Coevolutionary adaptations in avian brood parasites and their hosts

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Preface

Back in 1995 I listened carefully as Arne Moksnes presented an available cuckoo study to new MSc students in the auditory at NTNU, Rosenborg. I was immediately fascinated and went to visit Arne the same day to tell him about my interest in the topic. Soon after, I started planning how to carry out the study together with my two supervisors Arne Moksnes and Eivin Røskaft, and I have never since regretted that I chose to get involved in the "cuckoo-project". I want to thank both of them for an extremely well done job as supervisors, and we have also become very good colleagues and friends.

Geir Rudolfsen has helped me in my fieldwork during the whole period, and a better friend and assistant is hard to imagine. I also want to thank Oddmund Kleven for a great time in the Czech Republic and for valuable scientific discussions. I am indebted to our Czech collaborator Marcel Honza who has participated as a co-author in four of the five papers included in this thesis, and who also obtained permissions to carry out the fieldwork in the Czech Republic. Many thanks are also due to Per Harald Olsen who has helped me a lot in matters like production of artificial eggs and making of posters.

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I am grateful to the Nord-Trøndelag County Governor's environment department for permission to carry out investigations in nature reserves, and to all the landowners that kindly gave permission to do fieldwork on their properties.

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During my PhD-study I have shared office with Ingveig Langseth, Tonette Røstelien, Kristian Overskaug, John Odden and Henrik Jensen. Thanks to all of you for many cheerful moments.

Finally, I want to thank the staff and students at the Department of Zoology at NTNU for a great time during these three years; you have made my period as a PhD student a memorable time!

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II. Stokke, B.G., Moksnes, A., Røskaft, E., Rudolfsen, G. & Honza, M. (1999). Rejection of artificial cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among reed warblers (*Acrocephalus scirpaceus*). *Proc. R. Soc. Lond. B* **266,** 1483-1488.

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IV. Stokke, B.G., Honza, M., Moksnes, A., Røskaft, E. & Rudolfsen, G. (In review). Costs associated with recognition and rejection of parasitic eggs in two European passerines. Submitted *Behaviour.*

V. Røskaft, E., Moksnes, A., Stokke, B.G., Moskát, C. & Honza, M. (In press). The spatial habitat structure of host populations explains the pattern of rejection behaviour in hosts and parasitic adaptations in cuckoos. *Behav. Ecol.* **xx,** xxx-xxx.

Sammendrag

Dette prosjektet har satt søkelyset på to problemstillinger knyttet til samevolusjonen mellom parasitt og vert; 1) utvikling av vertstilpasninger som mottrekk mot tilpasninger hos parasitten, med spesiell fokus på eggtilpasninger, og 2) mekanismer som kan forklare den store variasjonen i forsvarsatferd mot kullparasittisme blant ulike verter.

1) Flere gjøk- (*Cuculus canorus*) stammer eller gentes har utviklet egg som er veldig like vertens egne egg, såkalt eggmimikry, for å vanskeliggjøre vertenes eggavvisning. For å svare på dette har mange verter på sin side gjort det vanskeligere for parasitten ved å utvikle en lavere variasjon i utseende mellom sine egg innen kullet (innenkull-variasjon), og en høyere variasjon mellom egg fra kull til kull (mellomkull-variasjon). Mange nordamerikanske spurvefugler blir benyttet som verter av brunhodetrupialen (*Molothrus ater*), men denne parasitten har ikke utviklet eggmimikry i forhold til vertseggene. Vi sammenlignet kullvariasjonen mellom spurvefugler i Europa og Nord-Amerika og fant en høyere innenkull-variasjon og en lavere mellomkull-variasjon i eggutseende hos nordamerikanske spurvefugler, selv om forskjellen i innenkull-variasjon mellom kontinentene var mindre enn forventet. Hos europeiske spurvefugler er det i tidligere eksperimenter funnet at det er en sammenheng som forventet mellom avvisningsraten overfor parasittiske ikke-mimikry egg og kullvariasjonen i eggutseende. Vi fant at det ikke var noen slik sammenheng hos spurvefugler i Nord-Amerika. Resultatene gir støtte til hypotesen om at parasitter med eggmimikry utøver et betydelig seleksjonstrykk for utvikling av bestemte eggkarakterer hos sine verter.

Vi undersøkte om det var noen forskjell i innenkull-variasjon hos avvisere og akseptorer av parasittegg innen bestemte populasjoner av tre europeiske spurvefugler; rørsanger (*Acrocephalus scirpaceus*), bokfink (*Fringilla coelebs*) og munk (*Sylvia atricapilla*). Det ble funnet at det var en signifikant forskjell i innenkull-variasjon i eggutseende mellom avvisere og akseptorer av kunstige ikke-mimikry gjøkegg i en rørsanger-populasjon i Tsjekkia; avviserne hadde en lavere innenkull variasjon enn akseptorer av slike egg. Denne vertspopulasjonen har en intermediær avvisningsrate overfor ikke-mimikry egg. Et tilsvarende forsøk ble utført hos en bokfink-populasjon i Norge og en munk-populasjon i Tsjekkia. Begge artene er meget gode avvisere av ikke-mimikry egg, noe som indikerer at de aller fleste individer er i stand til å avvise

slike egg. Vi valgte derfor å benytte egg fra artsfrender i forsøkene med disse artene. I motsetning til hos rørsangeren fant vi at det ikke var noen forskjell i innenkull-variasjon mellom akseptorer og avvisere av fremmede egg hos bokfink og munk. Hos begge artene ble det funnet at avvisningen av fremmede egg i stor grad avhenger av kontrasten (grad av mimikry) mellom egne egg og parasittegget. Dette viser at selv om individene er i stand til å avvise parasittegg, så finnes det kognitive begrensninger som medfører at egg som utseendemessig ligger under en viss terskelverdi med hensyn til likhet med egne egg vil bli akseptert. Det ble ikke funnet noen indikasjoner på at avvisningsatferden var avhengig av vertenes alder eller av kondisjonelle stimuli for noen av de tre artene. Dette kan tyde på at det er en genetisk basert kobling mellom det å kunne gjenkjenne fremmede egg og innenkull-variasjon.

2) Mange vertsarter viser ingen eller kun intermediære avvisningsrater overfor fremmede ikke-mimikry egg. En slik tilsynelatende suboptimal atferd kan skyldes at det er kostnader forbundet med avvisningen som forhindrer evolusjon av perfekt avvisningsatferd. Slike kostnader kan være feilaktig avvisning av egne egg i uparasitterte reir (gjenkjenningsfeil), eller avvisning av egne egg i tillegg til parasittegget i parasitterte reir (avvisningskostnader). Hos gjøkverter, som ved suksessfull gjøkparasittisme har en reproduktiv suksess tilnærmet lik null, vil kun gjenkjenningsfeil være kilde til et potensielt seleksjonstrykk mot utvikling av høy avvisning av fremmede egg. Vi undersøkte om slike kostnader forekommer hos bokfink og munk; to arter som antas å ha blitt benyttet av gjøken tidligere, men som i dag ikke blir regelmessig parasittert. På grunn av at avvisningsatferden opprettholdes i fravær av parasittisme, forventet vi at disse artene begår få gjenkjenningsfeil. Undersøkelsen gav støtte til denne prediksjonen; avvisningskostnader i parasitterte reir var relativt høye, men gjenkjenningsfeil i uparasitterte reir var meget sjeldent forekommende.

En hypotese ("spatiell habitat-struktur hypotesen") basert på metapopulasjons-dynamikk og med vekt på karakteristikker vedrørende vertsartenes hekkebiotop ble framsatt for å forklare de store variasjonene i avvisning hos europeiske spurvefugler. Hypotesen bygger på at gjøken benytter de verter som hekker nær utkikkspunkter for parasitten, dvs. nær trær. Arter som hekker både nær og langt fra trær er de beste gjøkvertene, i og med at genflyt fra uparasitterte populasjoner vil forhindre utvikling av perfekt avvisning i parasitterte populasjoner. Arter som alltid hekker nær trær har høye avvisningsrater fordi få eller ingen populasjoner har unnsluppet parasittering, og det har derfor vært sterk seleksjon for utvikling av vertsforsvar. Data for gjøkverter i Europa gav god støtte til hypotesen. Grad av parasitt eggmimikry og parasitteringsrater er høyest hos de vertsarter som kan hekke både langt fra trær og nær trær, noe som tyder på at gjøken har størst suksess hos slike arter.

Abstract

This thesis deals with two topics in the coevolution between brood parasites and their hosts: 1) evolution of host adaptations against parasite egg mimicry, and 2) sources that could explain the considerable variation in rejection behaviour found among various passerines.

1) Several common cuckoo (*Cuculus canorus*) tribes or gentes in Europe have evolved eggs that are remarkably similar to the host eggs in both size and appearance (i.e. egg mimicry). To counter this adaptation in the parasite, hosts can produce eggs with similar appearance within clutches (low intraclutch variation) as well as eggs with diverging appearance between different clutches (high interclutch variation). Many North American passerines are utilised as hosts by the brown-headed cowbird (*Molothrus ater*). However, this parasite generally lays non-mimetic eggs. As predicted, we found that European passerines had a lower intraclutch variation and a higher interclutch variation in egg appearance than North American passerines. However, the difference in intraclutch variation between the continents was less than expected. A relationship has previously been found among European passerines between the rejection rate of non-mimetic eggs and clutch variation in egg appearance, and this is thought to reflect the stage in the coevolution between parasite and host. We found no evidence of such patterns among North American species. These results provide support for the hypothesis that specific host clutch variation is a counteradaptation against parasite egg mimicry.

We investigated whether there was any difference in clutch variation between acceptors and rejecters of parasitic eggs within populations of three European passerines; reed warblers (*Acrocephalus scirpaceus*), chaffinches (*Fringilla coelebs*), and blackcaps (*Sylvia atricapilla*). In a Czech reed warbler population with an intermediate rejection rate of non-mimetic cuckoo eggs, it was found that rejecters had a statistically significant lower intraclutch variation than acceptors of such eggs. Age or conditional stimuli did not seem to have any influence on the rejection behaviour. A similar experiment was carried out in a Norwegian chaffinch population and a Czech blackcap population, which, however, were experimentally parasitised with foreign conspecific eggs because they are both very good rejecters of non-mimetic parasitic eggs. We found no difference in intraclutch variation among acceptors and rejecters of foreign eggs in chaffinches and blackcaps. However, it was

found that the rejection of conspecific eggs greatly depends upon the contrast (i.e. mimicry) between the parasitic and their own eggs. It therefore seems that even though individuals have the ability to reject foreign eggs, limitations in their cognitive system entails that parasitic eggs that are too similar to the host eggs will be accepted. We also looked for potential effects of age on rejection behaviour and intraclutch variation, but no relationship between these variables was found. The results indicate that in these three species both rejection behaviour and clutch variation are more or less innate features, and also that there is a genetically based linkage between recognition of odd eggs and intraclutch variation in egg appearance.

2) Many hosts of brood parasites show no or only intermediate rejection rates of foreign non-mimetic eggs. Evolution of proper rejection behaviour could be prevented by costs related to egg rejection. Important in this respect are erroneous rejection of their own eggs in non-parasitised nests (recognition errors) and rejection of their own eggs in addition to the parasitic egg in parasitised clutches (rejection costs). Because successful cuckoo parasitism usually is detrimental to the breeding success of the host, only recognition errors are believed to be important as an opposing selective pressure against proper host defence in cuckoo hosts. We examined whether such costs exist in chaffinches and blackcaps. These species maintain a high rejection rate of foreign eggs, even though they are not currently used as hosts by the cuckoo. We therefore predicted that recognition errors should be absent or at least rare in these species. We found support for this prediction; rejection costs were relatively high but recognition errors were at best rare events.

In another investigation, we proposed a hypothesis (the "spatial habitat structure hypothesis") based upon metapopulation dynamics and characteristics concerning host breeding habitats to explain the variation in rejection behaviour found among European passerines. This hypothesis is based upon the fact that the cuckoo, as well as other avian brood parasites, needs access to vantage points in trees to monitor host nests, and thus only species breeding near trees are available as hosts. Our results were very much in accordance with this hypothesis. Species that breed both near and far away from trees are the best cuckoo hosts, because gene flow from non-parasitised populations breeding far from trees will prevent the evolution of proper rejection behaviour in parasitised populations breeding near trees. However, species that always breed near trees have high rejection rates because the majority of the populations have been utilised as hosts, and thus there has been a strong selection for the evolution of host defences. Furthermore, the level of parasite egg mimicry and the level of parasitism was found to be highest among hosts breeding both near and far away from trees, indicating that the cuckoo is most successful when utilising such species as hosts.

Introduction

Avian brood parasitism

Coevolution is defined as specialised relationships between species that leads to a reciprocal evolutionary change (Janzen 1980, Thompson 1994). Such interactions have intrigued researchers since the publication of Charles Darwin's "The origin of species" (1859). One of the most suitable model systems for studying coevolution is the interaction between avian brood parasites and their hosts (Rothstein & Robinson 1998). Brood parasitism can occur between individuals of the same species (intraspecific or conspecific brood parasitism, CBP), or between individuals of different species (interspecific brood parasitism, IBP). CBP occurs especially in colony-breeding birds and species with precocial young, and has been documented in 236 (2.4%) (Rohwer & Freeman 1989, Yom-Tov 1980, 2001) of 9672 bird species (Sibley & Monroe 1990). Recently, new molecular techniques have been developed for revealing CBP (Andersson & Åhlund 2001), and the number of species in which such parasitism occurs is expected to increase as more studies are carried out. IBP has evolved independently 5-7 times, and is found in several distantly related taxa (Hughes 1996, 2000, Payne 1997). In general, CBP is hypothesised to be the precursor of IBP (Hamilton & Orians 1965, Payne 1977, Yamauchi 1993, 1995, Cichón 1996, Robert & Sorci 2001). In detailed field studies on two North American ducks (*Anatidae*), Sorenson (1998) showed a possible route in which CBP can lead to IBP. However, IBP could also evolve directly by parasite exploitation of smaller species with a longer incubation period (Slagsvold 1998). In contrast to CBP, obligate IBP occurs almost exclusively among altricial birds (Lyon & Eadie 1991). The only exception is the black-headed duck (*Heteronetta atricapilla*) (Weller 1968, Mallory 2000). Even though there are about 100 species of obligate avian brood parasites (Payne 1977, Johnsgard 1997, Davies 2000), only a few of these have been thoroughly studied. Among the best-studied brood parasites are the common cuckoo (*Cuculus canorus*) and the great spotted cuckoo (*Clamator glandarius*) in Europe, and the brown-headed cowbird (*Molothrus ater*) in North America.

Costs of parasitism

The costs inflicted on the hosts as well as the benefits for parasites are basically the same in both intraspecific and interspecific brood parasitism (Petrie & Møller 1991, Power 1998). Hosts suffer costs related to egg loss, misdirected parental care and overcrowding. However, in some cases, hosts of conspecific parasites may in fact receive some benefit from being parasitised through kin selection accompanied by an increase in the inclusive fitness of the host (Andersson 1984, Andersson & Åhlund 2000, Lyon & Eadie 2000). In any case, the costs associated with interspecific brood parasitism generally exceed those related to intraspecific brood parasitism, and are in many cases severe. Thus, in common cuckoos the parasitic chick ejects all the eggs and young of the host so that it becomes the sole occupant of the nest (Wyllie 1981). Cowbird chicks, on the other hand, generally grow up together with the young of the hosts (but see Dearborn 1996), but often outcompete these because of earlier hatching which results in a size advantage, especially in small hosts (Payne 1997, Rothstein & Robinson 1998).

In addition to costs in current reproduction, hosts may suffer costs in terms of lowered future survival and reproduction (trade-offs in life history theory, Stearns 1992), but no efforts have so far been made to measure such costs (Rothstein & Robinson 1998, Winfree 1999). However, it has recently been shown that increased egg production in one breeding season (e.g. due to abandonment and relaying after being parasitised) is costly, and may severely reduce future fitness in birds (Nager et al. 2001, Visser & Lessells 2001).

Coevolutionary adaptations and counteradaptations

Due to the costs inflicted upon hosts by the brood parasite, there will be a strong selection favouring evolution of host defences. The parasite, on the other hand, will reply by evolving more sophisticated trickery. This coevolution between brood parasites and their hosts has led to a variety of adaptations on both sides, and has traditionally been described as an evolutionary arms race (Dawkins & Krebs 1979, Rothstein 1990). This arms race and the various adaptations and counteradaptations in parasites and hosts can best be described as containing several stages (Davies & Brooke 1989b), as summarised below:

1). Host rejection and evolution of cuckoo egg mimicry

When brood parasites first start to parasitise new host species with no prior history of such interactions, the hosts will accept the parasitic eggs regardless of the degree of mimicry (i.e. resemblance) between host and parasitic eggs. As an example of such a scenario, azure-winged magpies (*Cyanopica cyana*) in Japan accepted non-mimetic cuckoo eggs when the population was first parasitised a few decades ago (Yamagishi & Fujioka 1986, Nakamura 1990). However, because the population suffered high levels of parasitism, the rejection behaviour soon changed and a higher proportion of rejecters of such eggs was found (Nakamura et al. 1998). In addition, species that are generally considered unsuitable as hosts for brood parasites (e.g. seed eaters and hole nesters) also mainly accept non-mimetic eggs (Davies & Brooke 1989b, Moksnes et al. 1990). The brown-headed cowbird in North America is a generalist brood parasite (Gibbs et al. 1997, Alderson et al. 1999, Hahn et al. 1999) that has expanded its range dramatically during the last few centuries (Mayfield 1965). Many of its hosts accept non-mimetic parasitic eggs, probably because they have only recently been utilised as cowbird hosts (Rothstein 1990, Hosoi & Rothstein 2000).

Due to the negative effect on host reproduction, there will be a selection in hosts for evolving rejection of parasitic eggs. The rate of spread of such behaviour will depend upon genetic predisposition, metapopulation dynamics, the costs of parasitism and rejection, and the level of parasitism (e.g. Kelly 1987, Davies & Brooke 1989b, Takasu et al. 1993, Lotem & Nakamura 1998, Martinez et al. 1999). The arms race between the cuckoo and its hosts can lead to differences in coevolved traits among populations of a single host species. Thus, the rejection rate of great spotted cuckoo eggs among their magpie (*Pica pica*) hosts varies among populations depending on the level of parasitism (Soler & Møller 1990, Soler et al. 1999), and has increased in southern parts of Spain in the last decades (Soler et al. 1994). Davies & Brooke (1989a) found that non-parasitised pied wagtails (*Motacilla alba*) and meadow pipits (*Anthus pratensis*) in Iceland showed less discrimination against foreign eggs than did parasitised conspecifics in Britain. Such differences in rejection behaviour among various host populations have also been found in other studies (e.g. Briskie et al. 1992, Sealy 1996, Lindholm & Thomas 2000).

When hosts start to reject non-mimetic parasitic eggs, parasites laying mimetic eggs will have a selective advantage (Brooke & Davies 1988, see also Peer et al. 2000). The rate of spread of mimetic eggs in the parasite population is expected to be faster than the spread of rejection behaviour in the host population, because every cuckoo encounters a host, while only a few hosts encounters the parasite ("the rare enemy effect"; Dawkins & Krebs 1979). The cuckoo will therefore usually be one step ahead in the arms race with its hosts (Kelly 1987). However, it is important to note that if the level of parasitism is high the hosts may evolve counteradaptations quite rapidly and perhaps drive the parasite to extinction before it has evolved proper countermeasures (see below). Takasu et al. (1993) modelled the population dynamics of cuckoo-host interactions based upon population genetics, and found that hosts in high abundance (denoting carrying capacity) and with exposed nests (denoting risk of parasitism) should evolve defences most rapidly.

