

Reviewing 30 years of studies on the Common Cuckoo: accumulated knowledge and future perspectives

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Abstract In Europe, eggs of the Common Cuckoo (*Cuculus canorus*) have been found in more than 125 different host species. However, very few species are frequently parasitized. The Cuckoo is divided into several distinct races termed gentes. Females of each gens specialize in parasitizing a particular host species. More than 20 such gentes are recognized in Europe. Each female Cuckoo lays eggs of constant appearance. Most gentes can be separated based on their distinct egg types, which in many cases mimic those of their hosts. Different gentes may occur in sympatry or may be separated geographically. Some gentes may occur in restricted parts of the host's distribution area. These patterns raise some fundamental questions like: Why are some passerine species preferred as hosts while others are not? Why does a host population consist of individuals either accepting or rejecting Cuckoo eggs? Why is there marked variation in egg rejection behavior between various host populations? How distinct and host-specialized are Cuckoo gentes? These questions are discussed in relation to existing knowledge and future perspectives.

Keywords brood parasitism, host defense, coevolutionary arms race, Common Cuckoo gentes

Introduction

The Common Cuckoo (*Cuculus canorus*) has a large breeding area across the Eurasian continent from the Atlantic to the Pacific Ocean (Payne, 2005). It breeds throughout China (Yang et al., 2012) and Japan except for the most extreme alpine areas. Especially in Asia it is sympatric with other cuckoo species, but in most of western and central Europe it is the only interspecific brood parasite.

The Common Cuckoo (hereafter Cuckoo) is an obligate interspecific brood parasite laying its eggs in the nest of other bird species, mostly smaller passerines. In Europe, eggs of the Cuckoo have been found in more than 125 different host species. However, the number

of species that are regularly parasitized is much lower (Moksnes and Røskaft, 1995a). Several distinct Cuckoo races termed gentes (e.g. Jourdain, 1925; Baker, 1942; Lack, 1968; Brooke and Davies, 1988) exist, in which females of a particular gens utilize one particular host species. About 20 such gentes are so far recognized in Europe (Alvarez, 1994; Moksnes and Røskaft, 1995a; Antonov et al., 2007). Each female Cuckoo lays eggs of constant appearance (Moksnes et al., 2008), and many gentes can be separated based on their distinct egg types, which in many cases mimic those of their hosts (Chance, 1940; Baker, 1942; Moksnes and Røskaft, 1995a; Davies, 2000). Different gentes may occur in sympatry (Honza et al., 2002; Antonov et al., 2010a; Fossøy et al., 2011) or may be separated geographically (Davies, 2000). Some gentes may occur only in restricted parts of their host's distribution area (Stokke et al., 2007a; Vikan et al., 2010).

Since the Cuckoo chick normally ejects all the host eggs or young from the nest, successful parasitism results in no reproductive success for the host and mis-

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directed parental care (Wyllie, 1981; Øien et al., 1998). This leads to a strong selection pressure among hosts to evolve defense mechanisms against Cuckoo parasitism, of which the most conspicuous behaviors are aggression towards the Cuckoo and recognition and rejection of the Cuckoo egg (Davies and Brooke, 1989a; Moksnes et al., 1991a; Røskaft et al., 2002a). Host rejections of Cuckoo eggs are in most cases carried out by either ejecting the parasite egg from the nest or by abandoning the nest altogether (Moksnes et al., 1991b).

When hosts evolve the ability to reject non-mimetic parasite eggs, individual Cuckoos that lay eggs which hosts cannot recognize (i.e. better mimics) will have a selective advantage (Brooke and Davies, 1988). Evolution of even better egg recognition among hosts may subsequently select for further improvements in Cuckoo egg mimicry with host eggs. Such reciprocal interactions through several stages result in a coevolutionary arms race between parasite and host (Dawkins and Krebs, 1979; Davies and Brooke, 1989b; Rothstein, 1990). During this process individual Cuckoo females specialize on particular host species and the different genotypes mentioned above arise as “egg-mimicry races” (e.g. Chance, 1940; Baker, 1942; Lack, 1968; Gibbs et al., 2000; Antonov et al., 2010a; Fossøy et al., 2011).

Arms race stages may represent many intricate adaptations. For example when the Cuckoo has evolved seemingly perfect egg mimicry with host eggs, the host can respond by evolving more intricate surface patterns on their eggs like a form of “signatures” which make the eggs more difficult to mimic (Davies, 2000). Furthermore, the host may evolve a lower intraclutch variation and a higher interclutch variation in egg appearance (Davies and Brooke, 1989b; Øien et al., 1995; Soler and Møller, 1996; Stokke et al., 2002; Vikan et al., 2010, 2011). Low intraclutch variation will make it easier for hosts to recognize foreign eggs (Stokke et al., 1999) while high interclutch variation will make it more difficult for parasites to mimic the eggs of the host species (Davies and Brooke, 1989b).

