the Indian sub-continent (see Payne 2005), the Asian koel seems to parasitise many passerine species with which it is sympatric. However, the Asian koel only lays one type of egg. In this respect, the Asian koel seems to be more generalistic and more similar to the brown-headed cowbird than to the common cuckoo. The pied cuckoo, on the other hand, mainly parasitises babblers of the *Turdoides* genus, most commonly lowland species such as *T. striatus*, *T. caudatus* and *T. malcolmi* (Becking 1981). The common hawk cuckoo parasitises jungle babblers like the pied cuckoo. This cuckoo lays its eggs during spring rather than during the rainy season, which coincides with the breeding of jungle babblers. On the other hand, jungle babblers are parasitised by pied cuckoos during the rainy season (Gaston and Zacharias 2000), which may be an adaptation to reduce competition between two sympatric cuckoos. The Indian cuckoo mainly parasitises black drongos, a sympatric passerine found in mixed scrub forests (Paper III) (Baker 1942, Becking 1981). Black drongo eggs are variable in colour and markings (Becking 1981), which might be adaptations towards the mimetic eggs of the Indian cuckoo (Øien et al. 1995). The Indian cuckoo parasitises different hosts in several regions in Asia (Payne 2005).

In two host species, the Asian koel laid highly non-mimetic eggs (Paper I). In previous studies, Asian koels parasitised different host species, such as black-naped orioles (*Oriolus chinensis*) and black drongos, if crows were not available (Smith 1950, Holmes and van Balen 1996). The blue magpie (*Urocissa erythrorhyncha*) has also been recorded as a host (Lewthwaite 1996). Asian koels may, as discussed above, be regarded as a generalist brood parasite throughout its range. The frequency of koel parasitism was lower in house crows than in common mynas and long-tailed shrikes; however, all three hosts of Asian koel eggs can be regarded as equally suitable hosts because there were no significant differences in cuckoo breeding success (Paper I). In spite of the extensive costs of parasitism, long-tailed shrikes and common mynas seem not to have evolved rejection behaviour, with no observed cases of egg ejection, even though the parasite egg appeared to be highly non-mimetic compared to host eggs (Paper I). This situation is contrary to that in many hosts of the common cuckoo (e.g., Davies and Brooke 1989a,b, Moksnes et al. 1990). In the current cuckoo-host system, the absence of host responses or very low levels of anti-parasitic defence may be more similar to the cowbird-host system, which is probably a result of repeated or spatially and temporally non-random patterns of parasitism (Hauber et al. 2004). Moreover, habitat fragmentation, which is one of the main causes of habitat degradation (Muzaffar et al. 2007) in this region of Asia, may have forced hosts and parasites into high densities in the comparatively undisturbed areas, which may lead to an ‘unbalanced’ situation with high parasitism rates, multiple parasitism and poorly developed host defences.

Pied cuckoos, Indian cuckoos and most of the common hawk cuckoos selected hosts in mixed scrub forests, which differed from the Asian koel which parasitised hosts mostly near human habitations (Paper III). This might be another adaptation to reduce competition. Common hawk cuckoo nestlings evict host eggs or nestlings, while pied cuckoo nestlings do not evict. The pied cuckoo’s late arrival in the study area might theoretically be an adaptation to avoid common hawk cuckoo nestlings in the nest of the same host thus, promoting survival of their own chicks.

Nest Searching Activities

There have been substantial attempts to identify cues and searching methods that brood parasites use to find nests (Gill et al. 1997, Clotfelter 1998, Teuschl et al. 1998, Moskát and Honza 2000, Banks and Martin 2001, Antonov et al. 2007). Non-random parasitism across host populations has been widely linked to host nest-site characteristics (Øien et al. 1996, Grim 2002). Røskaft et al. (2002b) found that the host breeding habitat predicts the rate of parasitism by the common cuckoo. Other features such as host quality (Soler et al. 1995) and host behaviours around nests (Clotfelter 1998) affect the probability of parasitism. Asian koels may use a basic or focal nest search rule or may favour a simple nest visibility rule when looking for nests to parasitise (Aviles et al. 2009). Proximity to fruit trees was an important positive predictor of the probability of parasitism in all three host species. The perch proximity hypothesis states that brood parasitic females are better able to locate host nests that they can observe from nearby perches (Freeman et al. 1990, Øien et al. 1996, Clotfelter 1998, Larison et al. 1998). The fact that nests close to fruit trees were significantly more likely to be parasitised than those further away from such trees provides support for the 'perch proximity' hypothesis (Anderson and Storer 1976, Freeman et al. 1990, Øien et al. 1996). A short distance between the host nest and an Asian koel perching tree is perhaps essential and enhances the ability of the parasite to survey the nesting area and time its egg laying in the host nest (Paper II). The significance of parasite perch sites and proximity to host nests has been stressed in several studies of common cuckoos (Øien et al. 1996, Moska´t and Honza 2000, Antonov et al. 2006b, 2007) as well as in cowbirds (Freeman et al. 1990, Romig and Crawford 1996, Clotfelter 1998, Hauber and Russo 2000). Potential hosts breeding in habitats where vantage points are scarce or absent may suffer less parasitism than those breeding where vantage points are abundant (Røskaft et al. 2002b, 2006). This is well known for the hosts of several avian brood parasites, e.g., the common cuckoo (see e.g., Øien et al. 1996, Moskát and Honza 2000). Røskaft et al. (2002b) proposed the spatial habitat structure hypothesis, which explains the occurrence and extent of adaptation in host-brood parasite (common cuckoo) systems by the proportion of host populations breeding in the vicinity of trees with potential cuckoo perches and thereby are accessible to cuckoos. However, future experimental studies (for instance, including nest and clutch size manipulations) should be carried out to reveal in more detail the system involved in Asian koel host nest use.