2). Various theoretical outcomes of the arms race

a). With a high level of parasitism, the host population may become extinct before it evolves a proper defence (May & Robinson 1985).

b). The host could evolve rejection of eggs with relatively good mimicry. Theoretically, there can be three possible outcomes of this arms race:

i). The parasite may switch to a new host that accepts non-mimetic eggs (Davies & Brooke 1989a, Moksnes et al. 1990).

ii). The parasitic egg mimicry may evolve to be a perfect match of the host eggs. Thus, parasite gentes or tribes may arise, which specialise on one or a few host species (Jourdain 1925, Chance 1940, Baker 1942, Lack 1968, Gibbs et al. 2000). The common cuckoo in Europe can be classified into at least 16 such gentes (Wyllie 1981, Alvarez 1994, Moksnes & Røskaft 1995). As the mimicry becomes more common, the increase in host rejection rates may slow down and perhaps stall completely if mimicry reaches fixation (i.e. rejecters have the same fitness as acceptors; Kelly 1987, Rothstein 1990, Davies & Brooke 1998). However, a host counteradaptation at this stage could be to evolve eggs with a more intricate surface pattern (i.e. signatures, see Davies 2000), so that it is harder for the parasite to mimic its eggs. Alternatively, the hosts can evolve a lower intraclutch variation and/or a higher interclutch variation in egg appearance (Swynnerton 1918, Victoria 1972, Rothstein 1974, Davies & Brooke 1989b, Øien et al. 1995, Soler & Møller 1996, Rodríguez-Gironés & Lotem 1999, Marchetti 2000). The low intraclutch variation makes it easier for the hosts to detect and reject foreign eggs, whereas a high interclutch variation makes it more difficult for parasites to mimic the eggs of a specific host (Davies & Brooke 1989b). It is hypothesised that parasitism will first select for an evolution of a low intraclutch variation because it would then be easier for hosts to recognise their own eggs as well as detect the parasitic egg. The increasing interclutch variation would thus be a consequence of the reduced intraclutch variation (Soler & Møller 1996). At this point, it should be mentioned that in some birds (e.g. *Ploceus* weavers), intraspecific brood parasitism probably is responsible for the evolution of a low intra- and high interclutch variation (e.g. Victoria 1972, Freeman 1988, Møller & Petrie 1991, Jackson 1992a, 1998).

iii). A parasite gens can become extinct if the corresponding host population is becoming rare, or if it evolves strong discrimination against parasitic eggs. Many European passerines show strong specific aggression when confronted with adult cuckoos near their nest (Moksnes et al. 1990, Duckworth 1991, Braa et al. 1992, Røskaft et al. in review), as well as strong discrimination against foreign eggs (Moksnes et al. 1990, Moksnes & Røskaft 1992) even though many of them are not regularly parasitised at present.

A loss of host rejection behaviour in the absence of parasitism (e.g. Cruz & Wiley 1989) assumes that there is a cost connected with the maintenance of such behaviour, for example erroneous rejection of own eggs in the absence of parasitism (Marchetti 1992, Brooke et al. 1998). If there are few costs involved, the loss of "rejecter alleles" will be slow (Davies & Brooke 1988, Takasu et al. 1993). Alternatively, the rejection behaviour could be lost due to random genetic drift. However, it is also important to take into account factors that could select for the maintenance of rejection behaviour in hosts besides obligate parasitism, such as intraspecific brood parasitism (e.g. Freeman 1988, Rothstein 1990, Jackson 1992a, b).

Imperfect host behaviour; lag, equilibrium or other explanations?

Many hosts of brood parasites show no or only intermediate levels of rejection of foreign non-mimetic eggs (e.g. Rothstein 1975a, 1990, Von Haartman 1981, Davies & Brooke 1989a, Moksnes et al. 1990, Brooke et al. 1998, Alvarez 1999). Several hypotheses have been proposed to explain this phenomenon. According to the "evolutionary lag hypothesis", a lack of proper defences against parasitism is due to a time lag in the origin and spread of anti-parasite adaptations (Rothstein 1975b, 1990, Dawkins & Krebs 1979, Davies & Brooke 1989a, Lotem & Rothstein 1995). Thus, lag is more likely to explain lack of defences in young parasite-host systems than in systems where parasites and hosts have coexisted for a long time (Rothstein & Robinson 1998, Winfree 1999). Many hosts of the brown-headed cowbird are acceptors of non-mimetic eggs (Rothstein 1990). This parasite is a relatively young species compared with the common cuckoo, and in addition many new hosts have become available in the last few centuries due to anthropogenically induced habitat changes (Rothstein & Robinson 1998). Some hosts of the common cuckoo also show no or only moderate rejection of non-mimetic eggs, even though they are quite heavily parasitised. The dunnock (*Prunella modularis*) is an example of such a species, and the lack of defences against parasitism could be explained by the lag hypothesis (Brooke & Davies 1988).

An alternative hypothesis is the "evolutionary equilibrium hypothesis", stating that acceptance of parasitic eggs is a result of a balance between various opposing selective pressures (Zahavi 1979, Rohwer & Spaw 1988, Petit 1991, Lotem et al. 1992, 1995, Takasu et al. 1993, Lotem & Nakamura 1998, Takasu 1998a, b). Rejection costs and recognition errors are especially important in this respect (Lotem & Nakamura 1998). Rejection costs are accidental loss of their own eggs when rejecting parasitic eggs, whereas recognition errors are erroneous rejection of their own eggs when not parasitised (Lotem et al. 1995, Rothstein & Robinson 1998). Costs associated with the rejection of parasitic eggs are likely to be highest when the parasite lays mimetic eggs (Davies & Brooke 1988, Davies et al. 1996, Lotem & Nakamura 1998). The impact of such costs is likely to be dependent on the host-parasite system in question (Røskaft & Moksnes 1998). As common cuckoo hosts normally lose all their eggs and young when successfully parasitised, only recognition errors are assumed to be of importance as an opposing selective pressure against proper host defence. In these hosts, intermediate rejection rates could thus be the result of a balance between the costs of acceptance and the costs of making recognition errors. Many hosts of the brown-headed cowbird, however, grow up together with the parasitic chick, and thus rejection costs can also be important in this respect. A scenario, first proposed by Davies & Brooke (1988), where an equilibrium may exist is when young inexperienced breeders have not yet learned the appearance of their own eggs and thus accept most of the eggs laid (both their own and parasitic eggs) in their first breeding attempt (Lotem et al. 1992, 1995).

Due to recognition errors and rejection costs some hosts may need additional stimuli to the parasitic egg when deciding whether to reject such eggs or not (e.g. Rothstein 1982a, Davies & Brooke 1988, Moksnes & Røskaft 1989, Moksnes et al. 1993, 2000, Sealy 1995, Alvarez 1996, Brooke et al. 1998, Lindholm 2000, Soler et al. 2000a), especially when they are confronted with mimetic eggs (Davies et al.

1996). Øien et al. (1999) predicted that species with no or high rejection rates should show few costs and no conditional responses in relation to rejection behaviour (see e.g. Hill & Sealy 1994, Soler et al. 2000b); their response towards parasitic eggs should be more or less fixed. On the other hand, hosts with intermediate rejection rates towards foreign eggs should have larger costs and also show more conditional responses in rejection behaviour.

Zahavi (1979) proposed another hypothesis for the acceptance of parasitic eggs based upon the existence of costs associated with parasite retaliation or "mafia" behaviour, and Soler et al. (1995) found support for this in the great spotted cuckoo-magpie system. In addition, nest-site limitations (Petit 1991) and the length of the breeding season (Moksnes et al. 1993, Brooker & Brooker 1996, 1998) could also explain the acceptance of parasitic eggs in some situations.

Recently, researchers have acknowledged the importance of looking upon interactions between parasites and their hosts not only as isolated entities/populations, but also as metapopulations (Levins 1969, Lindholm 1999, Lindholm & Thomas 2000, Soler & Soler 2000). Taking migration, gene flow, local adaptations and other metapopulation dynamics into account, a new dimension is introduced to coevolutionary studies. A hypothesis that could explain the existence of both acceptors and rejecters within and among host populations based upon the existence of costs connected to rejection behaviour is the "intermittent arms race hypothesis" (Soler et al. 1998), also termed the "coevolutionary cycles model" (Rothstein 2001). According to this hypothesis based upon metapopulation dynamics, hosts evolve better defences as the level of parasitism increases, and as a consequence of this the fitness gains for parasites decrease. Parasites that disperse will therefore have a selective advantage if they encounter host populations that have no previous history of interactions with the brood parasite. When the level of parasitism declines, hosts will lose their defences against parasitism due to the costs associated with maintaining such traits (e.g. Peer & Bollinger 1997). However, many hosts retain rejection behaviour for a long time even though they are not currently parasitised, indicating no or negligible costs in retention of such behaviour (e.g. Braa et al. 1992, Moksnes & Røskaft 1992, Rothstein 2001). Rejection behaviour can even be retained through speciation events (Bolen et al. 2000, Rothstein 2001). This scenario of long time retention of rejection behaviour is termed the "single trajectory-model" (Rothstein 2001).

The metapopulation approach can also help to explain why some host populations have a mixture of acceptors and rejecters of parasitic eggs, not because of costs associated with rejection behaviour but rather because of gene flow of "acceptor alleles" from non-parasitised host populations preventing the evolution of proper host defence in parasitised populations. Martinez et al. (1999) found that the amount of gene flow between different magpie populations in Europe (the most common host of the great spotted cuckoo) is high, and Soler et al. (1999) obtained further support for the "rejecter-gene flow hypothesis" regarding this parasite-host system. This hypothesis can explain the persistence of a high rejection rate in currently non-parasitised host populations, the coexistence of both acceptors and rejecters within a population, as well as the rapid increase in rejection rates in recently parasitised populations by gene flow of "rejecter alleles" from areas of sympatry to allopatry (see also Soler & Møller 1990, Briskie et al. 1992, Soler & Soler 2000). However, it has also been stressed that rapid changes in host defences within populations as well as differences in defences between populations may reflect phenotypic plasticity rather than or in addition to genetically determined evolutionary changes (e.g. Soler et al. 1994, Brooke et al. 1998, Robert & Sorci 1999, Lindholm 2000, Lindholm & Thomas 2000).

Study sites and study species

Data on European and North American passerine eggs for use in comparative studies were obtained at the Zoological Museum in Copenhagen, Denmark and the Western Foundation of Vertebrate Zoology in Camarillo, California, USA in 1996.

The studies on chaffinches (*Fringilla coelebs*) were carried out in Stjørdal, central Norway (63°10'N, 10°20'E) in 1999 - 2001. The study area consists of three lowland alder (*Alnus incana*) woodlands in which chaffinches are breeding in high densities.

Blackcaps (*Sylvia atricapilla*) were studied in a deciduous woodland near Dolní Bojanovice in the southeastern part of the Czech Republic (48°52'N, 17°00'E) during the 2000 and 2001 seasons. This area has a large population of blackcaps.

Finally, reed warblers (*Acrocephalus scirpaceus*) were studied near Luzice in the southeastern part of the Czech Republic (47°40'N, 16°48'E) in 1998. The area consists of several artificial fishponds with dense littoral vegetation (Hudec 1975), in which reed warblers breed in high densities (Øien et al. 1998).

Aims of the study and summary of papers

The main aims of the study were to reveal host adaptations in the coevolutionary arms race with brood parasites with a special focus on egg appearance (Papers I - III), and to explain the pronounced variation in rejection behaviour found among various hosts (Papers IV - V).

Evolution of egg characteristics among hosts of brood parasites (Papers I - III)

Here I tested the hypothesis that hosts of brood parasites with egg mimicry should lower their intraclutch variation and increase their interclutch variation in egg appearance as a counteradaptation against parasitism.

Paper I:

North American passerines are utilised by the brown-headed cowbird, a generalist brood parasite with no egg-mimicry. Thus, parasitic eggs are easily recognised even without specific host egg characteristics. In a comparative study it was found that European passerines suitable as common cuckoo hosts in general had a lower intraclutch variation and a higher interclutch variation than comparable North American species. In addition, in contrast to what has previously been found among common cuckoo hosts in Europe there was no difference in these traits between suitable and unsuitable hosts of the cowbird. Neither conspecific brood parasitism nor nest predation, both of which could influence the evolution of egg characteristics, explained the differences in clutch variation between European and North American passerines. This shows that specialist brood parasites with egg mimicry (e.g. the common cuckoo) are powerful selective agents for the evolution of such traits in passerine birds.

Paper II:

In a Czech reed warbler population, which rejects non-mimetic cuckoo eggs at an intermediate rate (56.3% in this study), a lower intraclutch variation in egg appearance was found among pairs that rejected experimentally added non-mimetic model cuckoo eggs than among pairs that accepted such eggs. There was no evidence of conditional responses; the rejection rate of artificial eggs was not correlated with the level of parasitism, and furthermore, we found no indication for a correlation between rejection behaviour and age. The results obtained suggest that a genetically based linkage between the recognition of odd eggs and intraclutch variation may exist in this host population.

Paper III:

Host age and intraclutch variation, and also mimicry of parasitic eggs, may be important for host rejection behaviour. Here we examined the role of these clues for the rejection of experimentally added conspecific eggs in a chaffinch population in Norway and a blackcap population in the Czech Republic. The chaffinch population is allopatric whereas the blackcap population is sympatric with the common cuckoo. However, the blackcaps are not regularly parasitised. Both species are good rejecters of non-mimetic parasitic eggs and generally have a low intraclutch and a high interclutch variation in egg appearance. We found that there was no difference in intraclutch variation in egg appearance between rejecters and acceptors of conspecific eggs. However, the ability to reject foreign eggs was highly dependent on the degree of mimicry between parasitic and host eggs; the better the mimicry, the lower the rejection rate. Acceptance of mimetic eggs is probably due to limitations in the cognitive system, indicating that the hosts need some clues (e.g. differences in egg colour or spotting pattern) to detect the parasitic egg. No effect of age was revealed in the rejection behaviour or intraclutch variation. The results indicate that responses towards foreign non-mimetic conspecific eggs in chaffinches and blackcaps are more or less fixed.

Sources that could prevent the evolution of proper host defence (Papers IV - V)

Many hosts of brood parasites show imperfect rejection behaviour towards parasitic eggs. Here I examined two possible explanations for the lack of such behaviour; costs related to recognition and rejection of parasitic eggs and metapopulation dynamics preventing a proper spread of "rejecter alleles".

Paper IV:

Costs associated with the recognition and rejection of parasitic eggs were investigated in chaffinches and blackcaps, two species that are good rejecters of foreign eggs. Both species show specific aggression against the cuckoo, but are not currently parasitised. It is hypothesised that such hosts should show no or only few costs, because the rejection behaviour is retained even in the absence of parasitism by the common cuckoo. We found that both species experienced quite high costs when rejecting eggs from parasitised clutches, but that they made very few recognition errors in non-parasitised clutches. These findings supported our predictions since only the presence of recognition errors is believed to be important for a loss of rejection behaviour in the absence of parasitism. In addition, the influence of a conditional stimulus, the sight of a dummy cuckoo at the nest, was insignificant among chaffinches because no more recognition errors were made at nests presented with the dummy than at those without this treatment.

Paper V:

Here we proposed a hypothesis based upon metapopulation dynamics (local adaptations, gene flow, etc.), and with focus on the breeding habitat of the hosts, that could explain the extensive variation in host adaptations found among various passerines. The "spatial habitat structure hypothesis" assumes that common cuckoos and other parasites utilise only species or populations breeding near vantage points (i.e. mainly trees). This implies that parasite-host population dynamics could vary between different habitats. Data on hosts of the common cuckoo in Europe supported the hypothesis. We found that cuckoos are best adapted to utilise species in which some populations are breeding far from trees (i.e. cuckoo vantage points) and others are breeding near trees, because in such species gene flow from non-parasitised populations prevents the hosts from evolving a perfect rejection behaviour. On the other hand, hosts that always breed near trees will rapidly evolve rejection behaviour because the majority of individuals in most populations will experience brood parasites. Parasite egg mimicry and the level of parasitism was found to be highest among hosts breeding both near and far away from trees, indicating that the cuckoo is most successful when utilising these species.

Discussion

In this section, I discuss how our findings contribute to the knowledge about avian brood parasitism. Basically, our results have shed light on host counteradaptations to adaptive traits evolved by brood parasites, as well as focusing on the variation in host rejection behaviour against parasitic eggs among various passerines.

Host adaptations against brood parasitism

An advanced host counteradaptation against brood parasites that lay mimetic eggs is the evolution of specific clutch characteristics (Davies & Brooke 1989a, Øien et al. 1995, Soler & Møller 1996, Rodríguez-Gironés & Lotem 1999). Previous studies have shown that European passerines which have been involved in a coevolutionary arms race with the common cuckoo have evolved a low intraclutch variation and a high interclutch variation in egg appearance to be better able to recognise mimetic parasitic eggs (Øien et al. 1995, Soler & Møller 1996). Our findings provide further support for this hypothesis, by showing that hosts of a parasite with non-mimetic eggs (i.e. the brown-headed cowbird) have not evolved such clutch characteristics (Paper I). In addition, the results show that there is indeed a difference in both intraclutch and interclutch variation in egg appearance between hosts of the common cuckoo and of the brown-headed cowbird. Cuckoo hosts have a lower intraclutch and a higher interclutch variation than cowbird hosts (Paper I). However, the difference in intraclutch variation was less than expected. This suggests a new possibility for the evolution of a low intraclutch variation and a high interclutch variation. Previously, it was thought that a high interclutch variation is a direct consequence of selection for a reduced intraclutch variation (Soler & Møller 1996). The results from the present study could indicate that the evolution of a higher interclutch variation is more or less independent of the evolution of intraclutch variation. As a new host egg-type occurs in a population through mutation or immigration from another host population, the carriers will have a selective advantage when confronted with a parasitic egg that mimics the most common egg morph. Thus, this egg-type will spread in the host population, given that the level of parasitism is high enough.

The main conclusion from the comparative analyses presented in Paper I is that brood parasites with mimetic eggs are strong selective agents for the evolution of egg characteristics among their hosts. Additional support for this hypothesis is provided by the study on a reed warbler population in the Czech Republic (Paper II).

This was the first investigation that set out to examine levels of intraclutch variation within a population of a common cuckoo host in Europe, since previous studies have focused on comparisons between species (Davies & Brooke 1989a, Øien et al. 1995, Soler & Møller 1996). Several studies have shown that the reed warbler is an intermediate rejecter of non-mimetic eggs (Davies & Brooke 1988, 1989b, Brooke et al. 1998, Lindholm & Thomas 2000), which was further supported in the present study (Paper II). We found that rejecters of non-mimetic eggs among reed warblers had a significantly lower intraclutch variation in egg appearance than acceptors of such eggs. This study suggests that there exists some sort of genetic linkage between the evolution of clutch characteristics and the ability to recognise odd eggs (Paper II). The results indicate that there were few conditional responses in rejection behaviour within this population. The rejection rate was not related to the level of cuckoo parasitism in the area, nor was there any indication for a relationship between age and rejection behaviour. However, several other studies have shown that this species shows conditional responses in its rejection decisions (Davies & Brooke 1988, Lindholm 2000, Moksnes et al. 2000), suggesting a genetic basis for rejection behaviour combined with some flexibility in this behaviour triggered by clues in the environment.

Øien et al. (1999) proposed that species that are good rejecters of parasitic eggs should show few conditional responses towards foreign eggs, i.e. that their response is more or less fixed. We examined this hypothesis by studying the rejection behaviour in two European passerines, the chaffinch and the blackcap, which are both good rejecters of parasitic eggs (Braa et al. 1992, Moksnes 1992, Moksnes & Røskaft 1992, Moksnes et al. 1994, Paper III, but see Davies & Brooke 1989a, b). Our results supported the findings of Braa et al. (1992) and Moksnes (1992); rejection of foreign eggs was strongly dependent on the mimicry between parasitic and host eggs. The better the mimicry, the poorer the rejection ability. These results suggest that a threshold exists in the cognitive abilities (see McLean & Maloney 1998), and that mimetic eggs fell below this threshold and thus were not perceived as foreign. In accordance with Øien et al. (1999), we found no difference in intraclutch variation between rejecters and acceptors of parasitic eggs in these species (Paper III). Furthermore, there was no indication for an effect of age on the decision to reject such eggs, suggesting that these species do not need a prolonged learning period to recognise the appearance of their own eggs (see Rothstein 1974, 1978, Lotem et al.

1995). In addition, among chaffinches there was no relationship between age and intraclutch variation in egg appearance (Paper III). The low intraclutch variation in this species makes it very likely that all subsequent eggs laid by the female will look very similar to the first laid egg, and therefore a prolonged learning period is not required (e.g. Lotem et al. 1995, Rodríguez-Gironés & Lotem 1999). However, the situation is likely to be the opposite in species with higher intraclutch variation, especially when they are parasitised by parasites laying mimetic eggs (Lotem et al. 1995, Lotem & Nakamura 1998, Rodríguez-Gironés & Lotem 1999). The effect of age obviously differs among species, as Lotem et al. (1992, 1995) found that both rejection behaviour and intraclutch variation were correlated with age in a great reed warbler population in Japan, while several other studies have not revealed any effects of age on rejection behaviour (Marchetti 2000, Soler et al. 2000a, Amundsen et al. in review), or egg signatures (Gosler et al. 2000).