It is well known that avian brood parasites have stronger egg shells than those of their hosts (Lack, 1968; Spaw and Rohwer, 1987). This has traditionally been interpreted as a defense against puncture ejection by hosts (the puncture resistance hypothesis, see e.g. Antonov et al., 2006a; Spottiswoode, 2010).

The arms race between Cuckoo and host has hitherto mostly been restricted to the egg stage. However, a future arms race could theoretically also be extended

to the nestling stage where hosts may evolve chick discrimination which in fact has been observed in hosts of three Australian cuckoo species (Langmore et al., 2003; Sato et al., 2010; Tokue and Ueda, 2010; see also Grim, 2007). The parasite’s response to this host defense may be evolution of chick mimicry both in morphology and vocalization. Such traits have evolved among some African whydahs parasitizing indigobirds (Payne 1973a, 1973b, 1976) and also by Australian cuckoo nestlings (Langmore et al., 2008, 2011; Sato et al., 2010).

In this article we present a review of some central results from around 30 years of studies on the Common Cuckoo by the brood parasitism research group at the Department of Biology, Norwegian University of Science and Technology, NTNU, Trondheim, Norway. Our intention is to draw lines through this period showing the development in questions asked and methods used. Questions like “Why are some passerine species preferred as hosts while others are not?”, “Why does a host population consist of individuals either accepting or rejecting Cuckoo eggs?”, “Why is there often a marked variation in parasite egg rejection behavior between various host populations within the same host species” and “How distinct and host-specialized are Cuckoo genotypes?” have been central themes in our research. Finally, we point out some future perspectives in brood parasitism research.

Testing the arms race model

As mentioned above a central question is why the Cuckoo prefers some passerine species as hosts while others are rarely used or not parasitized at all. For example in our study area in Central Norway the Meadow Pipit (*Anthus pratensis*) was the main host with a parasitism rate of 6.4% (Moksnes and Røskaft, 1987) while some other seemingly suitable host species like the Willow Warbler (*Phylloscopus trochilus*) and Blackcap (*Sylvia atricapilla*) were not parasitized (Moksnes and Røskaft, 1992). Different populations of Reed Warblers (*Acrocephalus scirpaceus*) on the European continent showed parasitism rates varying between zero and 21% (Stokke et al., 2007a) and as a final example of this variation it could be mentioned that 34% of the nests of Great Reed Warblers (*Acrocephalus arundinaceus*) in southern Moravia, Czech Republic, was parasitized by the Cuckoo (Kleven et al., 2004).

There are several ecological mechanisms that can contribute to this variation in parasitism rates, but there

are at least four main factors that can be regarded as especially important. First, the stage of the coevolutionary arms race, as described in the introduction, could influence this variation. Host species at early stages in this race will easily accept Cuckoo eggs and therefore establish themselves as favorable hosts contrary to those at later stages where recognition and rejection of foreign eggs are more or less genetically fixed. Second, habitat differences could be important since the Cuckoo normally uses vantage points in trees to locate host nests and observe host activity (Øien et al., 1996; Røskaft et al., 2002c, 2006; Antonov et al., 2010b). Third, host population size and density including fluctuations is of crucial importance for their usefulness as Cuckoo hosts (Stokke et al., 2007a), and fourth, many aspects of the host species' life history traits might represent key factors in both utilization by Cuckoos and evolution of host defenses (e.g. Rutila et al., 2002). For example in Finland the nomadic Brambling (*Fringilla montifringilla*) is parasitized by the Cuckoo while the closely related but site fidelic Chaffinch (*Fringilla coelebs*) is not (Vikan et al., 2010, 2011).

When testing the arms race hypothesis we carried out field experiments where we acted as Cuckoos ourselves (Moksnes et al., 1991a). For this purpose we made artificial Cuckoo eggs from hard plastic. They had the same size and were painted to resemble real Cuckoo eggs found in Meadow Pipit nests. In addition we also made white model eggs. During the experiments we tried to copy the Cuckoo's egg-laying behavior as best we could (Moksnes et al., 1991a). Since the Cuckoo normally removes at least one egg from the nest during laying we exchanged one of the host eggs with a model Cuckoo egg, in each case choosing the color that appeared most non-mimetic compared to the host eggs. Furthermore, to copy Cuckoo behavior the model eggs were preferably inserted in the host's laying period or during early incubation. This experiment was carried out on as many potential Cuckoo host species as possible. Within a limit of six days after the experiment we recorded if the model egg was accepted and incubated or rejected either by ejection or desertion as explained in the introduction (see Moksnes et al., 1991a for details).

