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General Research Paper

Ecology and Evolution of Nest Parasitism in Indian Cuckoo

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ABSTRACT

Nest parasitism is a common phenomenon in many species of birds in which a female of one species lays her eggs in the nest of another species to be hatched and cared by the hosts. The nest parasitism evolved initially as a facultative strategy to use the nest of one species which has raised its brood or deserted nests and then further advanced into parasitism. The host species feed on a wide spectra of food resources, especially rich in protein and are insectivores, carnivores or omnivores in contrast to the very restrictive feeding habits of the parasite species. Parasitism cost for the host is often high which favour the evolution of host defence leading to a parallel evolution between adaptation and counter adaptation of host-parasite interaction. The understanding of breeding biology and ecology of nest parasitism provides important information for the population management of host and parasitic species to devise very specialized conservation strategies for the delicate interaction in the quickly evolving environmental scenario.

INTRODUCTION

Nest parasitism technically known as klepto-parasitism or brood parasitism, is a common phenomenon in many species of birds (David 1998) in which, a female lays her eggs in the host nest of different species to be cared by the host species. The host provides all parental care for parasite eggs and nestlings that decreases its own clutch size hatching success, nest success and fledgling success as the consequence of the parasitism (Lack 1968, Payne 1977, Rothstein, 1990).

The brood parasitism emerged first as a facultative strategy to use abandoned nests of host species and then further developed into parasitism (Hamilton & Orians 1965, Payne 1977, Yamauchi 1995). Parasitism cost for the host is often high which favour the evolution of host defences (Davies & Brooke 1989, Soler et al. 1999, Roskaft et al. 2002, Aviles et al. 2004, Moskat 2005) leading to a parallel evolution between adaptation and counter adaptation of host-parasite interactions (Davies & Brooke 1989, Soler et al. 1999).

Although basic information on parasitic birds was initiated in early twentieth century (Becking 1981) but the breeding biology of various birds still needs to be explored further. Studies on nest building, nest lodging sites, nesting height, nest construction material, nest composition, nest morphology, nesting territory and colonial nesting (Ali & Ripley 1987, Hanzak 1971) are of the practical importance in bird conservation biology. All these parameters lay emphasis on protecting and promoting the breeding and feeding habitats for the conservation of birds in their natural domain. The information on various aspects of nest parasitism has been integrated in the form of this review wherein the general nest ecology, feeding habits and breeding biology of host and parasite birds has been integrated and emphasized.

ORIGIN OF NEST PARASITISM

Brood parasitism occurs in over 200 species of birds (Yom-Tov 2001). As an alternative, typical nesting brood parasitism is a flexible life-history strategy in which female of one species lay eggs in the nest of another species. It was hypothesized that the nest parasitism originate when environmental conditions are unfavourable and phenotypic factors limit the ability to breed by typical nesting (Payne 1998). Several studies indicate that many birds prefer abandoned nest instead of making new nests (Erpino 1968, Marks & Yensen 1980, Knight et al. 1982, Becker 1987, Sige & Becker 1990, Xiang et al. 1991, Deng 2002, Prokop 2004, Zhou et al. 2009, Sharma & Sharma 2013). Hamilton & Orians (1965) suggested that brood parasitism could have evolved as a consequence of nest loss during the egg laying period and the physiological need to lay committed eggs would have promoted use of deserted nests of other birds. This further evolved to communal egg laying that involves facultative use of nests built by other cooperative species (Payne 1998). After the accidental cases of facultative nesting, the parasite female starts depending entirely on host females to raise their offspring and enjoy higher lifetime fitness because of the advantages of emancipation from parental care and enhanced lifetime fecundity (Dawkins 1980).

Because the parasite fitness depends on hosts, the parasitism potentially reduces host fitness, but still among birds species evolution favour the nest parasitism. This may be due to the reason that the cost of escape from parasitism was greater than the cost of rearing parasitized broods (De Marsico et al. 2013).