Variation in rejection behaviour among hosts of brood parasites

The profound variation in rejection rates of parasitic eggs among hosts of brood parasites is intriguing, and as explained previously there exist several hypotheses offering an explanation for such a variation. According to the "evolutionary lag hypothesis", a lack of proper defence against parasitism is due to a lag in the origin or spread of rejection behaviour (Dawkins & Krebs 1979, Davies & Brooke 1989a, Rothstein 1990). The "evolutionary equilibrium hypothesis" explains the coexistence of acceptors and rejecters within a host population by a balance between opposing selection pressures such as the cost of acceptance versus rejection costs and recognition errors (Zahavi 1979, Davies et al. 1996, Lotem & Nakamura 1998, Takasu 1998a). In hosts of brood parasites that lose their whole clutch when successfully parasitised (e.g. common cuckoo hosts), only recognition errors are important as an opposing selection pressure against evolution of proper defences (Rothstein & Robinson 1998). Common cuckoo hosts could therefore tolerate high rejection costs and it would still be most adaptive to reject foreign eggs. In chaffinches and blackcaps, a high rejection rate is maintained even though they are not currently used as cuckoo hosts, indicating that there are no costs associated with this behaviour. Our study supports this, as it was shown that recognition errors are extremely rare, but that rejection costs are high (Paper IV). These results correspond well with the "single trajectory model" outlined by Rothstein (2001). The loss of rejection behaviour in hosts that have previously been involved in a coevolutionary arms race with the cuckoo will thus only be due to random genetic drift as long as no costs are associated with the maintenance of such relict traits.

The occurrence of rejection costs has been thoroughly documented in previous studies (e.g. Molnár 1944, Rothstein 1976, 1977, Davies & Brooke 1988, 1989a, b, Rohwer et al. 1989, Røskaft et al. 1990, 1993, Lorenzana & Sealy 2001, Welbergen et al. 2001), but only a few studies have revealed recognition errors in non-parasitised host clutches, which are the best evidence for the existence of such costs (Davies & Brooke 1988, Marchetti 1992). However, loss of own eggs in non-parasitised nests can also occur in species that are acceptors of foreign eggs, and can be due to jostling, partial predation or other reasons (e.g. Rothstein 1982b, Kemal & Rothstein 1988, Lerkelund et al. 1993, E. Røskaft pers. obs., Paper IV). To make the picture even more complex, there could be different amounts of errors made among various populations of the same species. Thus, Davies & Brooke (1988) found that recognition errors occurred within a reed warbler population in England, whereas Røskaft et al. (in press) found no evidence for recognition errors even after exposure to a dummy cuckoo among reed warblers and great reed warblers in the Czech Republic.

A third hypothesis that could explain the variation in rejection behaviour among hosts is the "spatial habitat structure hypothesis" (Paper V). This hypothesis, based upon metapopulation dynamics, received support in our study and shows the influence of gene flow and local adaptations in the evolution of host defences (Paper V). Brood parasites must have access to perches in trees where they can be on the lookout for host nests that they can parasitise (Alvarez 1993, Øien et al. 1996, Clotfelter 1998, Hauber & Russo 2000, Moskát & Honza 2000, Clarke et al. 2001). Passerine birds that breed in the open are therefore believed to escape parasitism and should not have evolved defences against parasitism. Unfortunately, relevant data concerning such species do not currently exist. At the other extreme, we find species that breed only near trees (i.e. in woodlands and woodland borders). In such hosts, most populations are utilised by brood parasites and should thus rapidly evolve rejection behaviour. Initially there will be a high level of parasitism enforcing a strong selection pressure upon the hosts for the evolution of host adaptations against parasitism. The brood parasite might have problems in matching the speed of the evolution of host defences, and therefore only sporadically evolve adaptations like egg mimicry. The level of parasitism would thus decline as hosts evolve a proper defence. The most suggestive prediction from the "spatial habitat structure hypothesis" is the one concerning host species that can breed both near trees and far away from trees. Because only the populations that breed near trees are exposed to parasitism and thus experience a selective pressure for evolving host defence, gene flow from non-parasitised populations can prevent the evolution of a proper host defence in parasitised populations. This prediction also applies to single populations, in which some individuals breed near trees while others breed further away from trees. In populations fulfilling these criteria, we expect that host rejection behaviour is moderate, cuckoo egg mimicry is good, and the level of parasitism is high. Indeed, we found support for these predictions among European hosts of the common cuckoo (Paper V). Further support for the "spatial habitat structure hypothesis" was obtained in another study, where it was found that the level of aggression towards a dummy cuckoo generally was highest among suitable host species that always breed near trees and host populations that always breed in sympatry with the cuckoo (Røskaft et al. in review).

The three hypotheses outlined above ("lag", "equilibrium" and "habitat structure" hypotheses) to explain the existence of varying occurrences of rejection behaviour among hosts of brood parasites are all consistent with the hypothesis that the interaction between parasites and their hosts can be described as coevolutionary arms races. The obvious lack of antiparasitic adaptations among many hosts today can be explained by a lag in the evolution of such traits (Rothstein 1975b). With a strong selection (high costs of parasitism and/or high levels of parasitism) and a proper genetic background, hosts are assumed to eventually become good rejecters (i.e. "rejecter alleles" approach fixation). However, we can also think of cases where it is not necessarily more adaptive to be a rejecter of parasitic eggs than to be an acceptor (Lotem & Nakamura 1998), perhaps when host intraclutch variation in egg appearance is high and the parasitic egg is a good mimic of the host eggs (Lotem et al. 1995, Davies et al. 1996, Takasu 1998b, Rodríguez-Gironés & Lotem 1999). In such cases, the costs of recognition and rejection can be equal to or higher than the costs of acceptance and thus there could be a monomorphic host population constituted only of acceptors, or a dimorphic population with an equilibrium between equally adapted acceptors and rejecters (Lotem & Nakamura 1998). This equilibrium will be very dependent on the selection pressure enforced upon the hosts for evolving defence mechanisms, and in particular the level of parasitism is a critical factor (Lotem et al. 1992, Takasu et al. 1993, Davies et al. 1996). Thus, the equilibrium state could be unstable, and the proportion of individuals that reject or accept foreign eggs could fluctuate (Soler & Soler 2000). The situation is even more complicated when rejection behaviour is age dependent, or when hosts show conditional responses in their rejection behaviour, i.e. that individuals reject foreign eggs when receiving specific stimuli. In such cases, rejection is a better strategy on average, but the rejecter mutant will suppress rejection due to rejection costs when the stimulus expression is below a critical threshold determined by current perceptual abilities. There could alternatively exist a genotypic variability in adjustment of the conditional response, if different genotypes with different reaction norms are favoured in various environmental conditions (Lotem & Nakamura 1998). In summary, it is very difficult to separate the "lag" and the "equilibrium" hypotheses, and it could be argued that they really are not mutually exclusive but instead explain different stages in the coevolutionary arms race (Davies 1999, 2000, Winfree 1999). In situations where the costs of recognition and rejection outweigh the costs of acceptance (equilibrium), it can be argued that selection has not yet reduced the costs of rejection (lag) (Winfree 1999). If the hosts evolve a lower intraclutch variation in egg appearance or improve their perceptual abilities, the risk of making recognition errors may decrease, and the equilibrium state is distorted. Hosts that show high rejection rates against foreign eggs and also have a low intraclutch variation are thus likely to have overcome the costs associated with recognition and rejection of parasitic eggs, and can therefore be described as winners of the struggle against brood parasites (Paper III). The "spatial habitat structure hypothesis" described above is also based upon the arms race model (Paper V). From this hypothesis the level of parasitism and rejection behaviour in various host population or species can be predicted from characteristics of the host breeding habitat. Intermediate rejection rates are not necessarily due to the costs of recognition and rejection as stated by the "equilibrium hypothesis", but rather due to gene flow of "acceptor alleles" from non-parasitised populations into parasitised populations, thus efficiently preventing the evolution of proper defence in such populations even though rejection is adaptive. To enable us to separate the "equilibrium" and "spatial habitat structure" hypotheses, further studies should focus on obtaining more data on rates of gene flow between populations of parasites and hosts as well as data on recognition errors from unparasitised host nests. Only then is it possible to solve the enigma of apparently "improper" host defence.

Prospects for future studies

Future studies should focus more upon avian brood parasitism in a metapopulation context. The coevolutionary arms race between parasites and hosts can lead to a strong pattern of local adaptations among various host-parasite populations, especially when different host populations are isolated from each other. Theoretically, in the arms race between hosts and parasites, the latter can increase their mean fitness by specialising on the most common local host genotype (frequency-dependent selection). This would then give a selective advantage to rare host genotypes, allowing for counteradaptations by the hosts (Haldane 1949, Kaltz & Shykoff 1998). However, local adaptations in metapopulations as described above can be precluded by phenomena like extinction, recolonisation, gene flow, variable selection pressures and environmental stochasticity (Kaltz & Shykoff 1998, Martinez et al. 1999). The investigation of host-parasite dynamics in a metapopulation context is a recent idea which has been mainly applied to plants and their pathogens (see review in Kaltz & Shykoff 1998). Recently, the metapopulation approach has been applied to the coevolutionary interactions between great spotted cuckoos and their magpie hosts (Soler et al. 1998, Martinez et al. 1999, Soler et al. 1999, Soler & Soler 2000). Lindholm (1999) has studied common cuckoo-reed warbler interactions in Britain by a similar approach. In addition, the study presented in this thesis (Paper V) has shown that the spatial habitat structure is important for the evolution of adaptations and counteradaptations in common cuckoo and host metapopulations. There is need for more studies on local adaptations in a metapopulation scenario, because such investigations can reveal the primary causes of coevolutionary processes in host-parasite systems (Soler & Soler 2000). In addition, studies of local adaptations in a metapopulation context are very important for improving our understanding of biodiversity and conservation of this diversity (Hanski 1999).

Conclusions

The results presented in this thesis support the hypothesis that hosts of a specialist brood parasite with mimetic eggs (i.e. the common cuckoo) have evolved a low intraclutch and a high interclutch variation to be better able to recognise the parasitic egg. Hosts of generalist brood parasites without egg mimicry (i.e. the brown-headed cowbird) have not evolved such traits. Variation in intraclutch variation related to rejection behaviour against non-mimetic parasitic eggs can even be found within host populations of the common cuckoo, as illustrated by our study on reed warblers in which rejecters of non-mimetic eggs had a lower intraclutch variation than acceptors of such eggs. Reed warblers are intermediate rejecters of non-mimetic parasitic eggs. However, when cuckoo host species are good rejecters of non-mimetic eggs, the great majority of individuals are expected to have a low intraclutch variation, just as the chaffinches and blackcaps in our analyses. Failure to reject foreign eggs in these species is not because they lack the ability, but is rather due to cognitive limitations. Thus, parasitic eggs will not be rejected if they are too similar to the host eggs. Our results on three European passerines indicate that in these specific populations the age of the hosts has minor influence on rejection behaviour or intraclutch variation. This provides support for the view that these traits are more or less genetically fixed, with few conditional or learned components.

A high rejection rate is maintained in some hosts of the common cuckoo even though these species are not currently utilised by the parasite. The retention of rejection behaviour in blackcaps and chaffinches is probably due to the fact that recognition errors are negligible and thus this trait is more or less selectively neutral. The considerable variation in rejection behaviour among hosts of brood parasites can be explained by other means than the existence of costs related to such behaviour. Instead, metapopulation dynamics and host breeding habitats may influence the evolution of host defences. Species that breed both near trees (i.e. vantage points for parasites) and far away from trees are most suitable as hosts, because gene flow from non-parasitised populations prevent proper evolution of host defence in parasitised populations. Host species that always breed near trees rapidly evolve defences and thus the parasite may not be able to keep up with the hosts in the ongoing arms race. Such hosts are therefore not ideal from the point of view of the parasite.

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Paper I

Evolution **XX,** xxx-xxx

Obligate brood parasites as selective agents for evolution of egg appearance in passerine birds

by

B.G. Stokke, A. Moksnes & E. Røskaft

LRH: BÅRD G. STOKKE ET AL.

RRH: BROOD PARASITES AS SELECTIVE AGENTS

OBLIGATE BROOD PARASITES AS SELECTIVE AGENTS FOR EVOLUTION OF EGG APPEARANCE IN PASSERINE BIRDS

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ABSTRACT

Many passerine host species have counteracted the parasite egg mimicry in their co-evolutionary arms race with the common cuckoo (*Cuculus canorus*) by evolving increased interclutch and reduced intraclutch variation in egg appearance. Such variations make it easier for hosts to recognize a foreign egg, reduce the possibility of making recognition errors, and the ability of the cuckoo to mimic the eggs of a particular host. Here, we investigate if such clutch characteristics have evolved among North American passerines. We predict that due to the absence of brood parasites with egg mimicry on this continent, these passerines should 1) not show any relationship between rejection rates and intra- or interclutch variation, and 2) intraclutch variation should be lower and interclutch variation higher in European hosts exposed to cuckoo parasitism as compared to North American hosts parasitized by cowbirds. Here we present data that show support for most of these and other predictions, also when controlling statistically for effects of common descent. However, the effect of continent on intraclutch variation was less than predicted, and we discuss a possible reason for this. All things considered, the results demonstrate that parasitism by a specialist brood parasite with egg mimicry is a powerful selective force regarding the evolution of egg characteristics in passerine birds.

KEY WORDS: Brood parasitism, *Cuculus canorus*, *Molothrus ater*, co-evolution, rejection behavior, clutch variation, egg appearance.

The common cuckoo (*Cuculus canorus*) is considered as a specialist brood parasite. There are about 16 cuckoo gentes or tribes in Europe, and each gens generally parasitizes only one or a few host species (Wyllie 1981; Alvarez 1994; Moksnes and Røskaft 1995). Genetic evidence (Gibbs et al. 2000) indicates that it is the cuckoo female that specializes on specific host species and thus form the gentes. Several cuckoo gentes lay eggs that are remarkably similar to the host eggs. This egg mimicry has probably evolved as a response to host discrimination of unlike parasitic eggs (Brooke and Davies 1988), and the various adaptations and counter-adaptations evolved by the parasite and its hosts can be described as the result of a co-evolutionary arms race (Dawkins and Krebs 1979; Davies and Brooke 1989b; Moksnes et al. 1990; Rothstein 1990). This scenario may show several stages, among which the most advanced counter-adaptation by the host against the parasite egg mimicry is to evolve eggs with higher interclutch and lower intraclutch variation in appearance (Øien et al. 1995; Soler and Møller 1996). Such counter-adaptations against cuckoo parasitism should only have been evolved in host species that have experienced an arms race with the cuckoo, and thus can be regarded as suitable hosts (Davies and Brooke 1989b; Moksnes et al. 1990).

In North America, there are no brood parasites with egg mimicry. The brown-headed cowbird (*Molothrus ater*) is a generalist brood parasite, which utilizes many passerine species as hosts (Friedmann and Kiff 1985), and recent genetic studies have confirmed that individual cowbirds use multiple hosts (Alderson et al. 1999; Hahn et al. 1999). Because it has expanded its range over the last few centuries and encountered new host populations and even new host species (Mayfield 1965), many hosts have probably not had enough time to counteract the parasitism (Rothstein 1990; Hosoi and Rothstein 2000; but see Robert and Sorci 1999 for a case of rapid evolution of host defenses). Although some host species reject non-mimetic cowbird eggs, many species accept such eggs (Rothstein 1975, 1990). Because of the abundance of naïve hosts that accept non-mimetic eggs, there has not been a strong selection pressure on the brown-headed cowbird to evolve eggs that resemble those of the host. Hence, the co-evolutionary arms race between the cowbird and its hosts is probably still at an early stage compared to that between the cuckoo and its hosts in Europe. Thus, there has not been a similar selection pressure on egg variability within and between clutches of North American passerines as in their European counterparts. Even rejecters of the non-mimetic cowbird eggs have probably not experienced a strong selection pressure to evolve a pattern of egg variability similar to that in the European cuckoo hosts, because cowbird eggs are generally easily distinguishable from host eggs. The probability of making recognition errors is thus negligible (Lotem et al. 1992).

By performing comparative analyses, we tested the hypothesis that hosts of specialist brood parasites with egg mimicry, like the cuckoo, should evolve a high interclutch and a low intraclutch variation in egg appearance to facilitate the recognition of the parasitic egg. Previously, this hypothesis has received support from a study concerning the European cuckoo and its hosts (Øien et al. 1995; Soler and Møller 1996). Here, we go one step further, and investigate if there are any differences in clutch variation among hosts of a generalist brood parasite.

It is assumed that different rates of rejection of parasitic eggs by different host species may represent different stages in this arms race. In hosts of parasites with egg mimicry, high rejection rates have therefore been found to be positively correlated with a high level of interclutch variation and a low level of intraclutch variation and vice versa (Øien et al. 1995; Soler and Møller 1996). However, such a relationship is not expected in hosts of parasites without egg mimicry. From this we predict (1) that there should not be any relationship between rejection rates and clutch variation among North American passerines. Another prediction that follows from the hypothesis is (2) that the intraclutch variation in egg appearance should be lower, and the interclutch variation should be higher in European passerines suitable as cuckoo hosts than in North American passerines suitable as cowbird hosts. Furthermore, we expect (3) no such differences to be found between unsuitable host species on the two continents.

It is reasonable to argue that not every suitable host species in Europe has participated to the same degree in an arms race with the cuckoo. Therefore, we have partitioned host species on both continents into three groups according to their rejection rates of non-mimetic eggs. We predict (4) that European species in the group with highest rejection rates ($\geq$ 80 %) should have a lower intraclutch and a higher interclutch variation than North-American species within this group. In species with intermediate rejection rates, there could potentially also be some differences between the continents. However, this is probably not as pronounced as in the former group, because many individuals in cuckoo host species are still acceptors without any adaptations against brood parasitism (e.g. Stokke et al. 1999). However, we expect (5) to find no differences in clutch variation between European and North American passerines with the lowest rejection rates ($\leq$ 20 %), because here the majority of the individuals are acceptors.

MATERIALS AND METHODS

Data collection and classification of species

Data on clutch variation in 99 European passerines were obtained from the egg collection at the Zoological Museum in Copenhagen, Denmark. Corresponding data for 122 North American passerines were acquired from the Western Foundation of Vertebrate Zoology in Camarillo, California, USA. Only species that breed in open nests were used, because hole-nesters might have been subject to different selection pressures than those experienced by open nesters (Lack 1968). The clutches were photographed and the egg variation within and between clutches was assessed on a scale from 1 (low) to 5 (high) by four experienced persons as described by Øien et al. (1995). The mean value of the scores attained by these persons was used in the further analyses. This was justified because the various assessments were highly consistent (interclutch variation; repeatability = 0.757, s.e. = 0.012, F = 7.244, d.f. = 219, 660, $p < 0.0001$, intraclutch variation; repeatability = 0.718, s.e. = 0.035, F = 6.076, d.f. = 219, 660, $p < 0.0001$). In a recent paper, the method of assessing egg characteristics based upon human vision has been questioned (Cherry and Bennett 2001). Birds and human colour vision are different in several ways, including sensitivity to UV-wavelengths (Bennett and Cuthill 1994). The egg classification in the present study would therefore probably have derived advantage from use of such measurements, which we unfortunately were unable to do due to lack of equipment. However, many results obtained earlier using data generated with the traditional method have been in accordance with what it should be expected that the birds perceived (see e.g. Jackson 1998; Stokke et al. 1999; Welbergen et al. 2001), and supporting our assumption that the method used in this study is satisfactory for quantifying the actual appearance of eggs.

Data on the rejection rate of experimentally added non-mimetic parasitic eggs for 34 European and 37 North American passerine species were obtained from the literature (sources available from the authors on request).

It is believed that the evolution of a mimetic egg by the parasite leads to the selection for a lowered intraclutch variation in the host, and thereby automatically also a higher interclutch variation (Soler and Møller 1996). In the European species it could therefore be argued that rejection rates of mimetic eggs should be included in our analyses. However, several studies have shown that the rejection of mimetic and non-mimetic eggs are highly correlated (e.g. Braa et al. 1992; Moksnes and Røskaft 1992; Moksnes et al. 1993; Soler et al. 1999, but see Brooke and Davies 1988; Davies and Brooke 1989a for other findings). In addition, North American passerines are always parasitized with non-mimetic eggs (e.g. Rothstein 1975), and only experimental data on such eggs could be obtained. To standardize the methods on both continents we therefore only used rejection rates of non-mimetic eggs.

In the present study we divided the species into two different groups according to their suitability as hosts; suitable and unsuitable. European passerines were classified as suitable or unsuitable as cuckoo hosts according to Moksnes and Røskaft (1995), while the North American species were classified as suitable or unsuitable as cowbird hosts according to data obtained from Ehrlich et al. (1988) and Terres (1996). A species was regarded as a suitable host if it feeds its offspring with insects, breeds in open or semi-open nests, and has eggs and young that are small enough for the parasitic chick to evict (cuckoo) (Davies and

Brooke 1989a; Moksnes et al. 1990; Moksnes and Røskaft 1995), or successfully compete with (cowbird) (e.g. Friedmann 1963). Species that feed their young with regurgitated food (e.g. Hirundinidae) were regarded as unsuitable hosts (Davies and Brooke 1989b). We also classified as suitable hosts 13 species (six in Europe and seven in North America) that in some parts of their range are available as hosts, but in other parts are unavailable because they here may nest in holes/semi-holes with small entrances inaccessible to brood parasites. In such species gene flow from unparasitized to parasitized populations could potentially slow down the evolution of proper host defense, and thus lower the expected difference in clutch variation between Europe and North America (Røskaft et al. in press). We therefore did our analyses both including and excluding these species (Table 2).