Host aggression against Cuckoos was recorded by placing a stuffed Cuckoo dummy close to their nests. In general host individuals showed three types of responses: a) no aggression, b) vigorous mobbing against the dummy from a short distance and c) direct attack with physical contact. Individuals showing responses b) or c)

were classified as aggressive (methodological details in Moksnes et al., 1991a).

When making predictions for this test of the arms race model we classified the potential host species in groups. First we sorted out species with characteristics in their breeding biology that should make it impossible or very difficult for them to raise a Cuckoo nestling. One such category was the hole-nesters like the tits (Paridae) which nests should be inaccessible for the Cuckoo. Even if the parasite should succeed in placing an egg in the nest cavity, the narrow entrance would prevent the young Cuckoo from fledging. Another category consists of species which feed their young with a diet that is indigestible for Cuckoo chicks, for example those feeding their chicks with seeds (e.g. Carduelinae finches). Finally, in those passerine species with sufficiently large nests the newly hatched Cuckoo chick would have problems in ejecting the host eggs or young from the nest. We have classified the thrushes of the genus *Turdus* to belong in this category (Moksnes et al., 1991a; Grim et al., 2011; but see Davies and Brooke 1989a). All these species expected to be unfavorable host for the Cuckoo, were pooled together in a group named "unsuitable hosts", and we expected that they had not experienced any coevolutionary arms race with the Cuckoo. Therefore we predicted that they should not show any antiparasite adaptations, i.e. they should accept non-mimetic model eggs in their nests and show no aggressive behavior against Cuckoo dummies.

The host species assumed to have experienced a coevolutionary arms race with the Cuckoo, were termed "suitable hosts". They were classified into three groups in accordance with their parasitism rate as "most common hosts" (highest rates), "frequently used hosts" (medium rates) and "rare hosts" (lowest rates). Here we predicted that the "most common hosts" should accept a higher proportion of non-mimetic model eggs than the "rare hosts" and also that the former group should show less aggression against stuffed Cuckoos than the latter one. In relation to these two groups the "frequently used hosts" should show an intermediate behavior both in model egg acceptance and aggression (Moksnes et al., 1991a).

The results of the field experiments are shown in Table 1. As predicted the group of unsuitable hosts showed a clear lack of defense behavior against Cuckoo parasitism while the three groups of suitable hosts showed egg rejection abilities and aggression against Cuckoos in accordance with the predictions. The antiparasite

Table 1 Host acceptance of non-mimetic model Cuckoo eggs and host aggression against stuffed Cuckoo dummies at their nests. The number of species tested is shown in parenthesis. For closer details about the species tested, see Moksnes et al. (1991a).

	Median % (<i>n</i>)	
	Acceptance	Aggression
Most common hosts	86 (4)	50 (3)
Frequently used hosts	33 (5)	100 (3)
Rare hosts	10 (9)	100 (8)
Unsuitable hosts	100 (15)	0 (8)

adaptations were most pronounced among the rare hosts where both the egg rejection rate and frequency of aggression were significantly stronger than those of the unsuitable hosts. When comparing all tested species there was also a significant positive correlation between egg rejection rate and aggression against Cuckoos, indicating that both reactions are real antiparasite defense behaviors. In summary, the cumulative results from these studies therefore provide strong support for the arms race model, and the results are in accordance with those obtained by Davies and Brooke (1989a, 1989b) in similar experiments.

Importance of life history traits in suitable Cuckoo hosts

In a case study of how host life history traits can affect parasitism rate, we compared two closely related finches, the Chaffinch and the Brambling. These two species have evolved a strong defense against parasitism both in aggression against Cuckoos and a fine-tuned rejection ability against foreign eggs, including even real conspecific eggs with relatively small deviations in color and spotting pattern compared to host eggs (Vikan et al., 2010, 2011). The Chaffinch is distributed all over Europe except for the northernmost areas and is one of the most common passerines on the continent. Chaffinches typically show pronounced site fidelity to their breeding areas. The northern populations are winter migrants. Chaffinches are rarely parasitized by Cuckoos (Moksnes and Røskoft, 1995a).

Bramblings have a more northern distribution area restricted to Fennoscandia and northern parts of Russia. They are winter migrants but contrary to Chaffinches they do not show site fidelity but are rather nomadic. This is due to an opportunistic breeding strategy for exploitation of favorable but unpredictable resources

for breeding like the temporal outbreaks of caterpillar moths in boreal forests. We have carried out extensive studies of Bramblings at four study sites in Fennoscandia situated at a gradient from 63°N, 12'E to 70°N, 28'E (see Fig. 1 in Vikan et al., 2010) but parasitism by Cuckoos has been recorded only in Kittilä, northern Finland (68°N, 25'E). Here, in a restricted area of the Brambling's breeding range, it was parasitized at a rate of 6% by a distinct Cuckoo gens laying excellent mimics of Brambling eggs. However, rejection behavior, aggression against Cuckoos and egg characteristics were similar in all study areas, indicating a strong gene flow among populations, which also should be expected from the nomadic life of Bramblings (Vikan et al., 2010).