NEST PARASITISM BY PIED CUCKOO (*CLAMATOR JACOBINUS*)

Pied cuckoo (*Clamator jacobinus*) (Fig. 1) revealed nest-parasitism as it infested the common babblers (*Turdoides caudatus*) nest. Other hosts include the Red-vented Bulbul (Osmaston 1916), *Pycnonotus barbatus, P. capensis* (Kruger 2004), *Turdoides fulvus, Turdoides rubiginosus* (Huels 1982), *Lanius collaris, Andropadus importunus, Terpsiphone viridis, Dicrurus adsimilis* (Skead 1962), *Cinclus pallasii* (Ali 1967), *Turdoides affinis* (Legge 1983, Harrrison 1999) and a few other species (Payne 2005, Ali & Ripley 1981, Friedmann 1964).

Babblers build a shallow cup shaped nest in a low and thorny bush at a height of 2 to 4 meters (Gaston 1978). The host feeds on grasshoppers, hairy caterpillars and sometimes berries (Gaston 1976) whereas the parasite diet includes fruits, berries, nectar, figs, seeds and grains (Anthal & Sahi 2013). The dietary requirements of most chicks in birds are protein rich insect larvae. A pied cuckoo chick has been recorded to be fed by jungle babbler (Bates 1938, 1959) and common babbler. Sandun & Perera (2007) observed single pied cuckoo fledgling being fed by a flock of yellow-billed babblers, which also had their own fledglings. The flock feeding habit of the babbler reduces energy demands of the parents and division of labour ensures a good health of the fledging and the host species.

Pied cuckoo's peak breeding season therefore got evolved between February and May (Harrison 1999) whereas the breeding season of common babbler extends from March to August in north India. During the monsoon season i.e., from July onwards, crested cuckoo migrates to the plains of north India and breeds (Vogl et al. 2003, Soler 1990). The insects and their larvae are plenty during rainy season thus maximizing the reproductive success in both host and parasitic species. The babbler lays four eggs of turquoise blue colour. The female crested cuckoo (Fig. 2) lays two eggs by sitting on the rim of the babbler's nest.

Morphologically, the shape and size of the crested cuckoo eggs are identical, but slightly larger in dimensions than those of the common babbler *Turdoides caudatus* or the jungle babbler *Turdoides striata*. The colour of the eggs matches with those of the host, typically turquoise blue. Sandun & Perera (2007) documented that colour pied cuckoo eggs closely resemble those of the yellow-billed babbler.

Eggs are laid hurriedly in the morning in the nest of the host often dropped from while the bird perches on the rim of the nest and over the host eggs often resulting in the cracking of one or more host eggs (Gaston 1976). The males distract the host while the female lays the egg (Payne 2005). Multiple eggs may be laid in the nest of a host and two young cuckoos were found to fledge successfully on several occasions (Gaston 1976).

The babbler hatches these eggs for 11 to 12 days and feed the fledglings of crested cuckoo. These fledglings grow very fast and foster parents give full parental care to these growing birds (Sharma & Sharma 2011).

The cuckoo is unable to fly on its own for long distances,

Fig. 1: Pied Cuckoo (*Clamator jacobinus*) (Sharma and Sharma unpublished work).

Fig. 2: Crested cuckoo (*Clamator jacobinus pica*)revealed nest parasitism as it infested the babblers nest (Sharma & Sharma 2011).

and its gape still appears yellow in colour. However, the yellow-billed babbler fledglings are more active and seemed to grow faster than the cuckoo, causing the foster parents to pay more attention to the cuckoo. The flock of yellow-billed babblers defend the cuckoo from dangers, and babblers feed and train the cuckoo chicks (Sharma & Sharma 2011).

NEST PARASITISM BY ASIAN KOEL OR BLACK CUCKOO (*EUDYNAMYS SCOLOPACEA*)

Instead of constructing its own nest, the Asian koel (*Eudynamys scolopacea*) (Fig. 3) lays eggs in nest of the house crow (*Corvus splendens*). Asian koel also found to parasites jungle crow, *Corvus macrorhynchos* (Lamba 1976, Grimmett et al. 1998, Ali 2002), common myna, *Acridotheres tristis* (Inglis 1908), golden oriole, *Oriolus oriolus* (D' Abreu 1927) and magpie, *Pica rustica* (Harington 1904).