Comparative and statistical analyses

Treating each species as an independent data point may lead to an overestimation of the true number of degrees of freedom in statistical analyses (Felsenstein 1985; Harvey and Pagel 1991; Martins and Garland 1991). To control for possible effects of common descent, data used in the analysis were also assessed in light of phylogenetic relationships among species. When testing for relationships between rejection rates and intra-/interclutch egg variation, we produced a tree based on molecular data (DNA-DNA hybridization) (Sibley and Ahlquist 1990), with additional information from the literature (sources available from the authors upon request). We used three different methods to assign branch lengths; the method of Grafen (1989), the method of Pagel (1992), and constant branch lengths (= 1). We selected the branch lengths that yielded absolute values of contrasts that were not related to their standard deviations ($p < 0.05$) for any of the traits analyzed (Garland et al. 1992). When testing for any differences in clutch variation between the continents, we also made a tree (as above), but then all the species from both continents were merged into the same tree. A dummy variable was created for continental occurrence, where 0 = North America and 1 = Europe. We used the computer program package PDAP (Phenotypic Diversity Analysis Programs) version 5.0 (Garland et al. 1993; Garland et al. 1999) to generate the trees and to load variable data into them. This package also contains Felsenstein`s (1985) independent comparison method, which allowed us to obtain pairwise contrasts of the variables between nodes in the phylogenetic trees that were independent of each other. These contrasts were then used in the statistical analyses, and the relationship between the variables was analyzed by multiple regression (rejection rate versus clutch variation) and multivariate GLM (continent versus clutch variation). The regressions using independent contrasts were based on forcing the regression line through the origin (Garland et al. 1992).

We also analyzed the data by using a conventional multiple regression-analysis, and a multivariate GLM approach, where each species was treated as an independent data point.

Intraclutch variation was square root transformed, and the rejection rate was arcsine transformed before the analyses (Test for normality using Kolmogorov-Smirnov test with Lilliefors significance correction, n.s.). Interclutch variation already had an approximate normal distribution. All the tests were two-tailed. SPSS for Windows, version 10.0 (SPSS Inc. Chicago, Illinois, USA) was used for the data analyses.

RESULTS

Both when using the independent contrasts method and a conventional multiple regression using each species as an independent data point, we found as predicted (1) that there was no statistically significant relationship between the rejection rate of artificial, non-mimetic parasitic eggs and the variation in egg appearance in North American passerines (Table 1).

Insert Table 1 approximately here

Three of the North American species with high rejection rates can be considered as unsuitable cowbird hosts (e.g. Friedmann 1963); blue jay (*Cyanocitta cristata*), scrub jay (*Aphelocoma coerulescens*) and American robin (*Turdus migratorius*). We therefore did the same analyses excluding these species, because the evolution of rejection in these cases can be due to factors other than cuckoo-/cowbird parasitism. However, the results did not differ from those obtained when these species were included in the analyses (Table 1).

When using a conventional multivariate test, we found as predicted (2), that there was a statistically significant difference in clutch variation between Europe and North America among the species regarded as suitable hosts; intraclutch variation: mean = 1.66 ± 0.33 (n = 67) versus 1.89 ± 0.44 (n = 101) respectively, interclutch variation: mean = 3.25 ± 0.75 (n = 67) versus 2.92 ± 0.83 (n = 101) (Table 2). This difference was even more pronounced when the 13 species that can be both available and unavailable to the brood parasite were excluded; intraclutch variation: mean = 1.64 ± 0.31 (n = 61) versus 1.88 ± 0.44 (n = 94), interclutch variation: mean = 3.32 ± 0.75 (n = 61) versus 2.91 ± 0.85 (n = 94) for Europe and North America respectively (Table 2). Among unsuitable hosts, as predicted there was (3) no difference in clutch variation between European and North American passerines (intraclutch variation: mean = 2.02 ± 0.49 (n = 31) versus 1.86 ± 0.54 (n = 21) respectively, interclutch variation: mean = 2.97 ± 0.69 (n = 31) versus 2.69 ± 0.74 (n = 21), Table 2). When analyzing data based on independent contrasts, we obtained mostly similar results (Table 2). There was a statistically significant difference in clutch variation between European and North American passerines when suitable species were compared. As in the conventional analyses, the exclusion of partially available species resulted in a greater difference between the continents. However, continental occurrence was only related to interclutch variation while contrary to our predictions (2 - 3), there was no statistically significant difference in intraclutch variation.

Insert Table 2 approximately here

The division of 71 species with known rejection rates towards non-mimetic parasitic eggs into three groups, yielded as predicted (4 - 5) only differences among continents in the group with the highest rejection rates (≥ 80 %, Table 3). Again, the most profound effect of continent was on interclutch variation (Europe; mean = 3.50 ± 0.72 (n = 11), North America;

Insert Table 3 approximately here

mean = 2.39 ± 0.92 (n = 11)), while the effect of continent on intraclutch variation was in the predicted direction but not statistically significant (Europe; mean = 1.57 ± 0.27 (n = 11), North America; mean = 1.64 ± 0.46 (n = 11)).

DISCUSSION

In accordance with our prediction (1), and contrary to what was previously found among European passerines (Øien et al. 1995; Soler and Møller 1996) we found no statistically significant correlation between intra- and interclutch variation in egg appearance and the rejection rate of non-mimetic parasitic eggs in North American passerines. This supports the idea that the common cuckoo is responsible for the evolution of these differences in egg characteristics among the European passerines. The division of the species into groups according to their suitability as hosts or to their level of rejection of foreign eggs also supported our predictions (2 - 5). Statistically significant differences in clutch variation between European and North American passerines were only found when comparing suitable species, or species with high rejection rates. When comparing suitable species by using conventional statistics, there was a difference between continents in both intra- and interclutch variation. However, when controlling for phylogeny, this difference was only statistically significant for interclutch variation. Continental differences among species with high rejection rates, gave only a significant effect on interclutch variation regardless of the method used to analyze the data (i.e. conventional or independent contrasts). The support for our predictions with regard to interclutch variation but only partial support regarding intraclutch variation is hard to explain, because it has previously been thought that a high interclutch variation is a direct consequence of selection for a lowered intraclutch variation (Soler and Møller 1996). However, our data indicates that there generally is less variation between the eggs within a clutch even among unsuitable hosts than previously thought. Another possibility for the evolution of a higher interclutch variation in the European passerines could be that when a new host egg type emerges through mutation, it would give the carrier a selective advantage when confronted with a cuckoo egg that mimics the ordinary host egg morph. Thus, the allele(s) responsible for this egg type would spread in the population and lead to a higher interclutch variation, given that the parasitism rate is high enough to enforce a selective pressure for the evolution of such host egg characteristics. The reason that hosts that are not parasitized with a mimetic egg do not evolve such egg characteristics could be that there are selective forces working against it. A relevant question in this regard is if there are other factors that could influence the evolution of egg characteristics. Two obvious variables besides interspecific brood parasitism are conspecific brood parasitism (CBP) (Yom-Tov 1980; Rohwer and Freeman 1989; Petrie and Møller 1991), and nest predation (Tinbergen et al. 1962; Lack 1968; Montevecchi 1976).

CBP is especially common in colony-breeding birds (Brown 1984; Møller 1987; Brown and Brown 1988, 1989; Yom-Tov 2001), and birds with precocial young (Weller 1959; Yom-Tov 1980, 2001; Andersson 1984; Rohwer and Freeman 1989; Sorenson 1998). It is reasonable to assume that in species where some individuals use the CBP-strategy, it would pay to evolve a low intraclutch- and a high interclutch variation in egg appearance to detect the parasitic egg, just as in species that are subject to interspecific brood parasitism. Interestingly, Jackson (1998) found that frequent CBP (23-35%) in the Northern masked weaver (*Ploceus taeniopterus*) caused evolution of a high interclutch variation in egg appearance. However, there is no obvious reason that CBP should occur more frequently in Europe than in North America. Yom-Tov (2001) found that CBP was detected in 36 passerine species distributed in Western Palearctic (13), North America (20) or on both continents (3). Out of the 220 species in our analysis, CBP has been found in only 20 species; four European and 16 North American species (Yom-Tov 2001). This implies that interspecific brood parasitism should enforce a greater selective pressure on most passerines than CBP, and therefore is the more likely explanation for the observed differences in clutch variation between Europe and North America. However, some of the species in our study have a high rate of rejection of foreign eggs, although they are often considered unsuitable as cowbird- or cuckoo hosts (e.g. *Turdus* sp., blue jay and scrub jay). CBP could thus be more widespread than previously believed, and be responsible for the evolution of high rejection rates in some passerines (e.g. Ringsby et al. 1993; Grendstad et al. 1999).

Nest predation could select for eggs with a less conspicuous ground color and more spots/markings so as to be more cryptic against the nest lining (Tinbergen et al. 1962; Montevecchi 1976). Thus, to obtain well-camouflaged eggs, species would evolve a low intraclutch variation in egg appearance. A high interclutch variation could also be adaptive because then the nest predators would have difficulty to evolve a search image for a particular egg type. However, in many cases predators search for nests, and not directly for the eggs (Collias and Collias 1984; Nilsson et al. 1985; Götmark 1992; Kim et al. 1995). Experiments have shown that there is no higher rate of predation on eggs in nests where one or several eggs deviates from the rest (Mason and Rothstein 1987; Davies and Brooke 1988; Røskaft et al. 1990). In addition, Weidinger (2001) found that nest survival was not related to egg color in three European passerines with open nests. A study by Martin and Clobert (1996) showed that the rate of nest predation among passerines with open nests was lower in Europe than in North America. If predation is important in the evolution of egg characteristics, this result could indicate selection for a lower intraclutch- and a higher interclutch variation in North America than in Europe, which is contrary to our results. Nest predation is therefore likely of minor importance as a selective agent for the evolution of the low intra- and high interclutch variation found among cuckoo hosts.

To conclude, the results indicate that passerines that have been involved in a long-term evolutionary arms race with a specialist brood parasite, have developed a higher interclutch variation in egg appearance than passerines which have been involved in interactions with a generalist brood parasite. There is also a trend towards a lower intraclutch variation among these passerines, although not significant in most of the analyses. In addition, there was a no significant relationship between clutch variation and rejection rate among North American passerines. This implies that the cuckoo can be regarded as a strong selective agent for the evolution of egg appearance in European passerines. Since there is no brood parasite with egg mimicry in North America, rejecters of foreign eggs on this continent are not dependent of evolving a low intra- or a high interclutch variation in order to recognize a parasitic egg.

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TABLE 1. Comparison of the relationship between host rejection rate of non-mimetic parasitic eggs (dependent variable) and intra- and interclutch variation in egg appearance (independent variables) among North American passerines. Three species with high rejection rates have been regarded as unsuitable hosts (see text), and could have evolved rejection behavior for other reasons than interspecific brood parasitism. The data are therefore also analyzed excluding these species. R_{inter} = regression coefficient for interclutch variation. R_{intra} = regression coefficient for intraclutch variation. Real data = data without controlling for phylogeny, Sibley-Ahlquist = data obtained by using the phylogenetic tree derived from Sibley and Ahlquist (1990; with additional information).

	R^2	F	p	d.f.	R_{inter}	p	R_{intra}	p
Real data	0.083	1.539	0.229	2,36	0.066	0.834	-0.342	0.283
excl. 3 species	0.099	1.696	0.200	2,33	-0.322	0.352	0.010	0.978
Sibley-Ahlquist	0.033	0.575	0.568	2,36	-0.267	0.359	0.126	0.664
excl. 3 species	0.062	1.017	0.373	2,33	-0.410	0.177	0.271	0.368

TABLE 2. A multivariate comparative analysis of the relationship between continent (independent variable) and intra- and interclutch variations in egg appearance (dependent variables) among European and North American passerines. The analyses are conducted with the species divided into two groups according to their suitability as hosts; suitable or unsuitable hosts. In addition, we have analyzed the suitable hosts excluding 13 species, which in some areas could be unavailable to the parasites, because they are partial hole-nesters (see text). F_{inter} = effect of continent on interclutch variation. F_{intra} = effect of continent on intraclutch variation. For other details see Table 1.

	F	p	d.f.	F_{inter}	p	F_{intra}	p
SUITABLE							
Real data	24.667	<0.001	2,165	7.161	0.008	12.817	<0.001
excl. 13 species	29.490	<0.001	2,152	9.110	0.003	13.368	<0.001
Sibley-Ahlquist	4.746	0.010	2,165	4.932	0.028	0.402	0.527
excl. 13 species	12.211	<0.001	2,152	13.108	<0.001	0.129	0.720
UNSUITABLE							
Real data	0.988	0.379	2,49	1.890	0.175	1.241	0.271
Sibley-Ahlquist	1.170	0.319	2,49	1.295	0.261	0.840	0.364

TABLE 3. Comparison of 34 European and 37 North American species divided into three groups according to their ability to reject foreign non-mimetic parasitic eggs; low = rejection rate ≤ 20 %, medium = rejection rate > 20 - < 80 %, high = rejection rate ≥ 80 %. Based upon this division a multivariate comparative analysis of the relationship between continent (independent variable) on intra- and interclutch variations in egg appearance (dependent variables) among European and North American passerines was performed. For other details see Table 1.

	F	p	d.f.	F_{inter}	p	F_{intra}	p
LOW							
Real data	0.220	0.804	2, 28	0.149	0.703	0.001	0.980
Sibley-Ahlquist	0.950	0.399	2, 28	1.529	0.226	1.255	0.272
MEDIUM							
Real data	1.357	0.287	2, 15	0.014	0.906	0.974	0.338
Sibley-Ahlquist	0.183	0.835	2, 15	0.014	0.906	0.344	0.565
HIGH							
Real data	6.689	0.006	2, 19	9.979	0.005	0.170	0.684
Sibley-Ahlquist	9.949	0.001	2, 19	8.997	0.007	1.554	0.227

Paper II

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Rejection of artificial cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among reed warblers (*Acrocephalus scirpaceus*)

by

B.G. Stokke, A. Moksnes, E. Røskaft, G. Rudolfsen & M. Honza

Paper II is not included due to copyright.

Paper III

Submitted manuscript (Ibis)

Chaffinches *Fringilla coelebs* and Blackcaps *Sylvia atricapilla*: Current winners in the evolutionary struggle against the Common Cuckoo *Cuculus canorus*?

by

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Chaffinches *Fringilla coelebs* and Blackcaps *Sylvia atricapilla*: Current winners in the evolutionary struggle against the Common Cuckoo *Cuculus canorus*?

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Chaffinches *Fringilla coelebs* and Blackcaps *Sylvia atricapilla* are good rejecters of foreign eggs and also generally have a low intraclutch variation and a high interclutch variation in egg appearance. These traits have most probably evolved as counteradaptations against brood parasitism by the Common Cuckoo *Cuculus canorus*, even though none of these species are regularly parasitised today. In this study, we investigated some cues and traits that could influence rejection of foreign conspecific eggs in these species. Since the rejection rates of parasitic eggs are high, the variation in rejection behaviour is low, indicating that the majority of individuals within the population are able to reject parasitic eggs. Thus, we predict that 1) the effect of age on the decision to reject foreign eggs is negligible, 2) the intraclutch variation should generally be low in all individuals, and that 3) rejection decisions should be highly dependent on the degree of mimicry between parasitic and host eggs. We found support for all these predictions in both species. Due to their highly sophisticated countermeasures against brood parasitism, Blackcaps and Chaffinches can probably be regarded as current winners of the arms race with the Common Cuckoo.

It has previously been shown that hosts of the Common Cuckoo *Cuculus canorus* may lower their intraclutch variation and increase their interclutch variation in egg appearance as an evolutionary response against interspecific brood parasitism (Øien *et al.* 1995, Soler & Møller 1996). This is thought to be an advanced adaptation to counter the evolution of mimetic eggs by the brood parasite, as described in the co-evolutionary arms race hypothesis (Dawkins & Krebs 1979, Davies & Brooke 1989a, Moksnes *et al.* 1990, Rothstein 1990). A lack of "proper" counteradaptations in hosts can be due to a lag in the origin or spread of such traits (the evolutionary lag hypothesis; Dawkins & Krebs 1979, Davies & Brooke 1989a, Rothstein 1990), or due to a balance between opposing selection pressures (the evolutionary equilibrium hypothesis; Zahavi 1979, Rohwer & Spaw 1988, Lotem *et al.* 1992, 1995, Lotem & Nakamura 1998, Takasu 1998). One possible scenario where an equilibrium may exist is when there are costs connected to recognition or rejection of foreign eggs (e.g. Rothstein 1982a, Davies & Brooke 1988, Marchetti 1992, Davies et al. 1996, Røskaft & Moksnes 1998). Due to such costs, some passerines may show conditional responses (see e.g. Lotem & Nakamura 1998) by rejecting parasitic eggs more frequently when being confronted with a parasite near their nest (e.g. Davies & Brooke 1988, Moksnes *et al.* 1993, 2000), or in periods when the probability of being parasitised is especially high (e.g. Alvarez 1996, Lindholm 2000). Lotem *et al.* (1992, 1995) obtained support for another scenario explaining the co-existence of both rejecters and acceptors in a host population. They found that young Great Reed Warbler *Acrocephalus arundinaceus* females breeding for the first time had a higher intraclutch variation in egg appearance and a lower rejection rate than older females. The difference in rejection behaviour was explained by an imprinting mechanism, in which young birds need experience to learn the appearance of their own eggs (see also Victoria 1972, Rothstein 1974, 1978). Since young Great Reed Warblers have a high intraclutch variation, the prolonged learning period could be necessary to reduce the costs of recognition errors (i.e.

erroneous rejection of own eggs from unparasitised clutches) (Lotem et al. 1992, 1995, Lotem & Nakamura 1998).

It has recently been shown that the rejection rate of parasitic eggs in a population of Reed Warblers *Acrocephalus scirpaceus* was significantly related to the intraclutch variation in egg appearance (Stokke *et al.* 1999). Those individuals that rejected parasitic eggs had a statistically significantly lower intraclutch variation than those that accepted such eggs. However, there were no indications that the rejection behaviour was dependent on age or conditional stimuli. In host species with intermediate rejection rates there might be considerable variation in rejection ability within and between populations (e.g. Brooke *et al.* 1998, Lindholm & Thomas 2000). In such species conditional responses could play a major role in defence against parasites (Øien *et al.* 1999). This has previously been found in the Reed Warbler (Davies & Brooke 1988, Lindholm 2000) and the Meadow Pipit *Anthus pratensis* (Moksnes *et al.* 1993), which are both intermediate rejecters of parasitic non-mimetic eggs (Davies & Brooke 1988, 1989b, Moksnes *et al.* 1990, Moksnes *et al.* 1994, Brooke *et al.* 1998, Stokke *et al.* 1999). The aim of the present study was to go one step further, and investigate what traits or cues that could influence egg rejection in species that are very good rejecters of parasitic eggs. Such species should, because of the minute variation in rejection ability between individuals within a population, show few conditional responses and their behaviour should be more or less fixed (Øien *et al.* 1999). We predict that since most of the individuals in the population are able to reject parasitic eggs, there should be **1)** no age-specific effects on rejection behaviour or intraclutch variation. In addition, we predict for the same reason that **2)** no relationship between rejection behaviour and intraclutch variation should be found. In other words, the intraclutch variation should generally be low in all individuals.

To examine these predictions, we studied two European passerines, the Chaffinch *Fringilla coelebs* and the Blackcap *Sylvia atricapilla*. Both are known to reject model Cuckoo eggs, both mimetic and non-mimetic, at high frequencies (in Norway 77-100%; Braa *et al.* 1992*,* Moksnes 1992*,* Moksnes & Røskaft 1992*,* Moksnes *et al.* 1994). Chaffinches have even been shown to recognise and reject foreign conspecific eggs that differ slightly from those of their own (Moksnes *et al.* 1991*,* Moksnes 1992, but see Davies & Brooke 1989b). Due to the high rejection rate of artificial Cuckoo eggs, which yields almost no variation in rejection behaviour in these species, we designed a more fine-tuned experiment by parasitising all clutches with an arbitrarily chosen conspecific egg. Both the Chaffinch and the Blackcap are known to have a low intraclutch variation and a high interclutch variation in egg appearance (Øien *et al.* 1995), and therefore the contrast between the parasitic and host eggs in this study varies from low to high among the different clutches. According to the arms race hypothesis, the evolution of such clutch characteristics by the hosts would make it easier to spot a foreign egg (low intraclutch variation) and in addition make it more difficult for the parasite to mimic the host eggs (high interclutch variation). We therefore predicted that **3)** the rejection behaviour should be highly dependent on the contrast between the parasitic and the host eggs; low contrast eggs should be difficult to detect and therefore should lead to acceptance while high contrast eggs should be easy to detect and thus lead to rejection. Such a response pattern has previously been found in the Chaffinch and the Brambling *Fringilla montifringilla* (Braa *et al.* 1992*,* Moksnes 1992), as well as in several other species (e.g. Davies & Brooke 1988*,* Higuchi 1989*,* Welbergen *et al.* 2001).