Nest height above ground may be another important predictor of parasitism. Nests situated in low positions in small trees or in low bamboo thickets where branches and foliage are sparse may be easier to detect from potential perches higher in the trees (Øien et al. 1996, Moskát and Honza 2000, Clarke et al. 2001). This would explain why long-tailed shrike nests at lower positions in the study area were more frequently parasitised than those situated higher in the trees

Furthermore in my study, I found that parasitised nests of the Asian koel were significantly larger than unparasitised nests (Paper II), and this result contrasts with earlier work (Uyehara 1996, Moskát and Honza 2000). For all three host species studied, we found a significant positive relationship between nest volume and the likelihood of parasitism. For example, nest size in magpies (*Pica pica*) is correlated with parasitism by the great spotted cuckoo (*Clamator glandarius*), apparently because nest size reflects host parental ability (Soler et al. 1995, Polacikova´ et al. 2009). Furthermore, larger nests are easier to locate by the parasite and are therefore a predictor of risk of parasitism. Peer and Sealy (2004) found that hosts with larger nests evolved egg rejection due to stronger selection imposed by parasitic brown-headed cowbirds. The quality of territories may be important in the common myna and house crow because it is unlikely that host activity was the cue for the Asian koel's preference for large nests. These species' nests were usually poorly camouflaged and easily visible, so the parasite was able to find them regardless of nest size and host activity. Thus, more data are required to fully test the generality of the ‘‘host quality’’ hypothesis in the Asian koel–host system.

The risk of parasitism in all three koel host species was influenced by the distance to active conspecific neighbours. All parasitised house crows and most parasitised long-tailed shrikes in our study area were solitary nesters with longer distances between conspecific breeding pairs. Host species that nest in colonies may experience reduced parasitism with increasing density through communal vigilance and nest defence (Martinez et al. 1996, Lawes and Kirkman 1996, Canestrari et al. 2009).

Host use Pattern

Obligate avian brood parasites may be host specialists if they use one or a few host species or host generalists if they parasitise many hosts (Davies 2000). Different parasitic cuckoo species living in sympatry show divergence in their selection of suitable hosts.

Friedmann (1967) was the first to propose the term ‘Alloxenia’ to describe the parasitism state in which parasitic species are likely to use different species of hosts. Host selection by different cuckoos varies because of preferences for host size, food, breeding site, egg-laying seasons and nest accessibility among different hosts (Lack 1963). In the common cuckoo, different sympatric gentes parasitise different host species with different habitat preferences (Honza et al. 2001). The four sympatric cuckoo species in my study area mainly parasitised different host species with different breeding strategies, habitat preferences or breeding sites (Paper III). These sympatric cuckoos overlapped in their use of different breeding habitats, including human habitations with orchards and gardens, mixed scrub forests and monotypic plantations. They did not keep themselves separate from each other through strict habitat separation or any avoidance behaviour, although they utilised separate ecological niches concerning their food habits (Ali and Ripley 1987, Payne 2005). Habitat isolation is not necessarily comprehensive in cuckoos, as they may occur in the same habitat with wide home ranges and hence, overlap in several types of habitats (Higuchi 1998). In Japan where four species of cuckoos occur in a wide variety of habitats, the cuckoos also largely overlap in breeding ranges. These cuckoos use primary hosts in different genera and therefore have different parasitic niches, which reduce the potential competition (Royama 1963). In our study area, the Asian koel arrived earlier than any of the other cuckoo species and parasitised three hosts, among which common mynas and house crows are early breeders, while long-tailed shrikes started breeding later (Paper I). However, if two or more cuckoos parasitise the same host species, we predicted that they should show other fundamental differences in their breeding ecology. In support of this prediction, we found that the breeding season of the common hawk cuckoo was much earlier than that of the pied cuckoo (Paper III). House crows, common mynas and jungle babblers laid their first eggs earlier in the breeding season when the Asian koel or common hawk cuckoo had not yet commenced breeding. Therefore, early breeding in hosts could be a strategy to avoid parasitism (Gill 1998, Paper I & Paper III). However, long-tailed shrikes and black drongos overlapped entirely with the Asian koel and Indian cuckoo, respectively, in their breeding seasons (Paper III). Asian koels breed in habitats where there are fruit-bearing trees (see also Blakers et al. 1984 and Coats 1985), and as a comparatively larger cuckoo, it also has a broader niche of potential hosts (Brooker and Brooker 1989). The Asian koel thus exploits different hosts with different breeding habitats, which may reduce intraspecific competition. The regional composition of habitats can directly influence the density of parasites and therefore, the risks of parasitism in different hosts. This has been shown for generalistic brood parasites such as the brown-headed cowbird, which requires specific habitats for feeding (Robinson et al. 1999).