When parasitized by Cuckoos with excellent egg mimicry, there will be a selection pressure on the host to evolve eggs deviating from those of the parasite. Figure 1 in Vikan et al. (2011) shows variation in appearance of Chaffinch and Brambling eggs, in addition to Cuckoo eggs from Brambling nests in Kittilä. The most common ground color of Chaffinch eggs is blue to red-brown while green is rare. In Bramblings it is opposite with green as a common ground color. We used a spectrophotometer to obtain reflectance spectra of the ground color of the eggs (see e.g. Vikan et al., 2010) and analyzed egg colors by applying a tetrahedral color space model (Stoddard and Prum, 2008). These analyses show that the Cuckoo eggs are best matching the most common egg types in Bramblings (Fig. 4 in Vikan et al., 2011). However, the pronounced variation in Brambling egg colors show that this host has a potential for evolving egg colors differing from those of the Cuckoo. This would happen if red and/or blue eggs became more common. Analyses of eggs stored at museums, however, show that the color distribution in both Brambling and Cuckoo eggs has been stable the last 100 years. Furthermore, as mentioned above, the distribution of Brambling egg types was the same also in the study areas where there was no parasitism. This lack of evolution of egg phenotypes "away from the Cuckoo" (Fig. 5 in Vikan et al., 2011) is actually what we should expect from the Brambling's nomadic behavior resulting in a strong gene flow and a very low probability of being parasitized during lifetime due to the restricted occurrence of the corresponding Cuckoo gens.

The site fidelic Chaffinches have, contrary to the Brambling, responded to selection from Cuckoos by evolving a markedly bimodal egg color distribution

(Fig. 4 in Vikan et al., 2011) where red and blue eggs are proportionally more common than in Bramblings. This is most probably a result of previous parasitism that has ended because the Cuckoo has not been able to track the host's evolutionary change in egg colors. It is reasonable to assume that a Chaffinch Cuckoo gens must have been related to the Brambling gens and therefore operated in the northern parts of Fennoscandia. This is supported by the fact that in museum collections there is a greater proportion of red and blue Chaffinch eggs from these northern areas than from South Scandinavia and Britain (Vikan et al., 2011).

An interesting question to ask is if the *Fringilla*-Cuckoo system could have the potential for disruptive selection resulting in evolution of marked egg polymorphism within a Cuckoo gens and its host species. An example of such a system is the Cuckoo and its host, the Ashy-throated Parrotbill (*Paradoxornis alphonsianus*) in China (Yang et al., 2010). However, this would probably require that the *Fringilla* finches evolved an even better egg recognition ability than the present one. For the Chaffinch the explanation could also be that it has beaten the Cuckoo completely before needing to evolve a clearer egg polymorphism.

Why is there variation in rejection rate of Cuckoo eggs between species of suitable hosts?

This question has been much debated and subject to many studies within the field of brood parasitism. It is a very common picture that within a Cuckoo host population some individuals accept and incubate parasite eggs in their nests while others are able to recognize and reject such eggs (Davies and Brooke, 1989a; Moksnes et al., 1991a). This dichotomy has often been described as an apparent "imperfect host behavior".

Several hypotheses, all of which are consistent with the arms race model, have been proposed to explain this phenomenon. These hypotheses have for a long time been subject to thorough analyses in the brood parasitism literature (see e.g. Rothstein and Robinson, 1998; Davies, 2000; Stokke et al., 2005) and will therefore only be briefly described here.

The "evolutionary lag hypothesis" (Davies and Brooke, 1989a; Rothstein, 1990) states that lack of defense behavior is due to the fact that this adaptation has not yet appeared and/or spread in the host population. Lag is therefore often expected to occur in early stages

of an arms race and to persist for longer when selection is weaker (i.e. low parasitism pressure). The complete lack of defense in the Dunnock (*Prunella modularis*) which is regularly parasitized by the Cuckoo, has often been explained by the lag hypothesis (Brooke and Davies, 1988). Lack of defense behavior in many host species of the Brown-headed Cowbird (*Molothrus ater*) in North America has also been explained by evolutionary lag (see e.g. Hosoi and Rothstein, 2000; Peer and Sealy, 2004).