House crows roost communally near human habitations and often over tall trees in the streets (Fig. 4). The preferred roost sites are in well-lit areas with a lot of human activity, close to food sources and in tall trees with dense crowns that are separated from other trees. The roost sites are often enclosed by tall buildings (Kelvin & Sodhi 2002). The host house crows feed largely on refuse around human habitations, small reptiles, and other animals such as insects and other small invertebrates, eggs, nestlings, grain and fruits (Chhangani 2004). Whereas the parasite Asian koel chicks are omnivorous, consuming a variety of insects, caterpillars, eggs and small vertebrates. Adults feed mainly on fruit (Pratt & Thane 1984).

Breeding season of the koel and the crow have evolutionary adjusted in such a manner that survival of chicks is ensured. The house crow breeding season extends from late May to early September. The koel remains cognizant of

Fig. 3: Breeding pair of Koel Cuckoo (*Eudynamys scolopacea*) (Sharma & Sharma unpublished work).

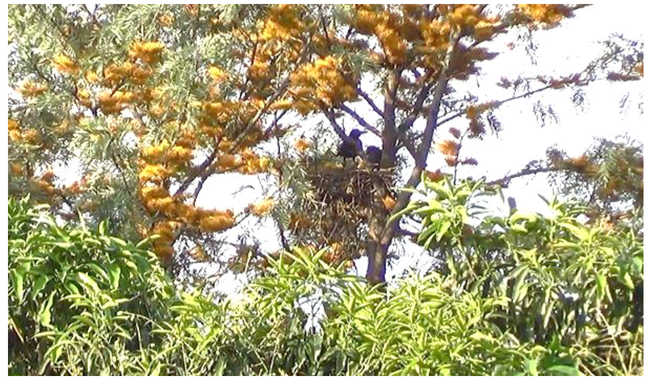

Fig. 4: House Crow (*Corvus splendens*) sitting in their nest (Sharma and Sharma unpublished work).

newly built nests of house crow in the vicinity and takes an early opportunity to lay its eggs in the crow nest (Ali et al. 2007). The koel's eggs resemble in coloration and texture with the host species. The ground colour of the crow eggs presents different shades of bluish green while that of the koel is olive green. Eggs of both host and parasite have similar brown markings in the form of blotches, specks and streaks which are more densely distributed towards the broader end. Although eggs of koel are smaller in size they exhibit remarkable mimicry with crow eggs (Ali et al. 2007).

Lamba (1976) and Ali et al. (2007) reported that no parasitised nest contained more than 3 eggs of cuckoo in a single nest. However, earlier works reported as many as seven (Jacob 1915), eleven (Abdulali 1931) and thirteen (Jones 1916, Baker 1935) eggs of cuckoo in a single nest. The parasite does not lay egg in the nest before the host egg (Ali et al. 2007).

The incubation period is 12-13 days for koel and 16-17 days for the crow. The koel chick emerge 1-4 days before the appearance of the first chick of host. Short incubation period is an advantageous adaptation in the koel. It is koel chicks that emerge earlier and get a better share of food from foster parents. Crow chicks may die of starvation, but koel chicks do not face this problem (Lamba 1963).

Egg fertility in koel is remarkably high and nestling mortality is extremely low. Chicks of cuckoo develop wings earlier, although their weight is quite less than crow chicks and it enables them to successfully fledge out earlier than crow (Ali et al. 2007).

NEST PARASITISM BY INDIAN HAWK CUCKOO (*HIEROCOCCYX VARIUS*)

Himmatsinhji (1980) has reported the brood parasitism by Indian hawk-cuckoo (*Hierococcyx varius*) and established *T. striatus* as favourite host (Ali 1968). *T. affinis*, *T. striatus* and *T. rufescens* species of laughing thrushes are host of Indian hawk-cuckoo.