Cuckoo Egg Mimicry and Host Responses

Host discrimination of parasitic eggs, the most common anti-parasite defence, appears to have been the main selective pressure on the evolution of egg mimicry in avian brood parasites (Rothstein and Robinson 1998, Davies 2000). Once the cuckoo has evolved egg mimicry, the host has the problem of distinguishing if there is a cuckoo egg in its clutch. Experiments with model eggs have revealed that hosts learn what their own eggs look like and then reject odd-looking eggs that differ from the learned set (Rothstein 1974, 1975a, Lotem et al. 1992, 1995). I tested host responses among ten species of passerines, which were potential hosts living sympatrically with the different species of cuckoos (Paper IV). Eggs of Asian koels are highly non-mimetic to eggs of both common mynas and long-tailed shrikes, but resemble eggs of house crows (Baker 1922, Paper I). Eggs of the common hawk and pied cuckoos resembled the eggs of jungle babblers quite strongly, and the eggs of Indian cuckoos were also good mimics to those of the black drongo. These cuckoos probably evolved egg mimicry in colour and size to overcome host defences. Black drongos were tolerant and accepted good-mimetic cuckoo eggs, but they rejected all non-mimetic model eggs, indicating that they have had a long history of coevolution with cuckoos in Asia. In all cases of parasitism, most parasitic eggs were accepted. However, common myna nests parasitised by the Asian koel were deserted more often than unparasitised ones (Paper I). Species that initially accept eggs into their nests may still reject parasitism by abandoning the parasitised clutch by deserting the nest (Rothstein 1975b, Ortega 1998) particularly if they have seen the parasite at the nest (Davies and Brooke 1988, Moksnes et al. 1993, 2000). Jungle crows, house crows and common mynas are reported to be the most frequently recorded suitable hosts of the Asian koel throughout the Indian sub-continent (Lamba 1976, Roberts 1991, Davison and Fook 1995, Wells 1999, Begum et al. 2011). Nest desertion with subsequent re-nesting has been observed in common mynas. However, it is not clear whether desertion is a defence mechanism against parasitism or not (Paper I and IV). Moreover, long-tailed shrikes and common mynas accepted highly non-mimetic Asian koel eggs. This could reflect that the koel is ahead in the co-evolutionary arms race with these hosts. This might be because they are not able to eject eggs from the nest. The common myna is, for instance, predominantly a cavity nester unable to eject foreign eggs (Paper IV). The long-tailed shrike rejected the model eggs in most cases (Paper IV), while it accepted Asian koel eggs. This species is probably a relatively new host in this region. Most likely, long-tailed shrikes were unable to grasp the large parasitic koel egg. Likewise, African subspecies of Jacobin cuckoos lay non-mimetic eggs larger than the host eggs, and it is unlikely that the former can be ejected by by the cape bulbul's (*Pycnonotus capensis*) grasping ejection method (Kruger 2011). Furthermore, size differences between a hosts' own and the parasite's eggs are apparently important in long-tailed shrike responses to the parasitic eggs, indicating that size can be a cue which may compel the hosts to evaluate physical capabilities in the egg rejection decision process (Stokke et al. 2010). This experimental study revealed that the jungle babbler accepted all non-mimetic model eggs. Although the eggs of common hawk and pied cuckoos were highly mimetic to the eggs of jungle babblers in colour pattern, their size varied (Paper III). Jungle babblers seem to either lack egg recognition abilities towards non-mimetic eggs or other host defences or have not yet developed any defences against cuckoo parasitism (Paper IV). If the jungle babbler is a secondary host that came into use by these two cuckoos after the cuckoos had already evolved their mimetic eggs, the babblers only defence would have been to either 1) prevent the cuckoo from laying or 2) destroy the nest content after the cuckoo had layed eggs. Further experiments are necessary to test these two hypotheses. In spite of the high degree of host acceptance of parasite eggs, the breeding success of both cuckoo and host should be studied in more detail.

For some hosts, it is simply difficult to puncture the cuckoo egg (Antonov et al., 2008) or they may fail to reject large eggs because rejection costs are too high (Røskaft and Moksnes, 1998; Stoddard and Stevens, 2011). This may force them to accept cuckoo eggs. As mentioned earlier, two major explanations are proposed for why potential host species accept brood parasitism. Under the evolutionary equilibrium hypothesis, nest parasitism is tolerated because of conflicting selection pressures (Zahavi 1979, Rohwer and Spaw 1988). Costs of ejection errors or abandonment of nests, representing losses of host eggs and energy expended in replacement nesting, may outweigh the costs of raising parasite young; thus, acceptance could be evolutionarily favoured (Lotem and Nakamura 1998). The present study of cuckoo-host systems showed remarkably high acceptance of parasitic eggs in some potential hosts, which might be explained by the existence of lag in the evolution of rejection responses, as suggested for many cowbird hosts (Rothstein 1990, Hosoi and Rothstein 2000). The study reveals that host populations are likely not able to recognise parasitic eggs (Rothstein 1982) or brood parasitic birds (Smith et al. 1984, Bazin and Sealy 1993) or lack appropriate responses to foreign eggs.

For the hosts of the parasitic species in this study, there are no results from previous research that can be used to compare the costs of accepting parasite eggs with the costs of rejecting them. Future studies on these costs are therefore necessary to obtain a better understanding of the mechanisms underlying acceptance versus recognition and rejection of parasitic eggs in the actual host species.

Prospect for future studies

This study is the first of its kind to reveal basic information on the interactions in several species of cuckoos and their host systems in Bangladesh. I studied three host species parasitised by Asian koel, all of which are regarded as successful hosts. The Asian koel is a host generalist, laying non-mimetic eggs and utilising several host species. There is a need to test for genetic differences among cuckoo nestlings raised by different hosts to find out whether individual females are host specialists. Furthermore, it is still unknown whether female cuckoo chicks raised in the nest of one specific host have a stronger tendency to parasitise the same host species as adults. Moreover, several hypotheses related to host imprinting, natal philopatry, nest site choice and habitat imprinting (Brooke and Davies 1991, Payne et al. 1998, Moksnes and Røskaft 1995, Teuschl et al. 1998, Vogl et al. 2002) should be studied in more detail in this cuckoo-host system. Prospective future directions for research should include further experimental work on the fitness costs of brood parasitism. Furthermore, interactions between parasitic chicks and their host parents should be studied, especially for the non-evicting cuckoo species. Experiments with artificial parasitism and model presentations, such as cuckoo dummy experiments, need to be conducted to acquire more accurate scenarios of anti-parasite defences in these host species.

Most of the research on the co-evolutionary arms race between cuckoos and their hosts have been conducted in Europe and Australia and are poorly studied on the Indian sub-continent (Moskát, 2005). The importance of studying hosts in a metapopulation context is crucial on the Indian sub-continent. Habitat degradation is pronounced, leading to large-scale deforestation throughout the continent (Muzaffar et al. 2007), while habitat fragmentation results in serious structural changes in forests. The 'spatial habitat structure' hypothesis (Røskaft et al., 2002b) is linked to the metapopulation structure. Hosts' metapopulation consists of both parasitised and non-parasitised populations. Immigrations of hosts from unparasitised to parasitised populations could protect hosts from local extinction (Barabas et al. 2004). It is therefore important to study local adaptations and co-existence in a metapopulation context for both the cuckoo and host over a long time.