The "evolutionary equilibrium hypothesis" (Lotem et al., 1992, 1995; Lotem and Nakamura, 1998; Takasu, 1998a, 1998b; Rodríguez-Gironés and Lotem, 1999) states that an equilibrium between individuals that reject parasite eggs and those which accept may be established in host populations. The reason for this equilibrium is that hosts have to make a compromise between the cost of parasitism and the cost of making recognition errors (see below). Mathematical modeling has provided some support for the evolutionary equilibrium hypothesis (Takasu, 1998a, 1998b), but all experimental tests must be based on the presumption that recognition errors or other rejection costs exist and can be documented. In hosts of evicting cuckoo species the only real recognition errors happen if rejection behavior is performed in an unparasitized nest by wrongly regarding it as parasitized. Recognition errors in parasitized nests are of less importance because the Cuckoo chick when hatched will evict its nest mates without regard to earlier events. The frequency of such recognition errors among hosts of the Cuckoo is not known, but we have no reason to believe that they occur frequently (Røskaft et al., 2002b; see also Davies and Brooke, 1988). The evolutionary equilibrium hypothesis may possibly have greater relevance for hosts of non-evicting brood parasites like the cowbirds.

The "Spatial habitat structure hypothesis" (Røskaft et al., 2002c, 2006) is based on the assumption that the Cuckoo and other brood parasites which are depending on finding a sufficient number of host nests, need access to suitable vantage points, usually perches in trees, from where they can observe host activities (Alvarez, 1993; Øien et al., 1996; Clotfelter, 1998). This means that hosts breeding near trees in woodland or its edges should have a high probability of being parasitized and therefore will experience a strong selection pressure for evolving defenses like Cuckoo egg rejection. We have mentioned above that several host species with high rejection rates today are not regularly used by the

Cuckoo because they are ahead of the parasite in their coevolutionary arms race (see “rare hosts” in Table 1; all of them breed in forests or near trees). Species breeding in completely open areas, on the other hand, faces a different situation. Even if being suitable Cuckoo hosts they experience no parasitism and have therefore not evolved any defense behavior. A good example is the Skylark (*Alauda arvensis*) (Antonov et al., 2010b).

From the spatial habitat structure hypothesis we can predict that species or single populations that are breeding both near and away from trees will show intermediate rejection rates. This is because parasitized individuals near trees will evolve host defense (rejection) while non-parasitized individuals away from trees will remain acceptors. Due to parasitism the host’s mean fitness will be lower near trees (sinks) which will result in a net gene flow of acceptors from areas away from trees where there are no parasitism and therefore higher mean fitness (sources). Røskaft et al. (2002c) have analyzed data from species breeding both close and far from trees and compared with data from species breeding only near trees, and this study has given support for the hypothesis. The spatial habitat structure hypothesis is also supported by theoretical models (Røskaft et al., 2006).

The three hypotheses mentioned above have been fundamental in explaining many patterns of variation in rejection rate between species. For a better understanding of the whole picture it is, however, necessary with a closer look on the process of decision-making taking place when an individual is faced with a “problem egg”; should it be rejected or not? (Stokke et al., 2005). In our discussion above we have mostly focused on the genetic foundation, but there is also convincing evidence for the importance of external cues which underline the importance of cognitive stimuli and abilities among hosts. We have for example, already in the introduction, when describing the arms race, focused on the intra- and interclutch variation in host egg appearance. In species with relatively high intraclutch variation it might be difficult for the host to identify a foreign egg and there is a high risk of making recognition errors. It is important for the hosts to know the appearance of their own eggs and Lotem et al. (1992, 1995) have proposed that first year breeders obtain this knowledge by going through a prolonged learning process. However, here we will not go further into this topic of egg recognition and learning (see Stokke et al., 2005; Stokke et al., 2007b) but rather focus on external conditional stimuli.

Conditional stimuli. The Cuckoo is well known for its cryptic egg-laying behavior (Wyllie, 1981; Davies, 2000). It lays its egg during the afternoon in the host’s laying period, when the host usually is away from the nest. The visit to the host nest is traditionally described as very short; in about 10 seconds or less it has deposited its own egg and taken one or more host eggs. This behavior indicates that it must be important for the Cuckoo not to be seen by the host. It also indicates that the sight of a Cuckoo near the nest must be an important cue that hosts use to disclose Cuckoo parasitism. In other words, it should be an important conditional stimulus which should lead to an extra careful inspection of the nest content by the host.