The babbler builds their nests at a height of 1.53 meters to 5.27 meters on jungle jalabi, mango, neem, *citrus* plants, jamun and *Acacia* species. Grasses, fine twigs and grass blades are used as nesting material. The trees like neem and mango which possess nests at a height of approximately 5 meters having open crown and well exposed branches are parasitized by hawk cuckoo (Sharma & Sharma 2014). Indian hawk-cuckoos feed mainly on insects and are specialized feeders that can handle hairy caterpillars. Caterpillar guts often contain toxins and like many cuckoos they remove the guts by pressing the caterpillar and rubbing it on a branch before swallowing it. The hair is swallowed with the caterpillar and separated in the stomach and regurgitated as a pellet (Payne 2005). The parasite species feed on spiders, cockroaches and other insects, wild figs, berries, grains and nectar of flowers (Ali 1964).

The cuckoos are faster in egg laying and it is believed that egg colour is inherited from maternal genes (Martin 1987). Most of the nests possess two eggs, but one and three eggs containing nests are also observed. The egg colour and size of the cuckoo matches closely to that of the babbler egg. The babblers fail to reject the eggs from the nest as morphologically the eggs are alike (Livesey 1938).

Sharma & Sharma (2014) observed that the parasitized nests contained only one cuckoo chick. Two to three members of babbler flock fed on the fledglings (Fig. 5). The feeding frequency was higher in the morning and evening hours, however, this activity continues for the whole day. The feeding demands of hawk cuckoo were higher as compared to the babbler chicks. Cuckoo chick perched at a height 2 meters to 12 meters. Contrary to the earlier findings cuckoo fledglings were observed even on ground begging for food (Sharma & Sharma 2014).

The size of the Hawk cuckoo chick is larger than the feeding foster parents. It is possibly because of the resemblance with hawk that cuckoo chick is less attacked by the predators like chikra, owl, crows, hawks and squirrels as reported earlier by John Singh et al. (1983).

EVOLUTION OF NEST PARASITISM

Avian brood parasites lay their eggs in the nests of other bird species which pay a fitness cost from raising the parasitic chicks (Rothstein 1990). Parasitism costs for the host are often high because (1) female parasites may remove or damage the host eggs, (2) parasitic chicks may eject all other eggs and chicks from the nest, (3) parasitic chicks may outcompete host nestlings for food, when raised alongside them (Davies et al. 1998, Kilner 2003), and (4) provisioning parasitic nestlings often requires longer and more demanding care than raising the host's own brood (Rothstein 1990). These high fitness costs favour the evolution of host defences such as recognition and ejection of alien eggs and/or mobbing of parasitic females (Davies & Brooke 1989, Soler et al. 1999, Roskaft et al. 2002, Aviles et al. 2004, Moskat 2005).

Behavioural evolution: Males of some cuckoos resemble with the host which help in distraction of host while female laying the eggs (Payne 2005). Cuckoos defend territories against other cuckoos and usually remove a host egg before laying one of their own (Robinson & Rothstein 2001). Cuckoos quickly drop their thick-shelled eggs onto host eggs to increase chances of breaking host eggs. Nestlings of some cuckoos mimic the begging calls or plumage of host young. Against the parasitism the hosts often respond aggressively to cuckoos (Robinson & Rothstein 2001).

Jacobin cuckoo females often lay their eggs by dropping them into the nest, sometimes from over 10 cm height, which is often the only way to lay as the fierce aggression of bulbuls against Jacobin cuckoos near their nests makes egg laying very difficult (Liversidge 1970). However, once the parasitic egg is laid, the rate of egg rejection by the host is very low because the investment in high level of aggression against the Jacobin cuckoo by bulbul might reduce selection in egg rejection (Welbergen & Davies 2009).

Eggs mimicry: Bird eggs vary considerably among females within a species in terms of size, colour and spot patterns (Underwood & Sealy 2002, Kilner 2006). Variability in egg colour and spot pattern facilitate recognition of foreign eggs (Victoria 1972, Freeman 1988, Davies & Brooke 1989a,b). Cuckoo eggs usually mimic their hosts' eggs in contrast to colour, shape, size and dimensions (Robinson & Rothstein 2001) and therefore the host usually fail to reject the para-

Fig. 5: Hawk Cuckoo (*Heirococcyx varius*) fledgling with open beak and begging for food from foster babbler parents. (Sharma & Sharma 2014).

sitic eggs (Livesey 1938).