Conclusions

The results from the present study show that different species of sympatric cuckoos co-exist along with passerine host populations in a diverse habitat in Bangladesh. They are reported to parasitise different host species in three different habitats and therefore avoid competition with each other through ecological niche segregation. Furthermore, the arrival date of cuckoos in different habitats varied, which indicates that they possess different breeding strategies. My study has shown that Asian koel parasitism rates were significantly higher than any other parasitic cuckoo, indicating that the koel has a larger and broader niche of potential hosts. In most cases, poorly mimetic koel eggs were accepted by the hosts, though common mynas were more likely to desert parasitised nests. House crows suffered low parasitism rates mainly because of a colonial nesting habit, which acts as an anti-parasite adaptation. Asian koels follow similar cues or patterns as other brood parasites while searching for host nests. Proximity of fruit trees is an important predictor for risk of parasitism for all three hosts, which supports the 'perch proximity' hypothesis. Common mynas, as predominantly cavity nesters, are unable to recognise the foreign egg and reject it, while long-tailed shrikes showed mixed responses (accepted 25%) to experimental eggs, supporting the hypothesis that this is a new host. Another explanation may be that this host lacks grasp-ejection abilities or is not able to puncture the large koel eggs to eject them from the nest. Black drongos ejected non-mimetic model eggs, while they accepted mimetic cuckoo eggs. Common hawk cuckoos and pied cuckoos parasitised jungle babblers where both parasitic cuckoos lay eggs highly mimetic to the host eggs. Jungle babblers accepted non-mimetic model eggs. Further experiments with cuckoo dummy models might reveal unknown questions as well as develop a better understanding of cognitive abilities of the hosts.

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Paper-I

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Paper-II

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Paper-III

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Paper- IV

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Asian cuckoo host responses against experimental parasitism

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ABSTRACT

In the arms race between avian brood parasites and their hosts several adaptations and counter-adaptations have evolved. The most prominent host defence is rejection of parasitic eggs. We experimentally parasitized nests of ten potential hosts breeding in sympatry with four different cuckoo species in an area in Bangladesh using different sized and coloured model eggs (brown, blue and white) in order to test host responses. Two species turned out to be strong rejecters of non-mimetic model eggs; Black Drongos (*Dicrurus macrocercus*) and Black-hooded Orioles (*Oriolus xanthornus*) which rejected all (100 %) model eggs. One species, the Long-tailed Shrike (*Lanius schach*) rejected 75 % of the model eggs. All model eggs were ejected within 24 hours after the introduction, indicating that these three hosts did not make any delay in rejection decisions. Most (90.9 %) of the House Crows (*Corvus splendens*) accepted the model eggs, while the remaining 9.1 % were abandoned. Jungle Crow (*Corvus macrorhynchos*) pairs accepted 56 % of the non-mimetic model eggs, while they deserted them in 44 % of the experiments. Common Mynas (*Acridotheres tristis*) and Jungle Babblers (*Turdoides striatus*) accepted (100 %) non-mimetic eggs, although they are common hosts in the area. Finally, Oriental Magpie Robins (*Copsychus saularis*), Red-vented Bulbuls (*Pycnonotus cafer*) and Asian Pied Starlings (*Gracupica contra*), which probably have no history of interaction with cuckoo parasitism, accepted 100 % of the non-mimetic model eggs.

Keywords: Experimental parasitism · model eggs · acceptance · rejection · non-mimetic · cuckoo · coevolution

INTRODUCTION

Avian brood parasites depend on their hosts for successful reproduction. Brood parasitism is in many instances inflicting high costs on the host because its reproductive success is dramatically reduced (Røskaft et al. 1990, Davies 2000). Due to these costs, natural selection will favour evolution of host defences (Davies & Brooke 1989a, Moksnes et al. 1990). Many host species are able to discriminate and reject eggs which are unlike their own, abandon parasitized clutches or sometimes bury the parasitic egg in the nest lining. Some hosts may even desert or eject the cuckoo chick (Grim et al. 2003, Langmore et al. 2003, Langmore et al. 2009, Sato et al. 2009). However, these host adaptations have resulted in evolution of counter-adaptations in parasites. Sophisticated deception strategies like egg colours that mimic those of their hosts or even producing young that mimic host offspring have evolved to overcome the host defences (Baker 1942, Southern 1958, Brooke & Davies 1988, Moksnes & Røskaft 1995, Higuchi 1998, Davies 2000, Langmore et al. 2003). Hosts may then respond by producing eggs with low intra or high inter clutch variation to discriminate against the mimetic parasitic eggs (Øien et al. 1995, Stokke et al. 2002, Stokke et al. 2007). The result is a coevolutionary arms race between the brood parasite and its host(s), leading to more and more complex and sophisticated adaptations and counter adaptations (Stokke et al. 2005, Davies 2000). Host chicks with intricate gape patterns or other characteristics making chick mimicry a more difficult task for the parasite may also evolve (Davies 2000, Stokke et al. 2005).

Despite the heavy costs of parasitism, many brood parasite hosts show either no or only moderate rejection abilities towards even non-mimetic parasitic eggs (Moksnes et al. 1990, Alvarez 1999, Stokke et al. 1999, Davies & Brooke 1989a, Stokke et al. 2008). This behaviour might at first sight seem maladaptive (Rothstein 1975b, Brooker & Brooker 1996, Robert et al. 1999), because such species may be unable to recognize and reject odd-looking eggs which are added to their nests (e.g. dunnocks *Prunella modularis*, (Brooke & Davies 1988) and splendid fairy-wrens *Malurus splendens*, (Brooker & Brooker 1996, Langmore & Kilner 2009)). A common explanation for why some potential host species do accept parasitic eggs is that they have not had enough time to evolve the ability to recognize odd looking eggs (the evolutionary-lag hypothesis) (Rothstein 1982b, Rothstein 1975a, Dawkins & Krebs 1979, Kelly 1987, Davies & Brooke 1989b, Rothstein 1990). However, several alternative hypotheses seeking more adaptive explanations for the variation in rejection of cuckoo eggs in different host populations have been proposed. Hosts might have attained an evolutionary equilibrium which may exist within host populations of acceptors and rejecters due to different selective pressures (Lotem & Nakamura 1998, Lotem et al. 1992, Lotem et al. 1995, Rohwer & Spaw 1988, Marchetti 1992, Zahavi 1979, Røskaft et al. 1990). One model argues that acceptance of cuckoo eggs in the nest may be the best choice if the cost of resisting parasitism outnumbers the advantages gained (Lotem & Nakamura 1998, Takasu et al. 1993, Røskaft & Moksnes 1998, Røskaft et al. 1990). Furthermore, host fitness is not necessarily reduced to zero due to untimely laying of cuckoo eggs, alternatively, if costs of brood parasitism are sufficiently low it may drive the host to accept parasitic eggs (Røskaft et al. 1990, Kruger 2011). Finally the variation in host reactions may also be explained through different selection pressures in a spatial mosaic structure (Røskaft et al. 2002, Røskaft et al. 2006, Antonov et al. 2006, Antonov et al. 2010).