To test the relevance of this stimulus we carried out a field experiment in two groups of Meadow Pipit nests. In one group a Meadow Pipit egg was exchanged with a mimetic model Cuckoo egg. In the other group we did the same egg experiment, but in addition we exposed the hosts to a stuffed Cuckoo dummy placed close to the nest. In the group where nests only received a Cuckoo egg, desertion occurred in 5% of the cases, which was the “normal” rejection rate in the study area (Moksnes et al., 1993). But when the pipits in addition to receiving a parasite egg observed the Cuckoo at their nest, as many as 41% of them deserted their nest. Here the Cuckoo obviously functioned as a conditional stimulus leading the pipits to undertake a more careful check for parasitic eggs in their nests. It is worth mentioning that a Cuckoo mount alone at the nest (without egg manipulation) resulted in no nest desertions.

The results of this experiment were in accordance with a similar experiment carried out on Reed Warblers in Britain by Davies and Brooke (1988). Interestingly, some years later we got the opportunity to test these experimental results on Reed Warblers by video recordings of Cuckoo egg-laying in this species in the Czech Republic (Moksnes et al., 2000). In the recordings we could see if the host was present or not during the Cuckoo’s egg-laying, and the results were in accordance with those from the experiments; the warblers which detected the Cuckoo close to their nests rejected significantly more often than those that did not.

It should also be added that these recordings disclosed a Cuckoo behavior quite different from what is usually described in the literature (e.g. Chance, 1940; Wyllie, 1981; Davies, 2000). It seemed that the Cuckoo in several cases did not aim at performing a cryptic behavior at the host nest. When laying it even flushed

a couple of incubating Reed Warblers off the nest, and the duration of its stay at the nest varied between 7 and 158 seconds with a mean of 41.2 ($n = 14$). A common activity during “long” stays was to sit on the nest rim eating host eggs. We have no special explanation of this deviating behavior, or whether it really is deviating or not. The real behavior in nature is often more variable than described in the literature.

In the above discussion on conditional stimuli we mostly focused on variation between individuals. However, phenotypic plasticity in host defenses against Cuckoo parasitism has also been found when comparing different populations (Lindholm, 2000; Lindholm and Thomas, 2000). Reed Warbler populations in sympatry with Cuckoos showed more developed defense behavior than host populations where Cuckoos were absent. But it could not be ruled out that genetic differences between the host populations also could have contributed to varying defense behavior (Lindholm, 2000).

How distinct are Cuckoo gentes and egg morphs?

The Cuckoo gentes, or egg mimicry races, each specializing on different host species have received much attention from ornithologists and researchers (e.g. Jourdain, 1925; Baker, 1942; Lack, 1968; Brooke and Davies, 1988, 1991). As mentioned in the introduction, about 20 such gentes are recognized in Europe of which the blue egg-morph of the gens parasitizing Redstarts (*Phoenicurus phoenicurus*) is one of the most distinct (Moksnes et al., 1995b). The most prevailing and traditional hypothesis to explain the existence of gentes is the “host preference hypothesis” (Chance, 1940; Baker, 1942; Lack, 1968; Wyllie, 1981; Nakamura and Miyazawa, 1997; Davies, 2000; Gibbs et al., 2000; Fossøy et al., 2011). According to this hypothesis egg mimicry is evolved by natural selection due to host rejection of unlike eggs. Furthermore, because the genes coding for egg appearance are thought to be located on the female W-chromosome, females alone control egg color and marking pattern. Finally, female Cuckoo nestlings are imprinted on their foster host species and will return to the same species for egg-laying as adults. However, still no clear evidence exists for this inheritance of egg color and imprinting on hosts (Brooke and Davies, 1991; Gibbs et al., 2000; Fossøy et al., 2011).

In the literature, Cuckoo egg mimicry is often classi-

fied as quite good or even perfect (Baker, 1942; Wyllie, 1981; Davies, 2000). Therefore, we expected to find such a relatively good mimicry when we analyzed around 12000 egg clutches parasitized with Cuckoo egg(s) held in European museum collections (Moksnes and Røskaft, 1995a). However, to our surprise, we recorded a mimicry that was markedly poorer than expected. Only in 5% of the parasitized nests the mimicry was classified as “perfect”. The “correct” egg-morph corresponding to host eggs was found in “only” 44% of the nests. If we also include in the sample nests of other host species which use similar nest sites as the main host, we found 77% of the Cuckoo eggs in their corresponding host plus in host species using similar nest sites (Moksnes and Røskaft, 1995a).