METHODS

The study on Chaffinches was carried out in Stjørdal, about 30 km north of Trondheim in central Norway (63°10´N, 10°20´E) in 1999-2000. The study area consists of three minor lowland Grey Alder *Alnus incana* woodlands in which the Chaffinch is breeding in high densities. This host population is allopatric with the Cuckoo, and during our two-year study, no Cuckoos were observed in the study area. A total of 85 nests were used in the experiments. Catching and ringing revealed that we found the nest of the same female both years in three cases. To avoid pseudoreplication we only used data from the first year (1999) for these females, thus 82 clutches were included in the analyses. Ten additional clutches were used as controls. These nests were visited and the eggs handled in the same way as the experimental clutches, except that no parasitic egg was introduced.

The study on Blackcaps was carried out in a deciduous woodland (85 ha) near the village Dolní Bojanovice in the southeastern part of the Czech Republic (48°52´N, 17°00´E) in 2000. This host population occurs in sympatry with the Cuckoo, but no case of parasitism has been recorded. Experiments were carried out in 35 nests, but unfortunately no clutches were assigned as controls in this species.

Both the Chaffinch and the Blackcap normally have one brood per season (Cramp 1992*,* Cramp & Perrins 1994). The fact that few of the parasitised hosts deserted their nests (see Results) indicates that the probability of using the same hosts twice for experiments was very low, and thus we avoided pseudoreplication.

In the Chaffinch, as well as in several other species (e.g. Moksnes *et al.* 1994*,* Palomino *et al.* 1998), it is the females that are responsible for the rejection of parasitic eggs. Chaffinches were caught in mist nets, photographed, and ringed with colour rings for individual identification. We later aged the birds as one-year-old (inexperienced) or older (experienced), based on the photos, according to criteria described in Svensson (1992) and Jenni & Winkler (1994). By this method the age of 25 female Chaffinch nest owners was determined. Unfortunately, we were not able to collect such data for the Blackcaps.

As already mentioned we used foreign conspecific eggs in the experiments, instead of Cuckoo eggs. The purpose was to obtain a more equal distribution between acceptors and rejecters of parasitic eggs. We consider this design as a more fine-tuned test of the variation in general recognition ability among individuals. Intraspecific brood parasitism has not been documented in these species (Braa *et al.* 1992, Yom-Tov 2001). The host clutch was experimentally parasitised on the day after the last egg was laid. This should make it possible for the host to assess the whole clutch when deciding to reject the parasitic egg or not. In the Chaffinch experiments, one randomly chosen egg was exchanged with a foreign conspecific egg from another nest. The removed egg was later used in the next experiment. In the Blackcap experiments, one foreign conspecific egg was added to the host clutch, but no host egg was removed. In both species, the whole clutch including the parasitic egg was photographed at the same time as the parasitic egg was added. The clutches and adult birds were photographed in a standardised manner, using a Canon EOS 100 camera with a ML 3 flashlight and Fujicolor 100 ASA film. The nests were visited every day for the next six days. If the parasitic egg was not removed or damaged (selective ejection), or the nest was not abandoned (desertion) within the termination of this period, it was regarded as accepted. The intraclutch variation in egg appearance and the contrast between the parasitic egg and the host eggs were later judged based on the photos, by three (Blackcap) and four (Chaffinch) experienced test persons.

The intraclutch variation was measured on the following scale from one to five (Øien *et al.* 1995, Stokke *et al.* 1999): 1) No variation, all the eggs were similar, 2) At least one egg differed slightly from the others, 3) At least one egg showed marked differences from the other eggs, 4) At least one egg differed dramatically from the others, and 5) All the eggs were different from one another. The contrast between the parasitic and host eggs was scored on the following scale from one to three (Braa *et al.* 1992, Moksnes 1992): 1) No contrast between host and parasitic eggs. The foreign egg was indistinguishable from the host eggs, 2) Medium contrast between host and parasitic eggs. The foreign egg could be distinguished from the host eggs, but the difference was only moderate, and 3) High contrast between host and parasitic eggs. The foreign egg was easily distinguished from the host eggs.

The mean of the assessments of the test persons was used both for intraclutch variation and contrast. This was justified by the fact that the test persons were highly consistent in their assessments, as measured by calculation of repeatability (Lessells & Boag 1987). The repeatability of scores for intraclutch variation in the Chaffinch was 0.32 ($F_{81,327}=2.87$, $P<0.001$). The corresponding values for the Blackcap was 0.52 ($F_{34,104}=4.26$, $P<0.001$). The repeatability of scores for contrast in the Chaffinch was 0.74 ($F_{81,327}=12.40$, $P<0.001$), while in the Blackcap it was 0.83 ($F_{34,104}=15.87$, $P<0.001$).

Recently, the method of assessing clutch variation and mimicry-score based upon human vision has been questioned (Cherry & Bennett 2001). Indisputably, birds and human colour vision are different in several ways, including sensitivity to UV-wavelengths (Bennett & Cuthill 1994). The egg classification in the present study would therefore probably have derived advantage from use of such measurements, which we unfortunately were unable to do due to lack of equipment. However, we see one problem concerning use of photospectrometry. Cherry & Bennett (2001) focus on measurements of eggs in museum collections. When it comes to field studies the situation is more complex. In the present study it is probably important to reduce the disturbance of the hosts, particularly when the aim is to reveal rejection behaviour, which could be influenced by disturbance. The traditional method of taking photos of the clutch is a simple and quick process in contrast to photospectrometry, which involves mounting and use of more advanced equipment and thus is a more time-consuming and serious source of disturbance. Even if the traditional method is less accurate, the question is if it is accurate enough for the measurements in the present study. This question is difficult to answer. However, many results obtained earlier by the method have been in accordance with what it should be expected that the birds perceived (see e.g. Lotem *et al.* 1995, Øien *et al.* 1995, Jackson 1998, Stokke *et al.* 1999, Welbergen *et al.* 2001), and it is hard to believe that these relationships were only coincidences. We therefore assume that the method used in the present study has been satisfactory for quantifying the actual differences between eggs.

The data-material was analysed using SPSS 10.0 for Windows (SPSS Inc., Chicago, USA). All the tests are two-tailed.

RESULTS

Rejection behaviour and method of rejection

The parasitic egg was rejected in 42 (51.2%) out of the 82 Chaffinch clutches. In only 9 (11.0%) cases the nest was deserted, while the parasitic egg was selectively ejected in 33 cases (40.2%). There was no difference in mean contrast between the parasitic and host eggs between deserters ($\overline{x}$=2.53 ± 0.44 (SD), N=9) and ejectors ($\overline{x}$=2.40 ± 0.52 (SD), N=33) (Mann-Whitney U test: U=132, N_1=9, N_2=33, P=0.61). None of the 10 Chaffinch control clutches was deserted, even though they were visited just as often as experimental nests, indicating that desertions are genuine responses towards parasitic eggs. However, probably due to a small sample size, the difference in desertion rates between experimental and control clutches was not statistically significant (Fisher's Exact Test, P=0.59). Regarding the Blackcap, the parasitic egg was rejected in 13 (37.1%) out of the 35 experiments. In two of the experiments the nest was deserted (5.7%), while the foreign egg was selectively ejected from 11 clutches (31.4%). There was no statistically significant difference in the proportion of acceptors and rejecters of parasitic eggs between Chaffinches and Blackcaps in this study (Fisher's Exact Test, P=0.23).

Rejection behaviour, contrast and intraclutch variation

Insert Figure 1 and 2 approx. here

The mean contrast between parasitic and host eggs (Figure 1) differed significantly between acceptors and rejecters in both Chaffinches ($\overline{x}$=1.65 ± 0.52 (SD), N=40 vs. $\overline{x}$=2.43 ± 0.50 (SD), N=42, respectively, Mann-Whitney U test: U=251, N_1=40, N_2=42, P<0.001) and Blackcaps ($\overline{x}$=1.67 ± 0.48 (SD), N=22 vs. $\overline{x}$=2.26 ± 0.60 (SD), N=13, respectively, Mann-Whitney U test: U=62, N_1=22, N_2=13, P=0.005). However, the mean intraclutch variation in egg appearance (Figure 2) was not statistically significant between acceptors and rejecters in neither Chaffinches ($\overline{x}$=1.96 ± 0.68 (SD), N=40 vs. $\overline{x}$=1.86 ± 0.57 (SD), N=42, respectively, Mann-Whitney U test: U=778, N_1=40, N_2=42, P=0.56) or Blackcaps ($\overline{x}$=1.65 ± 0.62 (SD), N=22 vs. $\overline{x}$=1.54 ± 0.40 (SD), N=13, respectively, Mann-Whitney U test: U=139, N_1=22, N_2=13, P=0.88). We also investigated possible differences in intraclutch variation in egg appearance between individuals that accepted or rejected a moderately mimetic parasitic egg in order to control for the effect of contrast on rejection behaviour. We recoded the mean contrast into a class variable (1 = 1-1.44, 2 = 1.45-2.44, 3 = 2.45-3) to make these analyses, and selected the cases where contrast was moderate (i.e. = 2). The mean intraclutch variation in egg appearance was not statistically significant between acceptors and rejecters in neither Chaffinches ($\overline{x}$=2.06 ± 0.77 (SD), N=22 vs. $\overline{x}$=1.81 ± 0.66 (SD), N=18, respectively, Mann-Whitney U test: U=158, N_1=22, N_2=18, P=0.27) or Blackcaps ($\overline{x}$=1.62 ± 0.65 (SD), N=15 vs. $\overline{x}$=1.71 ± 0.30 (SD), N=7, respectively, Mann-Whitney U test: U=37, N_1=15, N_2=7, P=0.26). A binary logistic regression analysis was carried out to determine the combined effect of contrast and intraclutch variation (independent variables) on rejection behaviour (dependent variable). When regarding the Chaffinch, rejection behaviour was significantly affected by the contrast between parasitic and host eggs (Wald χ^2_1=20.53, P<0.001); as the contrast between parasitic and host eggs increased, so did the rejection rate of the parasitic egg (B=2.86 ± 0.63 (SD)). However, the intraclutch variation in egg appearance had no effect on rejection behaviour (Wald χ^2_1=1.55, P=0.21). Among the Blackcaps, there was also a statistically significant effect of contrast on rejection behaviour in the same direction as for the Chaffinches (Wald χ^2_1=6.10, P=0.01, B=2.46 ± 1.00 (SD)). Again, the intraclutch variation had no effect on rejection behaviour (Wald χ^2_1=1.04, P =0.31).

The effect of host age

One-year-old Chaffinch females had a slightly higher mean intraclutch variation ($\overline{x}$=2.10 ± 0.43 (SD), N=10) than older females ($\overline{x}$=1.88 ± 0.65 (SD), N=15), but this difference was not statistically significant (Mann-Whitney U test: U=53, N_1=10, N_2=15, P=0.24).

The ability to reject foreign eggs was not statistically different between one-year-old and older females. Six out of 10 one-year-old females, and seven out of 15 older females rejected the parasitic egg (Fisher's Exact Test, P=0.69). This comparison was justified by the fact that the mean contrast between the parasitic egg and the host eggs between one-year-old- and older females ($\overline{x}$=2.20 ± 0.63 (SD), N=10 vs. $\overline{x}$=2.00 ± 0.66 (SD), N=15, respectively) was not statistically significantly different (Mann-Whitney U test: U=60, N_1=10, N_2=15, P=0.40).

There were no age-specific differences in the way the females rejected the foreign egg. Five out of six one-year-old females selectively ejected the parasitic egg, while six out of seven older females used the same method of rejection (Fisher's Exact Test, P=1.00). One female in each age class rejected the parasitic egg by desertion.

The period from parasitism until rejection of the foreign egg between one-year-old and older Chaffinch females ($\overline{x}$=2.83 days ± 1.33 (SD), N=6 vs. $\overline{x}$=3.00 days ± 1.83 (SD), N=7, respectively) was not statistically significantly different (Mann-Whitney U test: U=21, N_1=6, N_2=7, P=0.94).

As stated in the Material and Methods section, we have no specific data on age in the Blackcap. However, there were no statistically significant difference in distribution of acceptors and rejecters throughout the breeding season (Table 1, χ^2_2=4.16, P=0.13). In addition, there was no statistically significant difference in mean clutch size between

Insert Table 1 approx. here

acceptors ($\bar{x}$=4.95 ± 0.62 (SD), N=19) and rejecters ($\bar{x}$=4.85 ± 0.80 (SD), N=13) of parasitic eggs (Mann-Whitney U test: U=113, N_1=13, N_2=19, P=0.68). These results may indicate that the possibility of age specific rejection behaviour within this Blackcap population is negligible.

DISCUSSION

The high rejection rates of non-mimetic conspecific eggs by Chaffinches and Blackcaps in the present study correspond well with what has been reported previously by other authors (Davies & Brooke 1989b*,* Braa *et al.* 1992*,* Moksnes 1992*,* Moksnes & Røskaft 1992*,* Moksnes *et al.* 1994). However, the response towards foreign eggs in these species is intriguing, because as far as we know none of them are currently regularly parasitised by the Cuckoo in Europe. As mentioned above we did not detect any intraspecific brood parasitism in neither Chaffinches nor Blackcaps (see also Yom-Tov 2001), which for the former species is consistent with previous studies (Braa *et al.* 1992). The high rejection rate of foreign eggs has therefore most likely evolved as a consequence of previous parasitism by Common Cuckoos. In support of this view is the fact that in a large-scale study of Cuckoo egg collections at European museums, Moksnes & Røskaft (1995) found 180 parasitised clutches of Blackcaps and 76 parasitised clutches of Chaffinches. All together, 117 (65%) of the parasitic eggs among Blackcaps belonged to the corresponding Cuckoo egg-morph (*Sylvia*). In the Chaffinch, nine (11.8%) of the Cuckoo eggs belonged to the *Fringilla* egg-morph. These clutches were mostly collected about a century ago, and indicate that both species were formerly more or less regularly parasitised at least in part of their range. Glue & Murray (1984) found that three out of 1696 (0.17%) Blackcap nests in Britain were parasitised by the Cuckoo, and Malchevsky (1960) reported that the Chaffinch is occasionally parasitised in the northwestern and central regions of former USSR, indicating that these species might still be parasitised sporadically in parts of Europe. Additional support for a former interaction between Cuckoos and these passerines is the fact that both Blackcaps and Chaffinches respond very aggressively towards dummy Cuckoos near their nests (Moksnes *et al.* 1990), and obviously look upon the parasite as a threat.

The results support prediction (1) that there is no effect of age on intraclutch variation or rejection behaviour in the Chaffinch population. The even distribution of rejecters and acceptors during the breeding season and similar clutch size in both groups (see also Stokke *et al.* (1999)) also indicates negligible effects of age in the Blackcap population. These findings are contrary to what was found by Lotem *et al.* (1992, 1995) in the Great Reed Warbler, but in close consistence with the results obtained by Stokke *et al.* (1999) for Reed Warbler; Marchetti (2000) for Yellow-browed Leaf Warbler *Phylloscopus humei*; Soler *et al.* (2000) for Rufous-tailed Scrub Robin *Cercotrichas galactotes*; and T. Amundsen, P.T. Brobakken, A. Moksnes & E. Røskaft (unpubl. data) for Bluethroat *Luscinia svecica* (see also Gosler *et al.* 2000). For Chaffinches and Blackcaps the results, therefore, do not support the existence of an evolutionary equilibrium between rejecters and acceptors based on a learning process among first year breeders. Regarding the Chaffinch, this is further supported by the finding that one-year-old females do not need longer time to reject foreign eggs than older females. In some species, like the Great Reed Warbler in Japan, first-year breeders seem to need a prolonged learning period, which enables them to learn the whole spectrum of variation among own eggs (Lotem et al. 1992, 1995). However, species with a low intraclutch variation, like Chaffinches and Blackcaps, do not need a prolonged learning period to recognise their own eggs due to the minor variation among them making the probability of recognition errors negligible (Rodríguez-Gironés & Lotem 1999).

Furthermore, as predicted (2) there was no relationship between rejection behaviour and intraclutch variation in egg appearance among the species in the present study, as would be expected if there was little variation in host defences within these host populations (Øien *et al.* 1999). In accordance with previous studies (Braa *et al.* 1992*,* Moksnes 1992) and our prediction (3), we found that rejection of foreign eggs was highly dependent upon the degree of similarity between parasitic and host eggs. When there was a marked contrast between the parasitic and host eggs, the majority of the individuals were able to recognise and reject the foreign egg (Chaffinches; 88.5%, Blackcaps; 60.0%). However, as the degree of mimicry between host and parasitic eggs became better, the ability to reject the foreign egg was poorer. It is therefore reasonable to assume that the failure to detect foreign eggs when they are too similar to own eggs, is based upon limitations of the cognitive system (e.g. McLean & Maloney 1998), and that there is a threshold regarding the visual system for detection and rejection of such eggs. Since neither Chaffinches nor Blackcaps in our study areas are currently parasitised and rarely (Blackcaps) or never (Chaffinches) encounter Cuckoos, conditional cues like Cuckoos near their nests are also of minor help as an aid in the detection of a foreign egg.

Our results for Chaffinches and Blackcaps support the hypothesis proposed by Øien *et al.* (1999), stating that good rejecters of non-mimetic eggs should be more or less fixed in their responses. This means that they will reject parasitic eggs as long as their cognitive system can discriminate between the parasitic and their own eggs. Their low intraclutch variation makes it easier to detect even a relatively good mimetic parasitic egg. In addition, their high interclutch variation makes it very difficult for brood parasites to successfully parasitise these species (Øien *et al.* 1995*,* Soler & Møller 1996). Even though the parasite deposits a perfect mimetic egg in one host nest, the high interclutch variation implies that the same egg type in another host nest would appear as non-mimetic. In a previous study, Moksnes (1992) found that Chaffinches really have the knowledge of how their own eggs look like, and that they reject any eggs that look different from this picture (see also Rothstein 1975, 1982b). In the Reed Warbler, which is an intermediate rejecter, some individuals are unable to recognise and reject even highly non-mimetic eggs, and thus may not have the genetic background necessary to detect such eggs (Stokke *et al.* 1999). It therefore seems that species like the Chaffinch and the Blackcap have evolved advanced counteradaptations against the Cuckoo. Since they presently are not utilised as hosts, but obviously look on Cuckoos as a threat, these species can be regarded as current winners in their co-evolutionary arms race with the brood parasite. However, intermediate rejecter species like the Reed Warbler, may on the other hand still be at an earlier stage in the arms race, or at an evolutionary equilibrium due to costs associated with recognition or rejection of eggs (Davies & Brooke 1988, Davies et al. 1996; but see Røskaft et al. 2002).

To sum up; when the defences of various host species (e.g. Reed Warbler (Stokke *et al.* 1999) and Chaffinch/Blackcap (this study)) against brood parasitism are considered, we basically agree with the conclusion made by Davies (2000); there could be a mixture of systems that are at equilibrium and/or at different stages of a continuing arms race. Some of the responses towards parasites are evolved adaptive responses, while some are proximate decisions based upon cognitive experience. Caution should therefore be taken in stating generalisations. Instead, studies on various specific host-parasite interactions will lead to a better understanding of such systems in general.

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Figure legends

Figure 1 (Stokke *et al.*)**.** Mean (± SD) contrast between parasitic and host eggs among acceptors and rejecters of foreign conspecific eggs in Chaffinches and Blackcaps. Sample sizes shown above the bars.

Figure 2 (Stokke *et al.*)**.** Mean (± SD) intraclutch variation in egg appearance among acceptors and rejecters of foreign conspecific eggs in Chaffinches and Blackcaps. Sample sizes shown above the bars.

Table 1. Distribution of Blackcap rejecters and acceptors of foreign conspecific eggs throughout the breeding season. Date of egg laying refers to the date when first egg was laid

	Date of egg laying		
	15 April-4 May	5-24 May	25 May-13 June
Acception	12	3	4
Rejection	4	6	3
Total	16	9	7

The distribution of acceptors and rejecters throughout the breeding season was not statistically significantly different (χ^2_2=4.16, P=0.13).