Performing egg experiments in host nests has been a suitable tool for obtaining a better understanding of the coevolutionary mechanisms in the arms race between brood parasites and their hosts. Many such experiments have therefore been carried out to observe host recognition of foreign eggs (see Davies (2000) and Payne (2005) for summaries). Studies on natural parasitism have also increased over the last decades (Moksnes et al. 2000, Antonov et al. 2006, Antonov et al. 2007, Brooker & Brooker 1996, Øien et al. 1998, Moksnes et al.

1993, Sealy 1995, Moskát & Honza 2002, Moksnes & Røskaft 1987). Most of these studies have been carried out in Europe, America and Australia, and very few in Asia (Japan, Korea and China only) (Nakamura 1990, Nakamura et al. 1998, Andou et al. 2005, Higuchi 1989, Lee & Yoo 2004, Yang et al. 2010). In Africa the first experiments were carried out early in the twentieth century (Swynnerton 1918) but there is still limited information about brood parasitism on this continent, especially regarding cuckoos. However, recently some experimental studies, mostly on weavers, on brood parasitism have been carried out in Africa (Lawes & Kirkman 1996, Jackson 1998, Victoria 1972, Din 1992, Collias 1993, Lahti & Lahti 2002, Noble 1995). There are furthermore some experimental studies on cuckoo finches and their hosts in Africa (Spottiswoode & Stevens 2010).

Concerning Asia ten species of parasitic cuckoos belonging to the family Cuculidae have been recorded in Bangladesh, but so far no experimental study has been undertaken for any of their hosts. In our study area, close to the capital Dhaka, host use by four sympatric cuckoo species, viz. Asian Koel (*Eudynamys scolopacea*), Common Hawk Cuckoo (*Cuculus varius*), Pied Cuckoo (*Clamator jacobinus*) and Indian Cuckoo (*Cuculus micropterus*) has been recorded (Begum et al. subm)

Research on behavioural responses to experimental brood parasitism by different hosts can clarify why some hosts are responsive or susceptible to parasitism while some others are able to recognise and reject the cuckoo eggs or abandon the nest. In light of that, we investigated the responses of ten different potential host species to experimental parasitism with artificial eggs. All these potential host species were Passeriformes; Long-tailed Shrike (*Lanius schach*), Jungle Crow (*Corvus macrorhynchos*), House Crow (*Corvus splendens*), Black-hooded Oriole (*Oriolus xanthornus*), Black Drongo (*Dicrurus macrocercus*), Oriental Magpie Robin (*Copsychus saularis*), Common Myna (*Acridotheres tristis*), Asian Pied Starling (*Gracupica contra*), Red-vented Bulbul (*Pycnonotus cafer*) and Jungle Babbler

(*Turdoides striatus*). Brood parasitism has been recorded in five of these species with a high degree of acceptance of parasitic eggs (Begum et al. subm). They are common breeders in open scrub jungles along with scattered monotypic plantation habitats as well as suburban gardens and orchards. These habitats are frequently visited by the four cuckoo species described above, which are widely distributed throughout Bangladesh although the Pied Cuckoo is a summer visitor only during the breeding season (Begum et al. subm).

The Common Hawk Cuckoo, Pied Cuckoo and Indian Cuckoo laid eggs which showed excellent mimicry with those of their hosts, and they were all accepted. The eggs of Asian Koel showed good mimicry with one host species, but poor mimicry with its two other hosts. In spite of this there was a high degree of acceptance (Begum et al. subm). In a coevolutionary perspective it would be very interesting to see if these host species would show better rejection abilities when confronted with foreign eggs of poorer mimicry. At the same time it is necessary to know more about the discrimination abilities of as many potential host species as possible in the area.

MATERIALS AND METHODS

Study area

The study was conducted in the campus of Jahangirnagar University, 32 km north of Dhaka city located in the central region of Bangladesh (30°16′N, 90°52′E). The 200 hectares study site is consisting of mosaic vegetation (Begum et al. 2011).

Experiments were carried out in 2008, 2009 and 2010. We systematically searched for nests of different potential host species during the breeding season from January until August each year. When nests were found during incubation the eggs were floated using the method of Hays and Lecroy (1971) to estimate the laying date. The nest types were classified as open or in holes.

All hosts occurring in sympatry with the four cuckoo species in the study area were considered for experiments. Such potential hosts were species with nests accessible to a female cuckoo and which also feed their young mostly with invertebrates which is an essential diet for the cuckoo chick growth (Davies & Brooke 1989a), although some of the cuckoos in our study area, like the Asian Koel, have a diet which is basically comprised of fruit (Begum et al. 2011, Payne 2005). Their nestlings however, may feed on bugs (Hemiptera), and various other insects (Ali & Ripley 1989). Eventually some of these potential hosts should have been in a coevolutionary process in which counter-adaptations towards parasitism should have evolved (Moksnes et al. 1990).

Model eggs

Model eggs that were different in colours, but which matched host eggs in size were introduced into host nests. Model eggs were made of synthetic plastic "Crea-Therm", following the procedure of Bartol et al. (2002) and Antonov et al. (2009). We used three colours of the experimental eggs painted with acrylic paint; 1) pale blue 2) dark brown, 3) pure white. Blue and brown model eggs are non-mimetic to the eggs of most hosts used in the experiments. However, eggs of Common Myna, Jungle Babbler and Asian Pied Starling are blue and glossy in texture, thus model eggs being pale blue but not glossy might to some extent mimic the eggs of those hosts. Pure white model eggs with no markings were only used in nests of Black Drongos in addition to blue and brown egg because this species lays eggs of variable colouration. Some of its eggs are pure white and spotless while some are white with blackish or brownish spots (Whistler 1949), thus the white model eggs might to some extent mimic the white eggs of the Black Drongo. Previous studies clearly indicate that hosts respond to real and model eggs in a similar way (e.g. (Davies & Brooke 1989a) and hence the use of model eggs may indicate a natural reaction by the hosts.