A natural question emerging from these observations was if Cuckoo host selection really could be explained by the “host preference hypothesis”, or if it was necessary that also more habitat-related hypotheses had to be taken into consideration. According to the “nest site hypothesis” introduced by Moksnes and Røskaft (1987, 1995a; see also Edvardsen et al., 2001; Honza et al., 2001) each gens parasitizes a group of host species with similar eggs and nest sites. The almost similar “habitat imprinting hypothesis” (Teuschl et al., 1998) states that adult Cuckoos establish their home range in habitats resembling their natal ones. When searching for nests in such habitats they will have an increased probability of parasitizing the host species by which they were raised. Another similar and not mutually exclusive hypothesis is the “natal philopatry hypothesis” (Brooke and Davies, 1991). According to this hypothesis Cuckoos search for nests at random in their natal habitat. With random searching it could be predicted that host species occurring at the highest densities or have easy-found nests, should have the greatest risk of being parasitized. Because maintenance of Cuckoo egg mimicry requires that most eggs are laid in the nests of one host species, this could happen in homogenous habitats where one or a few host species predominate. In diverse habitats it is unlikely that this hypothesis could explain Cuckoo egg mimicry.

An appropriate way of testing these hypotheses is to look at Cuckoos parasitizing host species living in close sympatry and see how differentiated they are in host preference. We have carried out two such case studies, in Czech Republic and Bulgaria. We studied four sympatric host species in Czech Republic and three in Bulgaria.

Case 1: South Moravia, Czech Republic 1992–1998

Four host species nested in close sympatry in relatively narrow reed beds surrounding several fish ponds (see e.g. Edvardsen et al., 2001; Honza et al., 2002; Kleven et al., 2004). The host species were Reed Warblers, Great Reed Warblers, Marsh Warblers (*Acrocephalus palustris*) and Sedge Warblers (*Acrocephalus schoenobaenus*). All four species were heavily parasitized by the Cuckoo and rejected Cuckoo eggs at an intermediate level (Kleven et al., 2004). However, Cuckoo egg mimicry was not very good (actually moderate to poor) in any of the host species, and Cuckoo eggs from different host species looked quite similar (Edvardsen et al., 2001). This finding was contrary to what can be predicted from the “host preference hypothesis”, that Cuckoo eggs more closely resembled the eggs of their respective host species than eggs of other sympatric hosts. We therefore performed a blind test where test persons were asked to assess the similarity between Cuckoo and host eggs. Although this was the only method available for us at that time, it should be mentioned that avian vision is very different to that of humans, and birds may not see differences and similarities between eggs in the same way as we do (e.g. Cherry and Bennett, 2001; Starling et al., 2006).

From pictures of parasitized clutches we cut out the Cuckoo egg. The test subjects were then asked to compare the Cuckoo egg pictures with pictures of host egg clutches without knowing from which host the Cuckoo egg originated. In addition to host clutches they were also shown pictures of Garden Warbler (*Sylvia borin*) clutches because according to museum collections this was the most common host in the region although not found parasitized in the study area (Edvardsen et al., 2001). The results from the scoring did not support the prediction from the “host preference hypothesis”. The Cuckoo egg samples were not assessed to most closely resemble the eggs of any of their actual hosts (Edvardsen et al., 2001). In fact, the results pointed more in the direction of support to the “nest site/habitat imprinting hypotheses”.

This conclusion was, however, dramatically changed after we had carried out radiotracking of egg-laying Cuckoo females equipped with transmitters. With a few exceptions the general picture was that individual females laid their eggs only in the nests of one host species (Honza et al., 2002). This support for the “host preference hypothesis” was further confirmed by DNA analyses using microsatellite DNA markers showing

that individual females specialized on parasitizing one single host species (Skjelseth et al., 2004). The final conclusion from the studies in the Czech Republic was therefore that Cuckoo genets are host specific even if this specialization has not resulted in evolution of clear egg-mimicry races.

Case 2: northwestern Bulgaria 2005–2012

Our study area consisted mostly of abandoned agricultural land which had developed into a mosaic of pastures, open bushland and large stands of reeds in moist places. There was a scattered occurrence of trees in the whole area. The host species, Marsh Warbler and Great Reed Warbler, nested at high densities preferably in reeds while the Corn Bunting (*Miliaria calandra*) preferred open meadow habitats. However, these three species nested in close vicinity of each other and in partly overlapping habitats, thus justifying to be classified as breeding in close sympatry.

To analyze Cuckoo and host egg phenotypes we used a spectrophotometer to obtain reflectance spectra of the background and spot color of the eggs and we analyzed egg colors by applying a tetrahedral color space model (Stoddard and Prum, 2008). The egg color analyses showed very good Cuckoo egg mimicry with the two *Acrocephalus* warblers. There was especially good accordance in background and spot color hue distribution between Cuckoo and host eggs both for Great Reed Warbler and Marsh Warbler (see Fig. 3 in Antonov et al., 2010a). For Corn Bunting Cuckoos the distribution was clearly different from that of its host both for background color and spots. Corn Bunting Cuckoo eggs were therefore poor mimics of hue in both background and spot color. Because the Corn Bunting also showed poor recognition abilities against foreign conspecific eggs (Antonov et al., 2006b), it seems to be a relatively recent host in the study area, and Corn Bunting Cuckoos have possibly originating from Cuckoos parasitizing *Acrocephalus* warblers (see Fig. 3 in Antonov et al., 2010a). It is also worth mentioning that there was a clear positive significant correlation between egg size in the Cuckoos and their respective three hosts (Fig. 1 in Antonov et al., 2010a). As a conclusion on this study of egg phenotypes it should be stressed that even if Cuckoo egg matching with host eggs was not perfect for all egg features, matching for color patterns and egg size was obvious and has been maintained in close sympatry in spite of the possibility for gene flow.