In case the host recognizes the eggs, it rejects cuckoo eggs through three known mechanisms (Rothstein 1974, Robinson & Rothstein 2001), (1) nest desertion, (2) ejection of the parasitic egg out of the nest, or (3) burial of the egg into the nest material.

Many hosts defend themselves against parasitism by removing foreign eggs from their nest either by grasping the egg whole, or first puncturing the egg and then gripping the broken shell (Davies 2000). The cuckoo has evolved massive eggs (double the size of bulbul eggs) with thick shells, making it very hard or impossible for the host to eject the cuckoo egg (Kruger 2011). Therefore, for some hosts, no other technique will be a suitable than abandoning the parasitized nests (Robinson & Rothstein 2001). Nest desertion seems to be the most workable option for the bulbul host once the cuckoo egg is laid (Servedio & Hauber 2006).

The grasp-ejection is generally prevented when the parasite's egg is too large relative to the host's bill (Rohwer & Spaw 1988, Underwood & Sealy 2006, Rasmussen et al. 2010). Similarly, puncture-ejection is not desirable when the parasite egg's shell is too tough to pierce (Mermoz & Ornelas 2004, Antonov et al. 2009). Facing such constraints, hosts abandon the nest and build a new one or add new nest material to cover over the parasitized clutch (Petit 1991, Guigueno & Sealy 2010, Hosoi & Rothstein 2000), but both of these strategies delay reproduction and do not guarantee that the replacement clutch will escape parasitism (Guigueno & Sealy 2010, Hosoi & Rothstein 2000, Hoover et al. 2006, Kruger 2011).

Operating constraints on egg removal have thus been proposed to play an important role in determining whether or not hosts evolve this defence (Rohwer & Spaw 1988). If the costs of abandoning or burying a parasitized clutch are greater than the costs of rearing parasitized broods, then egg acceptance will be maintained in the evolutionary equilibrium (Rohwer & Spaw 1988, Underwood & Sealy 2006, Petit 1991, Hosoi & Rothstein 2000, Hoover et al. 2006, Kruger 2011, De Marsico et al. 2013). A higher predation and parasitism risk later in the season makes desertion more costly than accepting the cuckoo egg.

Many cases have been reported in which the host fails to reject parasitic eggs, like the case of great spotted cuckoo (*Clamator glandarius*) where one of its hosts, the carrion crow (*Corvus corone*) does not show any defence behaviour and in another case where bulbul host accept the cuckoo eggs. This may be due to reasons that the host may not have been able to eject the alien eggs from the nest and nest desertion being too costly or, alternatively, costs of brood parasitism are sufficiently low to prevent the escalation of the arms race (Canestrari et al. 2009, Soler 1990, Soler et al. 2001).

Nestling and fledgling evolution: Nestlings in most cuckoo species have concave backs that they use to push host nestlings out of nests (Robinson & Rothstein 2001). However, if the host recognizes the parasite chicks, it forcibly pulls the resisting nestlings out of their nests and dump them as reported by Stao et al. (2009). This ejection behaviour is a consequence of the host's ability to discriminate morphological dissimilarity between the odd looking nestling of the cuckoo and that of its own nestlings (Stao et al. 2009). Langmore et al. (2003) suggested that the defence mechanisms at the nestling stage would evolve only after host defence at the egg stage had been breached by the parasite.

CONCLUSION

Brood parasitism raises fascinating questions about co-evolution and conservation. Studies of brood parasitism provides evidence of micro evolution. It is an example of parallel evolution between the adaptations and counter adaptations of the host and parasite species.

Each cuckoo, be it pied/crested cuckoo, koel cuckoo or hawk cuckoo, has its own specific host which may include mainly crows, babblers and bulbuls which serve as foster parents to parasite chicks. The understanding of breeding biology and ecology of nest parasitism provides important information on the biological population regulation of host species which otherwise out number the parasite species. It is worth mentioning the feeding habits of most of the host species are different from parasite species. Thus in nature, energetics of breeding are very specifically regulated.

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