Two different egg sizes were used in the experimental treatments. All species except for the House and Jungle Crows were treated with small sized model eggs (±24.96 mm x ±19.29 mm; which is the average size of eggs of the Indian Cuckoo). This size matches the size of the cuckoo eggs which were expected to parasitize these host species. In the House and Jungle Crows we used egg size of the Asian Koel which were larger than those of the other species (±30.60 mm x ±23.10 mm) (Table 1).

In the experiments we followed the general procedures of Moksnes et al. (1990). We found most of the nests during the nest building stage while some were found during the laying period or first day of incubation. The standard procedure was to add the experimental egg on the penultimate or final day of the hosts' own egg laying period. A single experimental egg was added to each active nest without removing any host egg. Eggs were added to the nests throughout the day (0600h – 1800h CST), as there is no evidence that a host's response is related to what time of the day the nest is parasitized (Davies 2000). Each experimental nest was inspected daily to determine whether the model egg was ejected and to detect any damage or disappearance of host eggs. The nest visits continued for six consecutive days and if the model egg remained in the nest after six days and the nest was still active, we considered the egg accepted. The egg was then removed on the sixth day. If the model egg was missing during any of the first five consecutive visits, we considered it ejected. If the nest was unattended, and the eggs were not at all incubated for at least two days while eggs were undamaged but cold, we considered the nest deserted. Each individual nest was used only once in the experiments. This study design was similar to most other studies (cf. (Davies &

Brooke 1989a, Moksnes et al. 1990, Lotem et al. 1992, Marchetti 1992, Stokke et al. 1999, Amundsen et al. 2002, Bártol et al. 2002, Honza & Moskát 2008)).

RESULTS

We experimentally parasitized nests of 10 different potential host species ($N_{E} = 223$) with more than five nests and up to 10 nests for each species and with each colour (Table 1). Rejection of the model egg occurred within 24 hours in rejecter species, such as Black Drongo (in all 44 experiments), Black-hooded Oriole (in all 11 experiments) and in all cases of rejection in Long-tailed Shrikes (15 experiments), while desertion occurred around the fourth day in the Jungle Crow. The model eggs were accepted by different potential hosts in 144 cases out of 223 experimental nests. Hosts accepted the artificial eggs statistically significantly more frequently than they rejected them (Table 1, $\chi^2 = 52.5$, df = 1, N = 223, $P < 0.001$).

Both the blue and brown model eggs were accepted (100 %) by all pairs of Oriental Magpie Robins, Common Mynas, Asian Pied Starlings, Red-vented Bulbuls and Jungle Babblers. Most House Crows (90.9 %) accepted the blue eggs as well as the brown eggs (90.9 %) (Table 1). All Jungle Crow pairs accepted blue model eggs while they deserted all the nests containing brown model eggs, a difference that was statistically significant (Table 1; $\chi^2 = 16.0$, df = 1, N = 17, $P < 0.001$).

All (100 %) experimental eggs introduced to Black-hooded Orioles and Black Drongos were ejected whether they were blue or brown model eggs (Table 1). Furthermore, Black Drongos ejected (100%) the white model eggs (Table 1) in nests where they laid either pure white spotless eggs or white eggs with black or brownish markings.

The Long-tailed Shrike was the only species which did not eject or accept all the eggs at a 100 % rate. The model egg was ejected from 15 (75 %) of the 20 experimentally parasitized nests and accepted in 5 (25 %) of the nests (Table 1). In 4 of the 5 nests where model eggs were accepted the experimental treatment was carried out when the host had laid its penultimate egg. However, in the remaining 15 experiments where the model egg was ejected the experimental treatment was carried out on the day when the host laid its final egg (Fisher's exact probabilities test, df = 1, $P < 0.001$). Model eggs were also ejected more frequently in small clutches (complete clutch size of 3 or 4 eggs; 4 out of 4 experimental eggs ejected), than when clutch size was large (5 or 6 eggs; model egg accepted in 5 out of 16 experiments). In 4 of these cases an additional host egg was found in the nest on the subsequent visit (Fisher's exact probabilities test; df = 1, $P = 0.026$). This indicates that the most important factor for egg rejection was that the clutch was not complete when the experimental egg was added, while clutch size had no effect.

No host eggs were found damaged or lost during rejection in any of the rejecter species, suggesting that all species selectively ejected the non-mimetic model eggs.

DISCUSSION

Jungle Crows, House Crows and Common Mynas are reported to be the most frequently used suitable hosts of the Asian Koel throughout the Indian sub-continent (Wells 1999, Roberts 1991, Davison & Fook 1995). We have discussed their parasitism rates in two other papers (Begum et al. 2011, Begum et al. subm). The present study reveals that such frequently used hosts as well as the Jungle Babbler, which was parasitized by the Common Hawk Cuckoo and Pied Cuckoo (Begum et al. subm) accepted most parasitic model eggs. The Jungle Crow, however, deserted all brown model eggs.

The reason why Common Mynas accepted model eggs may be because of their nesting habits as they are predominantly cavity nesters. The hole nesting habit is widely common in this species which may normally refrain individuals from being parasitized and thus to evolve rejection behaviour. The Common Mynas mostly nest inside the hole of dead tree trunks, wall holes or small building ventilators (Pell & Tidemann 1997, Begum et al. 2011). The urban area comprising open, grassy woodland, with remnant hollow-bearing trees may provide the ideal breeding habitat for the Common Mynas or other hole- nesters as well. However, in these urban habitats there is probably competition for such resources between hole-nesting species, such as the Common Myna, Jungle Myna (*Acridotheres fuscus*), Crimson-breasted Barbet (*Megalaima haemacephala*), Chestnut-tailed Starling (*Sturnas malabaricus*) and Spotted Owlet (*Athene brama*), which are all common breeders in the study area. Because of this competition most of the nests of Common Mynas were located either in building cornices or in the cup-shaped pockets at the junction where coconut or palm fronds meet the trunk. Such nests were easily accessed by Asian Koels. Sometimes Common Mynas are reconstructing large sized old nests of Asian Pied Starlings after they have finished breeding; hence most of the open nests of Common Mynas were parasitized by Asian Koels and no nests in tree cavities were parasitized in our study area (Begum et al. 2011).