To confirm if the recorded differences in Cuckoo egg characters represented real host specialization we carried out genetic analyses of Cuckoo chicks from nests of Corn Buntings, Marsh Warblers and Great Reed Warblers (Fossøy et al., 2011). When looking at mitochondrial DNA we used the 411 basepair control region as used by Gibbs et al. (2000). This analysis showed that Marsh Warbler Cuckoos were significantly different from those utilizing Great Reed Warblers and Corn Buntings, but the latter did not differ significantly from Great Reed Warbler Cuckoos (see Table 2 in Fossøy et al., 2011).

When analyzing nuclear DNA we used 13 microsatellite-loci. Interestingly, we found significant genetic differentiation between all the three Cuckoo groups also for biparentally inherited microsatellite markers (Table 2, Fossøy et al., 2011). As far as we know, this is the first time such differences in autosomal chromosomes are documented among Cuckoo host-specific races. This finding has important implications because it indicates that males may also contribute to the evolution and maintenance of different Cuckoo gentes. Hence, it opens for the possibility that the genes responsible for egg phenotype may be located on autosomal chromosomes rather than on the female-specific W-chromosome as traditionally assumed.

These two studies, of egg phenotypes and genetics, generate the conclusion that the Cuckoos parasitizing Marsh Warblers, Great Reed Warblers and Corn Buntings in Bulgaria belong to three distinctly different Cuckoo gentes. So, the final message from Bulgaria is the same as from the Czech Republic: a strong support for the “host preference hypothesis”.

Future perspectives

After the genetic story presented above (Fossøy et al., 2011) it should be unnecessary to stress that further genetic studies are highly needed for understanding the mechanisms in the maintenance of gentes. For a more complete understanding of this question it is also necessary to document if Cuckoo nestlings when reaching adult stage really return to parasitize the host species by which they were raised. Only in one study (Brooke and Davies, 1991) this question has been addressed without reaching any general conclusion. Natal dispersal and philopatry are relevant factors in this respect; do young Cuckoos return to areas where they can parasitize the host species by which they were raised? Use of

advanced satellite transmitters could be a useful tool in solving these questions.

Until now most studies have focused on systems with only one cuckoo species and its hosts. Research on systems with more cuckoo species living in sympatry, represents an exciting scientific challenge (e.g. Brooker and Brooker, 1989; Higuchi, 1998; Begum et al., 2012) which could focus on questions related to competition between sympatric cuckoo species and isolation in time and space. Southeastern Asia, for example China, offers excellent conditions for such studies (Yang et al., 2012). Such perspectives and possibilities represent promising prospects for brood parasite research in the years to come.

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对大杜鹃30多年研究的综述：知识积累和未来展望

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摘要：在欧洲，有超过 125 种宿主鸟类的巢里都发现有大杜鹃 (*Cuculus canorus*) 的卵，但其实常被大杜鹃寄生和利用的宿主种类并不多。寄生不同宿主的大杜鹃可分成显著不同的宿主专一类群 (*gentes*)，迄今欧洲已有超过 20 种宿主专一类群被报道。每一类群的大杜鹃雌鸟所产的卵的颜色和卵形 (如斑点) 都较为一致，并专门寄生某一特定的宿主鸟。宿主专一类群可同域出现，也可因为地理隔离而不同，甚至仅局限于宿主分布区的某一区域。不同的宿主专一类群可通过卵的不同而加以区分，在大多数情况下，每一宿主专一类群的卵都模拟其寄生的宿主的卵。为什么一些雀形目鸟类被寄生，而另一些却不被利用？为什么同一宿主种群内一些个体能识别和拒绝杜鹃卵，而另一些个体却接受？为什么同一宿主鸟的不同地理种群对杜鹃卵的识别和拒绝变化很大？大杜鹃不同的宿主专一类群之间的差异到底有多大？本文根据目前已有的知识探讨了这些问题，并对未来的研究进行了展望。

关键词：巢寄生，宿主防御行为，协同进化的军备竞赛，大杜鹃宿主专一类群