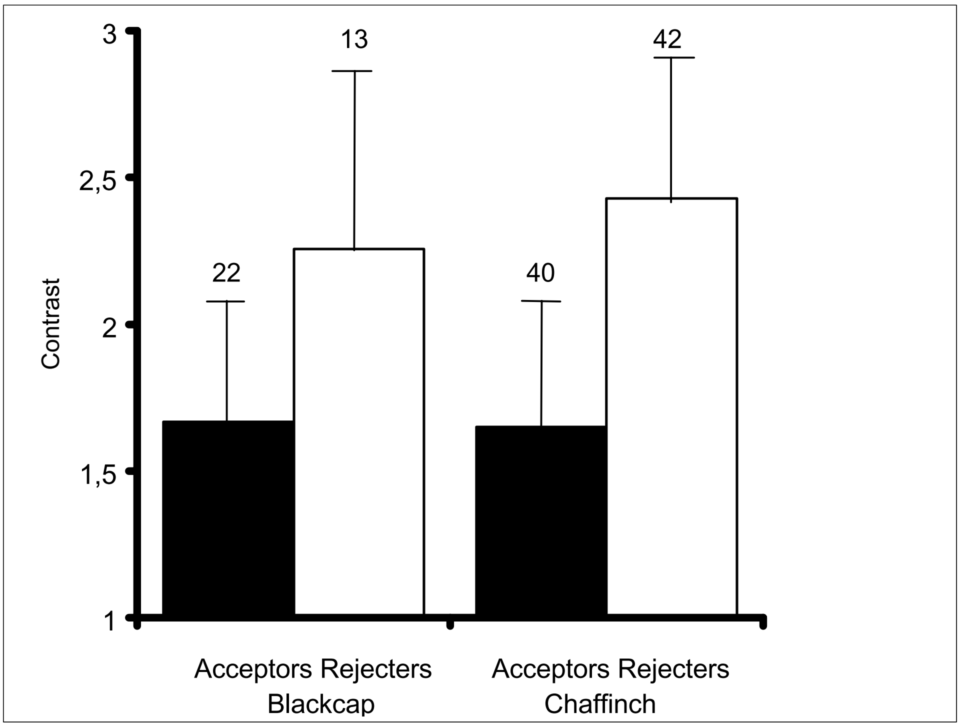
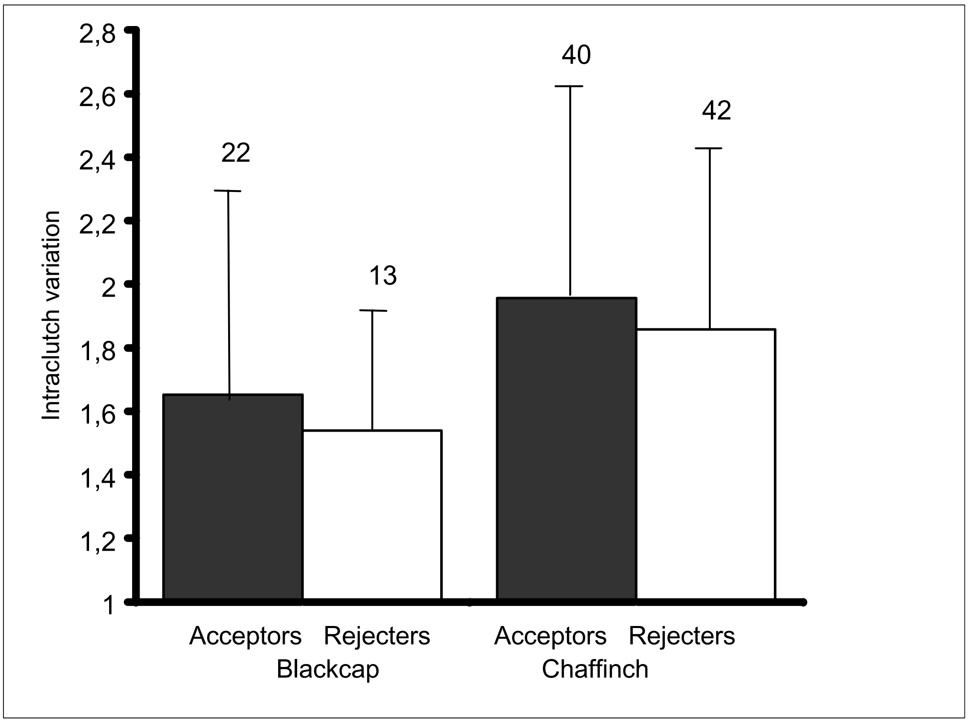


Fig.1 Stokke *et al.*

Fig. 2 Stokke *et al.*



Paper IV

Submitted manuscript (Behaviour)

Costs associated with recognition and rejection of parasitic eggs in two European passerines

by

B.G. Stokke, M. Honza, A. Moksnes, E. Røskaft & G. Rudolfsen

COSTS ASSOCIATED WITH RECOGNITION AND REJECTION OF PARASITIC EGGS IN TWO EUROPEAN PASSERINES

by

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Summary

Many hosts of avian brood parasites accept parasitic eggs even though successful parasitism frequently is detrimental to the hosts' own reproduction. Such behaviour seems suboptimal, but has been explained by the existence of opposing selective pressures operating against the evolution of proper host defence. Costs associated with rejection and recognition of eggs are central topics in this respect. Here we report cases of such costs in two European passerines (chaffinches and blackcaps), that are good rejecters of foreign eggs, even though the common cuckoo does not presently use them as hosts. Since high rejection rates are maintained in the absence of parasitism we predict that few recognition errors are made by these species. We tested this prediction by monitoring the occurrence of such errors in both experimentally parasitised and unparasitised host clutches. We found support for the prediction, as our results show that recognition errors are at best rare events in these two species. We discuss the role of intraspecific brood parasitism as well as other explanations for the retention of a high rejection rate in these species. Various studies have reported mixed support for the occurrence of recognition errors among hosts of the cuckoo, and we consider other explanations for the existence of both acceptors and rejecters of foreign eggs in host populations.

Introduction

The common cuckoo Cuculus canorus is regarded as a specialist brood parasite (Chance, 1922, 1940; Baker, 1942; Lack, 1968; Gibbs et al., 2000). This specialisation has led to the occurrence of at least 16 cuckoo tribes or gentes in Europe, each parasitising one or a few passerine species (Wyllie, 1981; Alvarez, 1994; Moksnes & Røskaft, 1995). In the coevolutionary arms race between the cuckoo and its hosts both sides have evolved adaptations and counteradaptations to enhance their reproductive success (Dawkins & Krebs, 1979; Davies & Brooke, 1989a, 1989b; Moksnes et al., 1990; Rothstein, 1990). Several cuckoo gentes have thus evolved eggs that mimic those of the host (Baker, 1942; Southern, 1954; Wyllie, 1981; Brooke & Davies, 1988). The hosts on the other hand, have evolved specific clutch characteristics like a low intraclutch and a high interclutch variation in egg appearance to be better able to discriminate against the mimetic parasitic egg (Øien et al., 1995; Soler & Møller, 1996; Stokke et al., 1999, 2002). Successful cuckoo parasitism is detrimental to the host reproduction (Lack, 1968; Payne, 1977; Wyllie, 1981), and thus there is a strong selection for evolving traits that could enhance the rejection of parasitic eggs. However, many hosts show no or intermediate rejection rates towards cuckoo eggs (e.g. von Haartman, 1981; Davies & Brooke, 1989a; Moksnes et al., 1990; Brooke et al., 1998; Alvarez, 1999; Stokke et al., 1999). Recently, much effort has been made in revealing selection pressures that could oppose the evolution of proper host defences against avian brood parasitism, and set the stage for an equilibrium between acceptors and rejecters of parasitic eggs within a host population (Zahavi, 1979; Rohwer & Spaw, 1988; Moksnes et al., 1991; Lotem et al., 1992, 1995; Lotem & Nakamura, 1998). Central topics in this respect are rejection costs and recognition errors in the process where hosts are evaluating and deciding if they are parasitised or not (e.g. Molnár, 1944; Rothstein, 1976, 1977, 1982a; Davies & Brooke, 1988, 1989a, 1989b; Rohwer et al., 1989; Moksnes et al., 1991; Marchetti, 1992; Røskaft et al., 1990, 1993; Lotem et al., 1992, 1995; Lorenzana & Sealy, 2001). Rejection costs are loss of own eggs in the process when hosts are rejecting parasitic eggs. This could be ejection or destruction of own eggs in addition to the foreign eggs or desertion of the whole clutch. Recognition errors are defined as erroneous rejection of own eggs (ejection or desertion) in cases when hosts are not parasitised (Rothstein & Robinson, 1998). Several attempts have been made to model which host behaviour that should be adaptive when confronted with brood parasitism, based upon the influence of these costs (e.g. Davies & Brooke, 1989b; Takasu et al., 1993; Davies et al., 1996; Lotem & Nakamura, 1998; Takasu, 1998; Røskaft & Moksnes, 1998; Rodríguez-Gironés & Lotem, 1999). However, rejection costs and recognition errors as opposing selection pressures in the evolution of proper host defences are likely to have different effects depending on the host-parasite system in question (Rothstein, 1990; Røskaft & Moksnes, 1998; Rothstein & Robinson, 1998; Takasu, 1998). In common cuckoo hosts, rejection costs are of minor importance as opposing selection pressure against evolution of host defences. Only recognition errors can tilt the selection in favour of acception, if the costs associated with such errors are high enough (Rothstein, 1990; Lotem et al., 1995; Rothstein & Robinson, 1998). In some cases it can be very difficult to separate these two terms, e.g. when hosts are parasitised but reject own eggs instead of the parasitic egg. Such cases could be interpreted as recognition errors, but could as well be defined as rejection costs (Røskaft et al., 2002). This is particularly true among small cuckoo hosts, which often have great difficulties in ejecting the thick-shelled parasitic egg (Moksnes et al., 1991). In the process of trying to eject the foreign egg, such hosts could instead accidentally destroy or eject some of their own eggs. Thus, even though these cases are rejection costs, they might appear as recognition errors. The only proper way to detect true recognition errors is thus to record hosts that reject own eggs in unparasitised clutches. Such errors are most likely to occur when the parasite has evolved mimetic eggs (Rothstein, 1982a; Brooke & Davies, 1988; Davies & Brooke, 1988), and/or when the hosts have a high intraclutch variation in egg appearance (Davies & Brooke, 1998). In such cases the parasite egg appearance can be within the range of the host egg intraclutch variation (Rothstein, 1982a). Even though recognition errors are hypothesised to be important for the evolution of host defences, very few studies have so far documented the existence of such costs (Davies & Brooke, 1988; Marchetti, 1992).

In the present study we investigate the occurrence of rejection costs and possible recognition errors in two common European passerines, the chaffinch Fringilla coelebs and the blackcap Sylvia atricapilla. Both species are rejecting foreign parasitic eggs at high rates (Davies & Brooke, 1989a; Moksnes et al., 1990, 1994; Moksnes, 1992), they have a low intraclutch variation and a high interclutch variation in egg appearance (Øien et al., 1995), but none of them are currently used regularly as cuckoo hosts in Western Europe. Both species are known to puncture eject parasitic eggs (Moksnes et al., 1994). The maintenance of a high rejection rate in spite of the absence of interspecific brood parasitism is intriguing, and we thus predict (1) that these two species should make no or at least very few recognition errors. Alternatively, the rejection behaviour is maintained because of high levels of intraspecific brood parasitism. However, no cases of such parasitism have previously been detected in neither chaffinches nor blackcaps (Braa et al., 1992; see also Yom-Tov, 2001).

We have focused mainly on the chaffinch, because our study population is allopatric with the cuckoo, and thus do not experience cuckoos in their breeding area. This implies that there is no partial egg loss due to egg predation by cuckoos, which could lead to a higher estimate of recognition errors than is really the case. However, chaffinches usually respond very aggressively to a cuckoo dummy mounted near the nest and obviously look upon the brood parasite as a threat (Moksnes et al., 1990; Braa et al., 1992). If recognition errors exist in this host population, we predict (2) that individuals that are exposed to a stuffed cuckoo dummy near their nest (i.e. receive a conditional stimuli) should be more prone to make errors than individuals that have not seen the dummy (Røskaft et al., 2002). In several other studies it has been found that such conditional stimuli increase the rejection of foreign eggs (Davies & Brooke, 1988; Moksnes & Røskaft, 1989; Moksnes et al., 1993, 2000; but see Braa et al., 1992; Lindholm, 2000).

Material and methods

A chaffinch population in Stjørdal, about 30 km north of Trondheim in central Norway (63°10´N, 10°20´E), was studied during the 1999-2001 breeding seasons. The study area consists of lowland grey alder Alnus incana forests in which the chaffinch is a common breeder. No cuckoos are present in this area, and thus this population does not experience these brood parasites in the breeding season. The blackcap study was carried out in a deciduous forest in the southeastern part of the Czech Republic (48°52´N, 17°00´E) during the 2000-2001 breeding seasons. This population occurs in sympatry with the cuckoo, but no cuckoo eggs were found in blackcap nests during our study.

When studying rejection costs, the host clutches were parasitised with a foreign conspecific egg on the day after the last egg was laid. It was thus possible for the host to assess the whole clutch when deciding to reject the parasitic egg or not. Both chaffinches and blackcaps reject foreign non-mimetic eggs at a high rate (Braa et al., 1992; Moksnes, 1992; Moksnes & Røskaft, 1992; Moksnes et al., 1994). We therefore used conspecific eggs instead of artificial cuckoo eggs to obtain a more equal distribution between acceptors and rejecters of parasitic eggs. We consider this design as a more fine-tuned test of the variation in general recognition ability among individuals. In the chaffinch experiments (N = 82), one randomly chosen egg was exchanged with a foreign conspecific egg from another nest. The removed egg was later used in the next experiment. In the blackcap experiments (N = 38), one foreign conspecific egg was added to the host clutch, but no host egg was removed. Both chaffinch and blackcap nests were visited every day for the next six days. If the parasitic egg was not removed or damaged, or the nest was not abandoned within the termination of this period, it was regarded as accepted. To keep track of rejection costs and possible recognition errors, we also monitored if host eggs disappeared from the nests within the six-day period. Abandonment of the clutch without destroying or ejecting the parasitic or own eggs is termed as desertion. Ejection of only the foreign egg with no harm to own eggs is defined as selective ejection or ejection without cost, while ejection of the parasitic egg in addition to damage or removal of own eggs is termed as unselective ejection or ejection with costs. Ejection of own egg(s) only without any harm to the parasitic egg is defined as rejection errors.

To reveal potential recognition errors in unparasitised clutches, we presented at 27 chaffinch and five blackcap nests a dummy cuckoo (<0.5 m from the nest; Braa et al., 1992) on the day that the host female had completed her clutch. In addition, 14 chaffinch nests were only visited and monitored without presentation of the dummy cuckoo. No egg experiments were done at any of these nests. All nests were visited for the next six days to look for recognition errors, which were defined as desertions or ejection of own eggs in these unparasitised nests.

In chaffinches, it is the females that are responsible for rejection of foreign eggs (Moksnes et al., 1994). At the start of the breeding season, chaffinch females were captured, ringed and aged so that we could look for possible age effects when calculating costs of rejection and recognition. Individuals were classified into two age-classes, first-year breeders and experienced breeders. Unfortunately, no such data were obtained for blackcaps.

All the statistical tests are two-tailed.

Results

Rejection costs and rejection errors at parasitised nests

Table 1 approximately here!

Table 1 summarises the rejection behaviour towards the foreign conspecific egg in the two host species. Chaffinches suffered rejection costs in 14 (33.3%) out of 42 rejections, while blackcaps suffered such costs in six (40.0%) out of 15 rejections (Table 1). The difference between the species in proportion of rejection costs was not statistically significantly different (Fisher's Exact Test, p = 0.76). Cost of rejection (including deserted nests) in chaffinches was 0.24 own eggs pr. rejected conspecific egg, while in blackcaps the cost was 0.30 own eggs pr. rejected egg. In five cases where rejection costs were observed in chaffinches, one host egg was ejected in addition to the parasitic egg. Two of these females were identified; one first-year breeder and one experienced breeder. In addition, nine parasitised clutches were abandoned, most likely as a response to the parasitic egg (Stokke et al., submitted; see also Hosoi & Rothstein, 2000). The age was known for two of the deserter females; one first-year breeder and one experienced breeder. In five cases where rejection costs were observed (two ejections and three desertions) the contrast between the parasitic and the host eggs was moderate, while in nine cases (three unselective ejections and six desertions) this contrast was high. Among the blackcaps, rejection costs because of unselective ejection occurred in three nests (Table 1). In two cases the hosts removed three host eggs together with the parasitic egg (low and moderate contrast between the parasitic and host eggs), while in one case a single host egg was removed together with the foreign egg (high contrast between the parasitic and host egg). In addition, three clutches were deserted when confronted with the parasitic egg. In two of these clutches the contrast between the parasitic and host eggs were moderate, while in one case the contrast was high.

In chaffinches rejection errors occurred in only one out of 40 clutches (2.5 %; 0.53 % of all egg laid (N=189)), while it was found in two out of 23 (8.7 %; 1.75 % of all eggs laid (N=114)) blackcap clutches (Table 1). There was no significant difference in the frequency of rejection errors between the two species (Fisher's Exact Test, p = 0.55). The only incidence of a rejection error in a parasitised chaffinch clutch occurred when all the three host eggs were ejected, while the host female continued to incubate the parasitic egg. In this case all the host eggs were infertile and a little deformed. The egg content was not evenly distributed, but concentrated in one end of the eggs. This particular host therefore probably looked upon its own eggs as abnormal, and thus chose to reject these eggs. In both cases where blackcap hosts made rejection errors, one host egg was removed while the moderately mimetic parasitic egg remained unharmed in the nest. The intraclutch variation in egg appearance as judged by the human eye was very low in both cases. The hosts continued incubating the rest of the eggs, including the parasitic egg.

Recognition errors in unparasitised nests

Table 2 summarises recognition errors made by chaffinches and blackcaps both with and without presentation of a dummy cuckoo near their nest. There were two cases of recognition errors by ejection of own eggs in chaffinches (one with and one without the cuckoo dummy treatment) both made by old, experienced females. However, the nest histories in these two cases are extraordinary. In the first case mentioned, two eggs appeared as normal in the nest on two consecutive days. Then there was, strangely, a period of seven days with no changes in the nest content (two cold eggs). On the eight day the third egg was laid, and a fourth egg appeared the next day. The following day one host egg had disappeared (the third laid egg). The cuckoo dummy was presented later on the same day. Nothing happened with the clutch until the fifth day after the cuckoo experiment. Then another host egg disappeared (the first laid egg), and the female continued to incubate the remaining two eggs. The last ejected host egg was somewhat different from the two remaining host eggs, in that it had more spots distributed at the pointed end of the egg. However, the ground colour was the same on all three eggs and it is unlikely that a second female had laid the egg that was ejected. The other female that made a potential recognition error also had an irregular laying-pattern. Three eggs were laid on three consecutive days, but then there was an interruption in breeding and three cold eggs remained in the nest for three days. However, on the fourth day one host egg had disappeared (the third laid egg) and the female incubated the remaining two eggs. The host egg that was ejected was not different from the rest of the clutch in appearance, at least to the human eye, indicating that the same female laid all the eggs. At a third nest, one of the chaffinch pairs that were exposed to a cuckoo dummy deserted their nest. The age of the deserter female was unknown. None of the pairs that did not receive such a treatment deserted their clutch. The difference in the frequency of potential recognition errors (desertions and ejections) between the two experimental groups was not statistically significant (Fisher's Exact Test, p = 1.00), and we have thus pooled the results from the two

Table 2 approximately here!

groups in the further analyses. Recognition errors in unparasitised chaffinch clutches thus occurred in three (7.3 %) out of 41 experiments, and out of a total of 194 eggs only eight (4.1 %) were erroneously rejected. None of the unparasitised blackcaps made any recognition errors. Unfortunately, the interpretation of the results for this species is not conclusive because of a small sample size.