Even if Common Mynas accepted all non-mimetic model eggs, nests that are naturally parasitized by the Asian Koel are significantly more often deserted than unparasitized ones (Begum et al. 2011). This reaction could, however, be a host response to the sight of the parasite at the nest (Davies & Brooke 1988, Moksnes et al. 1993, Moksnes et al. 2000) or because it in many cases, suffered from multiple parasitism (Begum et al. 2011).

In our study area, House Crows are also parasitized by Asian Koels (Begum et al. 2011) and the egg mimicry is better in House Crows than in Common Mynas (Begum et al. subm). House Crows accepted all non-mimetic model eggs, while Jungle Crows accepted blue eggs but deserted nests with dark brown model eggs, which seemed more mimetic than the blue eggs. This is difficult to explain, but it could be that dark brown model eggs are easier to discriminate than the pale blue model eggs, or perhaps more likely, that they are never parasitized by blue eggs so they have no experience with such eggs.

It has been discussed whether nest desertion with subsequent re-nesting, as observed in the naturally parasitized Common Mynas (Begum et al. subm), really is a defence mechanism against parasitism or not. Desertion is frequently associated with clutch reduction, which is often caused by the brood parasite itself (Rothstein 1975b, Rothstein 1982a, Rothstein 1982b, Øien et al. 1998), but is also regarded as a real response to parasitism (Moksnes & Røskaft 1992, Moksnes et al. 1991, Antonov et al. 2006). More experimental work is necessary to test whether this really is a defence towards parasitism.

Many species of babblers (*Turdoides spp*) are Pied Cuckoo hosts (Gaston 1976), while the Common Hawk Cuckoo has been recorded to parasitize the Jungle Babbler ((Ali 1969, Prasad et al. 2001) see also (Begum et al. subm)). Although the eggs of Common Hawk and Pied Cuckoos were highly mimetic to the eggs of Jungle Babblers in colour, though size varied a little (Begum et al. subm), Jungle Babblers seem to lack egg recognition abilities towards non-mimetic eggs and have probably not yet developed any defences against cuckoo parasitism. Thus there is a mystery why both cuckoo species have evolved such good mimetic eggs towards this host. Although further studies are necessary to develop at better knowledge and understanding about the lack of egg recognition in the Jungle Babbler, a possible explanation is that the egg appearance of these two cuckoo species has evolved as a response to rejection by other host species (e.g. other babblers) that also are laying blue eggs, and that the Jungle Babbler is a recent host of these two cuckoo species. However, we have observed that a pair of Jungle Babblers completely destroyed their nest after observing a Common Hawk Cuckoo near their nest (own unpubl. obs.). This may be an adaptation towards this cuckoo species. If the Jungle Babbler is a secondary host which was encroached by these two cuckoos after the cuckoos had evolved their mimetic eggs, their only possible defence is to 1) prevent the cuckoo from laying or 2) destroy the nest content after the cuckoo had been laying or 3) evolve chick rejection. Further experiments are necessary to test these three hypotheses.

Potential and suitable hosts like the Black Drongo and the Black-hooded Oriole rejected all model eggs. Black Drongo has been reported as a host of the Indian Cuckoo (Becking 1981, Lowther 2005). The eggs of the parasitic Indian Cuckoo were good mimics of those of Black Drongos (Begum et al. subm). Black Drongos were tolerant and accepted the mimetic cuckoo eggs, but they rejected all non-mimetic model eggs, indicating that they have had a coevolutionary history with cuckoos in Asia. Black-naped Orioles are potential hosts for the Asian Koel (Lowther 2005) and parasitism has also been recorded (Ali & Ripley 1969, Sethi et al. 2006), but not in our study area. However, a potential reason for this lack of parasitized nests could be that Black-hooded Orioles immediately rejected all cuckoo eggs. The Black-hooded Oriole and the Black Drongo can be regarded as grasp ejectors, because in three cases (two nests of Black Drongo and one nest of the Black-hooded Oriole) the model eggs were found within 50 meters from the nest without visual damage (own unpublished observation). These species therefore most probably grasped and ejected the non-mimetic model egg because they always removed only the artificial egg from the nest while all of their own eggs remained in the nest undamaged.

Other hosts like Oriental Magpie Robins and Red-vented Bulbuls may be parasitized by several cuckoo species in the Indian sub-continent (Lowther 2005). These two species accepted all non-mimetic eggs. The reason for why Oriental Magpie Robin accepts may be lack of evolutionary history with cuckoos because it usually nests in tree holes and also in the hole of concrete walls or buildings (Siddique 2008) which keeps parasites away. On the other hand, the Red-vented Bulbul is regarded as suitable and potential host of many species of cuckoos (Lowther 2005). It is therefore still a puzzle why rejection behaviour has not evolved in this species. The reason could be that Bulbuls are not able to eject cuckoo egg from the nest. A similar case has been reported in the Cape Bulbul (*Pycnonotus capensis*) parasitized by Jacobin Cuckoo (*Clamator jacobinus*) (Kruger 2011) and in Carrion Crow (*Corvus corone*) parasitized by Great Spotted Cuckoo (*Clamator glandarius*) where the host has not evolved any defence behaviour (Soler et al. 2001). Further studies are therefore necessary to understand the lack of rejection behaviour in this species and the other species discussed above. Finally The Asian Pied Starling has never been recorded as a host of any parasitic cuckoo, also probably due to their habit of being a hole nester with a very small entrance at one side of the nest. The nest is therefore, inaccessible to cuckoos, and hence it is an unsuitable host species which explains why it accepted all experimental model eggs.