Discussion

Our results show that both chaffinches and blackcaps experience considerable costs when rejecting foreign conspecific eggs from their nests (see also Braa et al., 1992). These costs are probably even higher when hosts are rejecting the thick-shelled cuckoo eggs instead of conspecific eggs (Moksnes et al., 1991; see also Rohwer et al., 1989). As stated previously, such costs can be tolerated in cuckoo hosts due to the detrimental effects when being successfully parasitised. More interesting in this respect are recognition errors associated with such rejection behaviour. The maintenance of a high rejection rate of foreign eggs despite the lack of parasitism in chaffinches and blackcaps suggests that there are few costs in terms of recognition errors associated with such behaviour in these two species. As predicted (1), our data on both experimentally parasitised and unparasitised clutches supports this hypothesis. Regarding the chaffinch, we found no support for increasing costs due to erroneous rejection of own eggs in unparasitised nests when exposed to a dummy cuckoo (prediction 2). In accordance with our results, Braa et al. (1992) who also parasitised chaffinches with real conspecific eggs (N = 24), found only one possible case of a recognition error where one host egg was ejected without any damage to the parasitic egg. Thus, real recognition errors are at best very rare in this species. In fact, all the three cases of potential recognition errors by ejection in our chaffinch population had nest histories that deviated from normal. The egg disappearance in these cases could therefore be due to other causes than suspicion of being parasitised. Furthermore, occasional disappearance of own eggs from unparasitised clutches also occur in species that accept foreign eggs, and can be due to jostling, partial predation and other reasons (e.g. Rothstein, 1982b, 1986; Kemal & Rothstein, 1988; Lerkelund et al., 1993; E. Røskaft, pers. obs.). However, the two cases of rejection errors in blackcaps, where one host egg was removed while the partially mimetic parasitic egg remained unharmed, could be interpreted as incidents where females suspected that they were parasitised but removed the wrong egg due to cognitive constraints (i.e. the parasitic egg was too similar to the host eggs) (e.g. McLean & Maloney 1998).

Data on other good rejecters of foreign eggs correspond well to our findings. Marchetti (1992) studied a yellow-browed leaf warbler Phylloscopus inornatus population and found that this species make a few recognition errors (one own egg in eight out of 180 unparasitised nests; 4.4 %). This population occurs in sympatry with the cuckoo, and could thus potentially still be occasionally parasitised or loose eggs due to partial egg predation by the brood parasite. The data on recognition errors made by this species could therefore be overestimated.

As stated previously, both blackcaps and chaffinches have a low intraclutch and a high interclutch variation in egg appearance (Øien et al., 1995). The low intraclutch variation makes it easier to recognise even a relatively mimetic parasitic egg. The maintenance of the high level of rejection and specific clutch characteristics in chaffinches and blackcaps is most certainly not presently selected for by intraspecific brood parasitism, because no cases of intraspecific brood parasitism were detected in neither chaffinches nor blackcaps (see also Braa et al., 1992; Yom-Tov, 2001). Instead, the behaviour is probably maintained because of the lack of opposing selection pressures in form of recognition errors. It thus seems likely that the co-evolution between the cuckoo and blackcaps/chaffinches best can be explained by the "Single trajectory model" (Rothstein, 2001; see also Welbergen et al. (2001) for retention of rejection behaviour in unparasitised populations). According to Rothstein (2001), host adaptations will be retained for long periods even in the absence of selection pressures favouring these traits. This retention will of course depend upon the costs associated with expressing such traits. If these adaptations are selectively neutral, they may be maintained in the population for a long time. Blackcaps and chaffinches are very common birds and holds large populations. It is thus unlikely that host adaptations will be lost through stochastic factors like random genetic drift as long as they have spread thoroughly.

Several studies have shown that hosts can modify their rejection behaviour according to conditional stimuli. However, in species with high rejection rates towards foreign eggs like chaffinches and blackcaps, it is hypothesised that there should be few such conditional responses (Øien et al., 1999). Both results from this study and from Braa et al. (1992) support this hypothesis. There were no more rejections of foreign conspecific eggs in another good rejecter of foreign eggs, the brambling Fringilla montifringilla when pairs were confronted with a dummy cuckoo at their nest than without such a treatment (Braa et al., 1992). In our study we have shown that the amount of recognition errors did not increase after the treatment with a dummy cuckoo. What then about species with intermediate rejection rates? Øien et al. (1999) hypothesised that such species should show more conditional responses in their rejection decisions. Support for such conditional responses have been found in several cuckoo hosts (Davies & Brooke, 1988; Moksnes & Røskaft, 1989; Moksnes et al., 1993; Alvarez, 1996). However, evidence for recognition errors in such species are few. The reed warbler Acrocephalus scirpaceus is a common host of the cuckoo showing conditional responses in rejection behaviour (Davies & Brooke, 1988; Øien et al., 1998; Moksnes et al., 2000). There is much variation in rejection behaviour both among and within various populations of this species, reflecting variation in the risk of being parasitised (Lindholm, 2000; Lindholm & Thomas, 2000). In a reed warbler population in England the rejection rate of foreign eggs has declined in recent years due to a lower level of parasitism (Brooke et al., 1998). The decline in rejection rate towards foreign eggs in this host population can be explained by high costs due to recognition errors (Davies et al., 1996), and some evidence for such errors have previously been found (Davies & Brooke, 1988). However, other studies have failed to reveal such errors in reed warblers (Lindholm, 1999; Røskaft et al., 2002), as well as other species (e.g. Lawes & Kirkman, 1996; Grendstad et al., 1999). The influence of recognition errors as opposing selection pressures against evolution of proper defence in hosts of the cuckoo is thus at present a matter of controversy among researchers. Recently, it has been found that cuckoo-hosts can show intermediate rejection rates not because of costs associated with rejection behaviour, but rather as a result of characteristics of the hosts breeding habitat ("the spatial habitat-structure hypothesis"; Røskaft et al., 2001). This hypothesis is based upon metapopulation dynamics (i.e. gene flow, local adaptations, etc.) and features of the parasite itself making it more suited to utilise hosts breeding in specific habitats. Brood parasites need access to observation posts in trees to discover host nests (Alvarez, 1993; Øien et al., 1996; Clotfelter, 1998; Hauber & Russo, 2000; Moskát & Honza, 2000; Clarke et al., 2001). Host populations or species breeding near trees are therefore most prone to parasitism, experience a higher level of parasitism and thus a stronger selection pressure on evolving defences than populations or species breeding far away from trees. Woodland-species like the chaffinch and the blackcap are therefore good rejecters of foreign eggs. Reed warblers on the other hand may breed both near and far away from trees (see e.g. Øien et al., 1996), and therefore gene flow from unparasitised populations may restrain an increase in the rejection rate in parasitised populations even without the influence of costs related to rejection behaviour. Needless to say, further studies into this topic with emphasise on metapopulation dynamics are called for. In addition, we strongly recommend that more data should be collected on the occurrence of real recognition errors in European passerines in the future, because such data are very important for the general understanding of evolution of host defences against brood parasitism.

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Table 1. Reactions of chaffinches and blackcaps towards foreign conspecific eggs. N = number of nests.

	Species	
	Chaffinch	Blackcap
Reaction	N (%)	N (%)
Conspecific egg accepted	40 (100.0)	23 (100.0)
Ejection of own egg(s) only	1 (2.5)	2 (8.7)
All eggs accepted	39 (97.5)	21 (91.3)
Conspecific egg rejected	42 (100.0)	15 (100.0)
Selective ejection (no costs)	28 (66.7)	9 (60.0)
Unselective ejection (with costs)	5 (11.9)	3 (20.0)
Desertion	9 (21.4)	3 (20.0)

Table 2. Potential recognition errors (ejections and desertions) in unparasitised nests (with or without the presentation of a cuckoo dummy) in chaffinches and blackcaps. N = number of nests.

	Species	
	Chaffinch	Blackcap
Reaction	N (%)	N (%)
No Cuckoo dummy	14 (100.0)	-
No recognition errors	13 (92.9)	-
Ejection of own egg(s)	1 (7.1)	-
Desertions	0 (0.0)	-
With Cuckoo dummy	27 (100.0)	5 (100.0)
No recognition errors	25 (92.6)	5 (100.0)
Ejection of own egg(s)	1 (3.7)	0 (0.0)
Desertions	1 (3.7)	0 (0.0)

Paper V

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The spatial habitat structure of host populations explains the pattern of rejection behaviour in hosts and parasitic adaptations in cuckoos

by

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The spatial habitat structure of host populations explains the pattern of rejection behaviour in hosts and parasitic adaptations in cuckoos

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Running headline: Røskaft et al. • Spatial habitat structure and cuckoo-host adaptations

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In this paper we present tentatively support for predictions derived from a "spatial habitat structure hypothesis" arguing that common cuckoos *Cuculus canorus*, the most common obligate brood parasite in Europe, only breed in areas where they have access to vantage points in trees. Thus, species where some populations breed near trees while other populations breed further from trees, have a different cuckoo-host population dynamic, than species where all populations always breed in the vicinity of trees. Parasitism rate, mimicry of brood parasite eggs with those of the hosts, and rejection behaviour of hosts varies with the host breeding habitat. Cuckoos are best adapted to exploit species where some populations breed near trees while other populations breed in open areas, because such hosts are not always accessible to cuckoos, and thus gene flow among unparasitised and parasitised populations delays the evolution of host adaptations. Adaptive behaviour in cuckoos as well as in their hosts can be predicted from the "spatial habitat structure hypothesis". *Keywords*: Host behaviour, *Cuculus canorus*, cuckoo parasitism, metapopulation, habitat structure, gene flow. *[Behav Ecol: 0: 000-000 (2001)]*

Theoretical analyses have shown that the spatial structure of populations may strongly influence their evolutionary processes, and analyses of host-parasite models have shown that patterns of gene flow among different local populations affect their ability to counteract the parasitism (Via et al., 1995; Gandon et al., 1996; Grenfell and Harward, 1997; Schlichting and Pigliucci, 1998). Thus, local microadaptations may affect the behavioural traits of different populations breeding in a metapopulation system.

In the Old World, the common cuckoo *Cuculus canorus* is an obligate brood parasite that lays its eggs in the nests of a variety of host species, mainly smaller passerines. As the cuckoo dramatically reduces the hosts' breeding success (Røskaft and Moksnes, 1998; Øien et al., 1998), there should be strong selection for the evolution of counter-adaptations by the hosts. Many investigations have shown that mechanisms of egg recognition have evolved among the hosts to counteract brood parasitism (Davies and Brooke, 1988; 1989a; b; Brooke and Davies, 1988; Moksnes et al., 1990; 1991). Such egg recognition behaviour of the hosts has led to selection for host-egg mimicry by the cuckoo (Baker, 1942; Lack, 1968; Davies and Brooke, 1989a; b; Moksnes and Røskaft, 1995).

It is reasonable to assume that the success of brood parasites will vary both temporally and spatially according to different environmental factors such as habitat structures and densities of host populations. It could be adaptive for hosts to modify their responses to parasitism according to variation in these factors (Øien et al., 1999). Experimentally parasitised hosts of the cuckoo are known to reject the foreign egg more frequently when they have seen a cuckoo female near the nest (Davies and Brooke, 1988; Moksnes et al., 1993a). The rejection rates of cuckoo hosts also vary with the degree of similarity between the parasitic and the host's egg (Davies and Brooke, 1988; Brooke and Davies, 1988). Furthermore, phenotypic plasticity may occur where individuals that either ejected or accepted the cuckoo egg in the first test, frequently changed their response in subsequent tests (e.g. rufous bush robin *Cercotrichas galactotes*; Soler et al., 2000). Since the parasitism pressure of brood parasites may vary spatially as well as temporarily, it has recently been stressed that host responses towards cuckoo parasitism have to be regarded in a metapopulation perspective (Lindholm, 1999; Lindholm and Thomas, 2000).

Many host populations show intermediate reactions towards the cuckoo egg, as both rejection and acceptance occurs (Davies and Brooke, 1989a; Moksnes et al., 1990). Such populations may be at an equilibrium between individuals that accept and individuals that reject, as a compromise between the cost of parasitism and the cost of recognition errors (Lotem et al., 1992; 1995; Takasu, 1998a; b; Takasu et al., 1993; Rodríguez-Gironés and Lotem, 1999). Recently a new hypothesis explaining the coexistence of acceptors and rejecters in the same host population (the intermittent arms race hypothesis; Soler et al., 1998) has been suggested. This hypothesis is based on the existence of spatially structured cyclic changes in parasitism over many years, where the host population will respond to the variation in parasitism pressure.

Although the equilibrium hypothesis may explain the intermediate rejection rates in some populations, it does not explain the dynamics of metapopulations, nor the plasticity different host populations show in their responses towards cuckoo eggs (Lindholm, 1999; Lindholm and Thomas, 2000). Furthermore, the equilibrium hypothesis can not predict the level of acceptance rate of different host species. Unparasitised host populations of several brood parasite species may accept almost all parasitic eggs experimentally laid in their nests (Davies and Brooke, 1989b; Soler and Møller, 1990; Lindholm and Thomas, 2000). Interpopulation variation has been attributed to phenotypic plasticity, but may as well be genetically determined and due to differences in gene flow between acceptor and rejecter populations. The degree of mimicry of cuckoo eggs with those of the hosts may also vary among populations (Moksnes and Røskaft, 1995).

In this paper we argue that the interpopulation variation in rejection behaviour within a species is determined by gene flow between unparasitised and parasitised populations. Differences in rejection rates of cuckoo eggs will affect the degree of host egg mimicry as well as the rate of parasitism. We have made some important prerequisites for this approach; 1) In many potential host species some populations are heavily parasitised by cuckoos whereas others are not parasitised at all (Davies and Brooke, 1989b). The metapopulation approach assumes that unparasitised populations are sources for parasitised ones, because everything else being equal (e.g. predation pressure) the average fitness will be lower in parasitised populations which will lead to vacancies and immigration of recruits from unparasitised populations. Thus gene flow from the sources where there is no selection for egg rejection to the sinks, where there is selection for rejection, leads to a dimorphic response in the sink populations. In parasitised populations the cuckoos will evolve mimetic eggs to lower the rate of egg rejection. 2) Because cuckoos are dependent on trees (or in recent time, electrical poles or wires) as vantage points for finding host nests, (Alvarez, 1993; Øien et al., 1996; Moskát and Honza, 2000), host populations breeding in the vicinity of trees will be more exposed to parasitism than host populations breeding further from trees. Thus, there will be a difference between species that always breed near trees and those breeding both near and far from trees, where some populations are exposed to cuckoo parasitism whereas others are not.

From this “spatial habitat structure hypothesis” we develop the following predictions; 1) In species where all populations always breed near trees, the host should rapidly evolve rejection behaviour, and the cuckoo should only occasionally match the speed of this evolution, and only sporadically develop matching mimetic eggs. Thus, in habitats with trees suitable hosts should always be good rejecters (≈ 100%), whereas cuckoo egg morphs matching those of the hosts will be rare. Parasitism rate should be low. 2) Among species breeding in habitats where some populations are breeding close to trees where they locally are heavily parasitised by cuckoos, whereas others are breeding far from trees where they are unparasitised, gene flow among populations should delay the evolution of rejection behaviour in parasitised populations. If the frequency of unparasitised populations is high, the result should be a high variation in rejection behaviour among populations. Cuckoos should evolve egg mimicry in parasitised populations. We expect the average mimicry of cuckoo eggs to be better among these species than among species always breeding near trees. 3) Host species that always breed in open areas far from trees should be acceptors, even though they in theory are suitable hosts. There should be no selection for egg mimicry and parasitism rate should always be very low (no data exists, however, to test this prediction).

MATERIALS AND METHODS

In this study we collected data from different sources. In the analyses we have used data on 24 different European cuckoo hosts, because available data on their rejection rates of non-mimetic cuckoo eggs exists (Table 1; see below).

Only suitable hosts are included in this analysis. Suitable hosts are defined as having nests that are accessible for the cuckoo. They are feeding their chicks with food that is digestible for the cuckoo chick, and they have a size of the nest and eggs making it possible for the young cuckoo to eject the nest content (Davies and Brooke, 1989a; Moksnes et al., 1990).

Rejection rates of different host species towards non-mimetic cuckoo eggs were collected from published papers or from own unpublished experiments in Norway, Hungary and the Czech Republic (von Haartman, 1981; Gärtner, 1982; Järvinen, 1984; Davies and Brooke, 1989a; Brown et al., 1990; Moksnes et al., 1990; 1994; Moksnes and Røskaft, 1992; Brooke et al., 1998; Alvarez, 1999; Moskát and Fuisz, 1999; Stokke et al., 1999). A hosts' rejection rate is defined as the proportion of eggs that was rejected (ejected or deserted), of the total number of experiments with artificial non-mimetic cuckoo eggs added to the clutch. In this paper experiments from different populations are pooled (Table 1).

Breeding habitats have been defined as A) always near trees (13 species, Table 1) where cuckoos in principal always have access to all host nests due to the proximity of trees (Figure 1), B) some populations (near trees) are accessible to cuckoos while others (far from trees) are not (eight species). Some host species as e.g. redstart *Phoenicurus phoenicurus*, robin *Erithacus rubecula,* pied wagtail *Motacilla alba* and wren *Troglodytes troglodytes,* are partly hole nesters or breed in cavities in some areas and are therefore inaccessible to cuckoos. They are included in this group. Altogether 11 species are therefore included in this group (Table 1). C) A third category of species always breeding far from trees (Figure 1), however, is not included in this analysis because no data exist. We used Snow and Perrins (1998) to determine the breeding habitats and nest sites of the different species. For simplicity we used only two habitats in the analyses (always near trees; near and far from trees).

The frequency of matching egg morphs of the different species was taken from a study of more than 12000 cuckoo eggs in European museums (Moksnes and Røskaft, 1995). A matching cuckoo egg morph is a cuckoo egg that is said to be similar to the eggs of the host (e.g. a blue cuckoo egg similar to the blue eggs in the redstart, Moksnes et al., 1995). Fourteen species have a matching cuckoo egg morph while 10 species have no matching cuckoo egg morph (Table 1). The information regarding the matching egg morph of the rufous bush robin *Cercotrichas galactotes* has been taken from Alvarez (1994).

We also used the mean degree of cuckoo egg mimicry from the museum collections. For each parasitised clutch the mimicry of the cuckoo egg with the host eggs was scored according to a scale from (1 to 5, where 1 is perfect mimicry, 2 is good mimicry, 3 is medium mimicry, 4 is poor mimicry, and 5 is maximum contrast; Moksnes and Røskaft, 1995; Table 1).

Rate of parasitism was obtained by using data from published papers averaged over the actual range (Wasenius, 1936; Lack, 1963; Wyllie, 1981; Glue and Murray, 1984; ; Moksnes and Røskaft, 1987; Davies and Brooke, 1989b; Moksnes et al., 1993b; Schulze-Hagen et al., 1996; Moskát and Honza, 2000). In addition we used a number of nests containing cuckoo eggs found in European Museums (Moksnes and Røskaft, 1995). Since in general, data on parasitism rates are poor, we used only two categories of parasitism rate; 1: normally parasitised at a rate less than 1 %, 2: normally parasitised up to 5 %, but frequently even above (Table 1).

Treating each species as an independent data point may lead to an overestimation of the true number of degrees of freedom in statistical analyses (Felsenstein 1985; Harvey and Pagel 1991). In order to control for possible effects of common descent, the species used in the analysis were organised in a phylogenetic tree. We produced one tree based on molecular data (DNA hybridisation; Sibley and Ahlquist 1991), and another based upon morphology (Howard and Moore 1991). In the latter tree, we assumed polytomies between species within a genus, between genera within a family, etc. In order to obtain a normal distribution, the rejection rate had to be arcsin transformed before the analysis. We used the computer program package PDAP (Garland et al. 1993; Garland et al. 1999; Phenotypic Diversity Analysis Programs) version 5.0 to make the tree and to load variable data. This package also contains Felsenstein`s (1985) independent comparison method, which allowed us to obtain paired contrasts of the variables between nodes in the phylogenetic trees that were independent of each other. The branch lengths were assigned by the method of Grafen (1989), by the method of Pagel (1992), or set as a constant (= 1). The branch length assignments that were used varied for each trait and also among the trees. We selected the branch lengths that yielded absolute values of contrasts that were not related to their standard deviations ($p < .05$) for any of the traits analysed (Garland et al. 1992). The relationship between the variables was analysed by multivariate General Linear Models (GLM). All the tests are two-tailed.

RESULTS

The mean rejection rate was 78.3 % (± 25.1, SD) for species always breeding near trees while it was 45.6 % (± 27.6, SD) for species breeding near trees as well as further away from trees, a difference which proved to be statistically significant (arcsin transformed data, ANOVA, $F_{1,23} = 9.21$, $p = .006$). The percentage of species that normally were parasitised at a rate above 1 % was much higher for species breeding in both kind of habitats (100 % of the species), while 10 of 13 species always breeding near trees (76.9 %) were normally parasitised less than 1 % (Fishers exact probabilities test, $p = .000$). The mean degree of mimicry of the cuckoo eggs towards those of the hosts was 3.6 (± 0.7, SD) for species always breeding near trees and 3.0 (± 0.5, SD) for species breeding in both kinds of habitats, a difference that proved to be significant (ANOVA, $F_{1,23} = 4.94$, $p = .037$; the mean of one species was used as a unit). Finally, the percentage of species with a matching cuckoo egg morph differed significantly between species always breeding near trees and those breeding both near and far from trees. A cuckoo egg morph similar to the eggs of the host was found among 90.9 % of the species breeding in both habitats, while it was found among only 30.8 % of the species always breeding near trees (Fishers exact probabilities test, $p = .005$).

A multivariate GLM-test using the habitat as the independent variable and (arcsin)-rejection rate, whether a species was frequently parasitised above 1 % or not, and the degree of mimicry of the cuckoo eggs, as dependent variables proved to be statistically significant (Wilk's Lambda, $F_{3,21} = 11.9$, $p = .000$). All the dependent variables were statistically significant ((arcsin)-rejection rate, $p = .006$; parasitism rate, $p = .000$; degree of mimicry, $p = .037$). Multivariate GLM-tests based upon phylogenetically independent contrasts obtained from trees based upon DNA-hybridisation or morphology, where habitat was the independent variable, and where rejection rate, parasitism rate and egg mimicry were dependent variables also proved to be statistically significant (DNA-hybridisation, Wilk's Lambda, $F_{3,21} = 8.34$, $p = .001$; morphology, Wilk's Lambda, $F_{3,21} = 6.92$, $p = .002$). In most cases the dependent variables were statistically significant ((arcsin)-rejection rate; DNA-hybridisation $p = .026$; morphology $p = .013$; parasitism rate DNA-hybridisation $p = .000$; morphology $p = .000$, degree of mimicry DNA-hybridisation $p = .033$), except for degree of mimicry in the test based on morphology ($p = .247$).

DISCUSSION

Our results tentatively support the “spatial habitat structure hypothesis”. The breeding habitat of the host species explains their rejection behaviour, the rate of parasitism by the cuckoo, and whether or not the cuckoo has developed a mimetic egg morph. The differences between species always breeding near trees or those breeding both near and far from trees were always in the direction of the predictions derived from the hypothesis. Thus, we have shown that important adaptations in both the cuckoos and their hosts can be explained by the spatial structure of habitats among breeding populations, even when controlling for phylogeny of different hosts.

Although the equilibrium hypothesis (Lotem et al., 1992; 1995; Takasu et al., 1993; Takasu, 1998a; b; Rodríguez-Gironés and Lotem, 1999) may explain the level of rejection in relation to parasitism rate of many species, it does not predict which species that should be parasitised or which species should have the highest level of rejection. However, the “spatial habitat structure hypothesis” does explain the variation between different species with regard to egg mimicry, as well as rejection- and parasitism rates. On the other hand, the support for the “spatial habitat structure hypothesis” also gives strong support to the “arms race hypothesis” (Davies and Brooke, 1989b; Moksnes et al., 1990).

The puzzle of why so many European hosts (and hosts ofother brood parasites; Rothstein, 1990; Brooker et al., 1990) have intermediate rejection rates has interested scientists for a long time. Recently the variation in rejection rates between host populations has been considered to be a result of phenotypic plasticity (Brooke et al., 1998; Lindholm, 1999) or conditional host strategies (Øien et al., 1999). These alternatives are, however, not mutually exclusive to the “spatial habitat structure hypothesis”, because plasticity in antiparasite behaviour may be higher for species where parasitism pressure is variable (e.g. among species breeding both near and far from trees).

In this paper we have only used a bimodal model, including two types of habitats. However, the metapopulation system is dynamic and we may regard a host species as representing a system where both the proportion of populations breeding near trees and the parasitism rate of populations, vary from zero to 100 % (Figure 2). One prediction that can be derived from the "spatial habitat structure hypothesis" is that there should be a close relationship between the proportion of populations that breed near trees, and the total rejection rate of the species (Figure 2). Species where about 50 % of the populations breed near trees and 50 % away from trees should have intermediate rejection rates. Species that always breed far from trees should be acceptors. Hole nesting birds are not accessible to cuckoos, although a few individuals that do not breed in holes may successfully rear young cuckoos. Hole nesters should therefore behave as they were breeding in more or less open habitats. Some of the European larks (Alaudidae) breed far from trees, and they are rarely parasitised by cuckoos (Moksnes and Røskaft, 1995), although, they in principle may be suitable hosts. We therefore predict that these larks would be acceptors.

Species that in principle always breed near trees should be close to 100 % rejecters. The definition of a tree is critical for this hypothesis, but it should be of a size that makes it easy for the cuckoo to use as a vantage point (above 3-4 meters high). The density of trees should be so high that cuckoos can use alternative vantage points. Cuckoos probably prefer to use vantage points giving them an overview of several host nests at a time (Clarke et al., 2001). Dense forests are probably not good cuckoo habitats, because dense vegetation will make it difficult for the cuckoo to observe host nests. Therefore open forests, or areas with scattered trees would be the best areas for cuckoos to use as vantage points. Normally, hosts are more exposed when breeding near trees (Alvarez, 1993; Øien et al., 1996; Moskát and

Honza, 2000). For species breeding in such habitats, the rejection rate will quickly evolve to a very high level, making it difficult for the cuckoo to successfully parasitise them. Therefore, parasitism rates should be highest for species breeding both near trees as well as far from trees (Figure 2). This explains why species like some of the *Acrocephalus* warblers may be locally parasitised at frequencies up to 15 % or more (Molnar, 1944; Moksnes et al., 1993b; Schulze-Hagen et al., 1996; Øien et al., 1999; Moskát and Honza, 2000). Mimicry of the cuckoo egg towards those of the hosts should be best among the species where about 50 % of the populations breed among trees.

However, none of the European species are always parasitised, even among species always breeding near trees. Among such species some populations may escape parasitism by the cuckoo, although, it would be hard to conclude whether this is a result of antiparasite behaviour of hosts, or cuckoos preferring other hosts because the host density of the most suitable hosts is too low. This phenomenon may explain why none or very few of the European host species have a 100 % rejection rate.

Data on one of the tested hosts do not support the "spatial habitat structure hypothesis". The dunnock *Prunella modularis*, a species that always breeds near trees, has in previous studies been found to be an exception to the patterns of other European hosts (Davies and Brooke, 1989b; Moksnes et al., 1990). Understanding why the dunnock is such an exception has been difficult. However, we suggest that one should look closer into their habitat and whether this species in some populations breeds in dense forests, in cavities, in very low densities, or if this species has not evolved antiparasite adaptations due to a time lag (Rothstein, 1982; 1990).

We conclude that the "spatial habitat structure hypothesis" explains the pattern of rejection behaviour in hosts and parasitic adaptations in cuckoos in Europe. This conclusion can be drawn despite the fact that the quality of data used in the present analyses is not optimal, because rejection rates, parasitism rates and degree of mimicry are not only taken from different host populations but often from populations far apart. In further research we recommend that researchers collect data on rejection rates, parasitism rates, cuckoo egg mimicry and even dispersal rates of adult and juvenile birds from both parasitised and unparasitised populations in areas that are not too far from each other (50 – 100 km).

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Table 1

Breeding habitats (A) always near trees, (B) both near trees and far from trees, or species which partly breed in cavity). Rejection rates in percentage of total experiments (with total number of experiments in parentheses), whether a matching cuckoo egg morph exists in some of the populations in European museum collections, mean degrees of mimicry of cuckoo eggs from museum collections and parasitism rates of different cuckoo hosts in Europe (1 = normally parasitised at a rate less than 1 %, 2 = frequently parasitised at rates up to 5 % and even above)

Host species	Breeding habitat	Rejection rate % (*n*)	Matching cuckoo egg morph	Mean degree of mimicry	Parasitism rate
Lanius collurio	A	96 (26)	Yes	2.8	2
Muscicapa striata	A	67 (18)	No	3.7	1
Erithacus rubecula	B	25 (20)	Yes	3.5	2
Cercotrichas galactotes	B	19 (54)	Yes	?	2
Phoenicurus phoenicurus	B	34 (65)	Yes	2.4	2
Luscinia svecica svecica	A	74 (17)	No	3.6	1
Troglodytes troglodytes	B	17 (6)	No	4.3	2
Phylloscopus trochilus	A	88 (16)	No	4.4	1
P. collybita	A	91 (11)	No	4.3	1
Hippolais icterina	A	78 (9)	No	3.8	1
Acrocephalus scirpaceus	B	41 (229)	Yes	3.1	2
A. palustris	B	87 (38)	Yes	3.1	2
A. arundinaceus	B	75 (28)	Yes	2.4	2
A. schoenobaenus	B	20 (5)	Yes	3.0	2

Host species	Breeding habitat	Rejection rate % (*n*)	Matching cuckoo egg morph	Mean degree of mimicry	Parasitism rate
Sylvia atricapilla	A	92 (48)	Yes	2.9	1
S. borin	A	67 (3)	Yes	2.5	2
Anthus pratensis	B	36 (82)	Yes	2.7	2
Motacilla alba	B	73 (41)	Yes	2.8	2
M. flava	B	80 (5)	Yes	2.6	2
Prunella modularis	A	3 (32)	No	4.9	2
Fringilla coelebs	A	77 (74)	No	3.6	1
F. montifringilla	A	90 (31)	Yes	2.6	1
Emberiza citrinella	A	100 (13)	No	3.6	1
E. schoeniclus	A	95 (20)	No	3.6	1

FIGURE LEGENDS

Figure 1

Distribution of different populations of three theoretical cuckoo host species;

A) Species always breeding near trees. Here cuckoo vantage points occur among all populations.

B) Species breeding both near trees as well as far from trees. Here some cuckoo vantage points occur among some of the populations, but not all. Note that reeds are not considered as a tree or a cuckoo vantage point. Therefore, species breeding in reed beds far from trees may not be parasitised at all.

C) Species always breeding far from trees with no cuckoo vantage points. Note that a tree or two may occur in some populations, but that is not enough for cuckoos to exist and to parasitise the majority of the population.

Figure 2

The relationship between a species' total rejection rate and the fraction of populations breeding near trees including the variation between populations (solid lines). The average parasitism rate of a species in relation to the fraction of species breeding near trees (dotted line) has a peak in the middle part, here parasitised populations may be heavily parasitised, while those populations breeding far from trees are not parasitised at all. Species where all populations always breed near trees on one hand, while other populations never breed near trees on the other hand, are never parasitised.

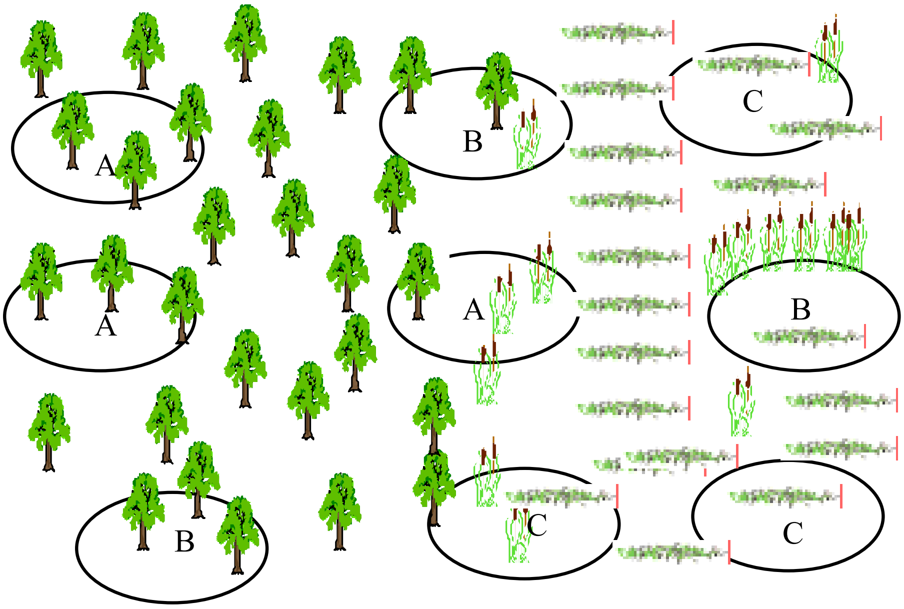
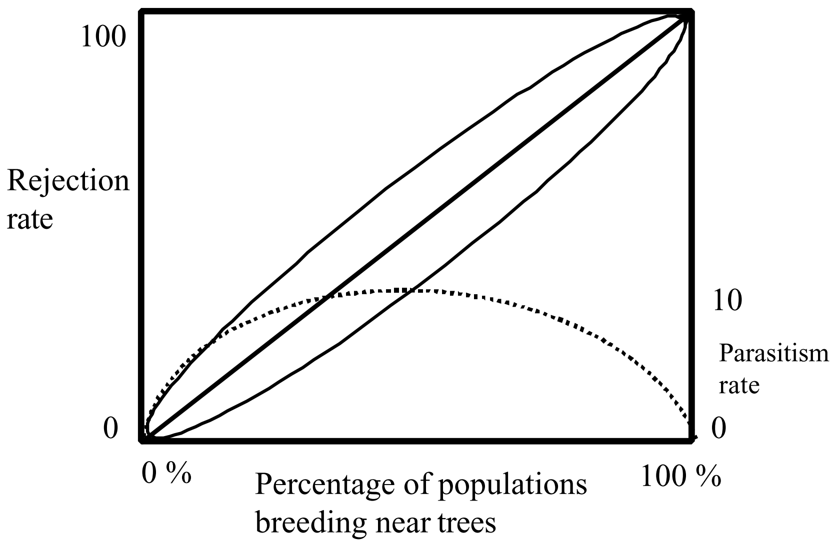


Figure 1

Figure 2


100
Rejection rate
0
10
Parasitism rate
0
0 %
Percentage of populations breeding near trees
100 %

URN:NBN:no.2134

Doctoral theses in Zoology
from the University of Trondheim / Norwegian University of Science and Technology

	Year	Name	Degree	Title
1	1978	Tore Slagsvold	Dr. philos.	Breeding events of birds in relation to spring temperature and environmental phenology.
2	1980	Arnfinn Langeland	Dr. philos.	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
3	1982	Dag Dolmen	Dr. philos.	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
4	1984	Eivin Røskaft	Dr. philos.	Sociobiological studies of the rook *Corvus frugilegus*.
5	1985	Randi E. Reinertsen	Dr. philos.	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
6	1985	Jarle Mork	Dr. philos.	Biochemical genetic studies in fish.
7	1986	Torleif Holthe	Dr. philos.	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
8	1986	John Solem	Dr. philos.	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
9	1986	Bernt Erik Sæther	Dr. philos.	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
10	1987	Olav Hogstad	Dr. philos.	Winter survival strategies of the Willow tit *Parus montanus*.
11	1987	Helene Lampe	Dr. scient.	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
12	1987	Bjørn Åge Tømmerås	Dr. scient.	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
13	1988	Tor G. Heggberget	Dr. philos.	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
14	1988	Hans Christian Pedersen	Dr. philos.	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
15	1988	Marianne V. Nielsen	Dr. scient.	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
16	1988	Ole Kristian Berg	Dr. scient.	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
17	1989	John W. Jensen	Dr. philos.	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.
18	1989	Reidar Andersen	Dr. scient.	Interactions betweem a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.

19	1989	Helga J. Vivås	Dr. scient.	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
20	1990	Arne Johan Jensen	Dr. philos.	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.
21	1990	Tor Jørgen Almaas	Dr. scient.	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
22	1990	Bengt Finstad	Dr. scient.	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
23	1990	Magne Husby	Dr. scient.	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
24	1990	Hege Johannesen	Dr. scient.	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
25	1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
26	1991	Jan Henning L'Abêe Lund	Dr. philos.	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
27	1991	Odd Terje Sandlund	Dr. philos.	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
28	1991	Trond Nordtug	Dr. scient.	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
29	1991	Tor Kvam	Dr. scient.	Population biology of the European lynx (*Lynx lynx*) in Norway.
30	1992	Bjørn Munro Jenssen	Dr. philos.	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.
31	1992	Arne Vollan Aarset	Dr. philos.	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
32	1992	Tycho Anker-Nilssen	Dr. scient.	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
33	1992	Torgrim Breiehagen	Dr. scient.	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
34	1993	Kjetil Bevanger	Dr. scient.	Avian interactions with utility structures, a biological approach.
35	1993	Thrine L. M. Heggberget	Dr. scient.	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
36	1993	Yngvar Asbjørn Olsen	Dr. scient.	Cortisol dynamics in Atlantic salmon, Salmo salar L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
37	1993	Tor Fredrik Næsje	Dr. scient.	Habitat shifts in coregonids.
38	1994	Arne Moksnes	Dr. philos.	Host adaptations towards brood parasitism by the Cockoo.

39	1994	Morten Bakken	Dr. scient.	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
40	1994	Peder Fiske	Dr. scient.	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
41	1994	Torbjørn Forseth	Dr. scient.	Bioenergetics in ecological and life history studies of fishes.
42	1994	Nils Røv	Dr. scient.	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
43	1995	Martha Kold Bakkevig	Dr. scient.	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
44	1995	Hanne Christensen	Dr. scient.	Determinants of Otter Lutra lutra distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
45	1995	Chris Jørgen Jensen	Dr. scient.	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
46	1995	Svein Håkon Lorentsen	Dr. scient.	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
47	1995	Vidar Moen	Dr. scient.	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
48	1996	Ola Ugedal	Dr. scient.	Radiocesium turnover in freshwater fishes
49	1996	Ingibjørg Einarsdottir	Dr. scient.	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
50	1996	Christina M. S. Pereira	Dr. scient.	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
51	1996	Jan Fredrik Børseth	Dr. scient.	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
52	1996	Gunnar Henriksen	Dr. scient.	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
53	1997	Ole Reitan	Dr. scient.	Responses of birds to habitat disturbance due to damming.
54	1997	Jon Arne Grøttum	Dr. scient.	Physiological effects of reduced water quality on fish in aquaculture.
55	1997	Per Gustav Thingstad	Dr. scient.	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
56	1997	Torgeir Nygård	Dr. scient.	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.

57	1997	Signe Nybø	Dr. scient.	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
58	1997	Atle Wibe	Dr. scient.	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.
59	1997	Rolv Lundheim	Dr. scient.	Adaptive and Incidental Biological Ice Nucleators.
60	1997	Arild Magne Landa	Dr. scient.	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
61	1997	Jarle Tufto	Dr. scient.	Gene flow and Genetic Drift in Geographically Structured Populations: Ecological, Population Genetic, and Statistical Models
62	1997	Trygve Hesthagen	Dr. philos.	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
63	1997	Trygve Sigholt	Dr. philos.	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
64	1997	Jan Østnes	Dr. scient.	Cold sensation in adult and neonate birds
65	1998	Thor Harald Ringsby	Dr. scient.	Variation in Space and Time: The Biology of a House Sparrow Metapopulation
66	1998	Erling Johan Solberg	Dr. scient.	Variation in population dynamics and life history in a Norwegian moose (Alces alces) population: consequences of harvesting in a variable environment
67	1998	Bente Gunnveig Berg	Dr. scient.	Encoding of pheromone information in two related moth species
68	1999	Kristian Overskaug	Dr. scient.	Behavioural and Morphological Characteristics in Northern Tawny Owls *Strix aluco*: An Intra- and Interspecific Comparative Approach
69	1999	Ingvar Stenberg	Dr. scient.	Habitat selection, reproduction and survival in the White-backed Woodpecker Dendrocopos leucotos
70	1999	Trina Falck Galloway	Dr. scient.	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and halibut (*Hippoglossus hippoglossus* L.)
71	1999	Marianne Giæver	Dr. scient.	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
72	1999	Ingrid Bysveen Mjølnerød	Dr. scient.	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
73	1999	Stein-Are Sæther	Dr. philos.	Mate Choice, Competition for Mates, and Conflicts of Interest in the Lekking Great Snipe
74	1999	Katrine Wangen Rustad	Dr. scient.	Modulation of Glutamatergic Neurotransmission Related to Cognitive Dysfunctions and Alzheimer's Disease
75	1999	Per Terje Smiseth	Dr. scient.	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)

76	1999	Gunnbjørn Bremset	Dr. scient.	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
77	1999	Frode Ødegaard	Dr. scient.	Host spesificity as parameter in estimates of arhrophod species richness
78	2000	Ingar Jostein Øien	Dr. scient.	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
79	2000	Sigbjørn Stokke	Dr. scient.	Sexual segregation in the African elephant (*Loxodonta africana*)
80	2000	Odd A. Gulseth	Dr. philos.	Seawater Tolerance, Migratory Behaviour and Growth of Charr, (*Salvelinus alpinus*), with Emphasis on the High Arctic Dieset Charr on Spitsbergen, Svalbard
81	2000	Pål A. Olsvik	Dr. scient.	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
82	2000	Sigurd Einum	Dr. scient.	Maternal effects in fish: Implications for the evolution of breeding time and egg size
83	2001	Jan Ove Evjemo	Dr. scient.	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
84	2001	Ingebrigt Uglem	Dr. scient.	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)