Clutch size of Long-tailed Shrikes varied from 3 to 6 (Whistler 1949). A great proportion of the Long-tailed Shrike individuals rejected the experimental eggs. They accepted the model eggs introduced when the clutch was still incomplete, while they rejected at a rate of almost 100 % when clutches were complete. One reason for this might be that it is easier to detect a new foreign egg in the nest when the host “know” that own egg-laying is terminated. Alternatively, this result suggests that individual females may wait until the clutch is complete, before making rejection decisions (Davies & Brooke 1988). This suggests that some females made rejection or acceptance decisions by comparing number of eggs in the nest and for that reason the females may wait and take their time until the clutch is complete (Marchetti 2000). In many cases, mimicry is an important cue for hosts when rejecting foreign eggs (Stoddard & Stevens 2010). However, it has been observed that in some hosts the egg shape and size seems to be a stronger cue for rejection (Marchetti 1992) than colour or any spotting patterns of parasitic eggs (Stoddard & Stevens 2010). This could be relevant for Long-tailed Shrikes because their eggs are considerably smaller than those of Asian Koels

(Begum et al. 2011). The Long-tailed Shrike is a preferred host of Asian Koels and suffered from multiple parasitism during the host's laying period (Begum et al. 2011), in fact all koel eggs were accepted. In our study area the Long-tailed Shrike has been recorded as a host of the Asian Koel for the first time (Begum et al. 2011). This species does therefore probably not have a long history of parasitic interactions with koels. As a result it might simply be lacking strong defences against parasitism by the Asian Koel as explained for many acceptor hosts of cowbirds (Takasu 1998).

It is important to note that the model eggs rejected by Long-tailed Shrikes were significantly smaller than the eggs of the Asian Koel that were always accepted. A possible explanation may be that Long-tailed Shrikes have difficulties in grasping the comparatively larger cuckoo eggs, but were able to grasp and eject most of the experimental eggs of similar size as their own. When ejecting model eggs they removed in most cases only the artificial egg from the nest while all of their own eggs remained undamaged. It may be that they did not even try to puncture the model egg because they were unable to do so according to the puncture resistance hypothesis (Spaw & Rohwer 1987). For some hosts it is simply difficult to puncture the cuckoo egg (Antonov et al. 2008) or they may fail to reject large eggs because the costs such rejections are too high (Røskaft & Moksnes 1998, Stoddard & Stevens 2010). This may have forced them to accept the cuckoo eggs (Antonov et al. 2009). A theoretical possibility is also that Long-tailed Shrikes have evolved their rejection behaviour against other cuckoo species than the Asian Koel, and then probably towards cuckoos with eggs they could manage to grasp eject. Due to its accessible nest and suitable invertebrate diet for a cuckoo chick, the Long-tailed Shrike can be classified as a suitable host for several cuckoo species such as the Pied Cuckoo and the Common Cuckoo (*Cuculus canorus*) (Baker 1942, Lowther 2005). Only further experiments can help to clarify the evolution of rejection behaviour in the Long-tailed Shrike, and what cuckoo species that are involved in this coevolutionary interactions. On the other hand, there is a theoretical possibility that the Asian Koel might have evolved mafia behaviour (Soler et al. 1995) by punishing rejecting hosts and thereby forcing the shrike to accept. This latter hypothesis, however, needs to be further tested.

In conclusion, the remarkably high rate of acceptance of non-mimetic model eggs among some of the potential hosts like Common Mynas and Jungle Babblers, in our study area might be explained by the existence of a lag in the evolution of rejection responses, which is also suggested for many cowbird hosts (Hosoi & Rothstein 2000, Rothstein 1982a, Rothstein 1990). It may also be that the Common Myna is normally a cavity nester, and thus avoiding parasitism, in most of its breeding range and has therefore not yet evolved rejection behaviour (see (Røskaft et al. 2002, Røskaft et al. 2006)). Furthermore, there is a close resemblance between host and parasitic eggs in the Jungle Babbler so only further experiments might reveal why this species accept non-mimetic eggs. The Black Drongo accepted good mimetic parasitic Indian Cuckoo eggs (Begum et al. subm) but rejected all non mimetic model eggs, which indicates that this species has an evolutionary history with Indian Cuckoos. Most individuals of the Long-tailed Shrike rejected the non-mimetic model eggs. As there are no data on acceptance- and rejection costs in this species, future studies should be concentrated on costs of parasitism and costs of rejection. Experiments should be carried out to unravel which cues are used to recognize parasitic eggs. The acceptance behaviour of Asian Pied Starlings and Oriental Magpie Robins can be explained by their inaccessible and cavity nesting behaviour. However, it is difficult to explain why Red-vented Bulbuls accepted all experimental eggs, and this question also needs further experimental work to achieve a better understanding. Finally, the reason why Jungle Crows deserted brown but not blue model eggs also needs further investigation.

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Table 1. Responses of different hosts to experimental parasitism by blue and brown model eggs; (A = Acceptance, E = Ejection, D = Desertion and R = Rejection; S, Small size eggs; L, Large size eggs; * including 16 out of 16 rejected small white eggs)

Host species	Egg size	blue				brown								Total nests
		A	E	D	R%	A	E	D	R %	A	E	D	R%	N
Long-tailed Shrike	S	2	8	0	80	3	7	0	70	5	15	0	75	20
House Crow	L	10	0	1	9.1	10	1	0	9.1	20	1	1	4.5	22
Jungle Crow	L	9	0	0	0	0	0	7	100	9	0	7	43.8	16
Black-hooded Oriole	S	0	6	0	100	0	5	0	100	0	11	0	100	11
Black Drongo	S	0	11	0	100	0	17	0	100	0	44*	0	100	44
Oriental Magpie Robin	S	10	0	0	0	10	0	0	0	20	0	0	0	20
Common Myna	S	12	0	0	0	10	0	0	0	22	0	0	0	22
Asian Pied Starling	S	11	0	0	0	15	0	0	0	26	0	0	0	26
Red vented Bulbul	S	9	0	0	0	12	0	0	0	21	0	0	0	21
Jungle Babbler	S	12	0	0	0	9	0	0	0	21	0	0	0	21
	Total									**144**	**71**	**8**		**223**

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*

1987	Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids

1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.

1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995 Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995 Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995 Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995 Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995 Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996 Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996 Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996 Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996 Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997 Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997 Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997 Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors
1997 Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997 Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators

1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*

1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts

Rangifer tarandus platyrhynchus

Castor fiber

2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A$_2$ in Monocytes During Atherosclerosis Development
	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania

2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway

2006 Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006 Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006 Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006 Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006 Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006 P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007 Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007 Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007 Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007 Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007 Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007 Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007 Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007 Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania

(Gadus morhua

2008 Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008 Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008 Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania

2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets

2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in *Arabidopsis thaliana*
2011	Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology