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Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

Thesis for the degree philosophiae doctor

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“Ja, dom jävlarna (bergfinkarna altså) beter seg ju inte som andra arter – dom lämnar häckningar (ock kommer tilbaka, ibland) och beger sig til ”Gud vet vart” mitt i altihopa”

- Roland Sandberg

”If you like to gamble, I tell you I’m your man
you win some, loose some, it’s all the same to me
(…)
Playing for the hard one, dancing with the devil
going with the flow, it’s all a game to me”

- Ace of Spades, Motörhead

Preface

I have a clear memory of that evening in June 2005 when I and Thomas Carlsen were searching restlessly for brambling nests around the hills of Isototovaara in Pallas-Ylläs national park. This was Finnish Lapland, and the childish excitement and naive optimism we had brought with us two weeks earlier was about to be displaced by melancholic despair. I suspect the shift of mood was due to a growing realisation that my first field season as PhD student was becoming an outright fiasco, although it could also have something to do with our whole-hearted attempts to master the Finnish sauna tradition. Anyhow, the phenology train had already left, the nests were much harder to find than we had imagined, and I had dispatched poor Arild Husby to survey an area near Kuusamo where bramblings were practically absent this year. And most discouraging of all: not the slightest sign of the mythical brambling-cuckoo which was the intended subject of my PhD and the main reason for my excursion. I was therefore already figuring out my alternatives - wondering if the job as village idiot of Vikanlandet was still open – when Thomas spotted the brambling nest. Concealed in a tiny goat willow amid mighty spruces, it contained a cuckoo egg that was remarkably similar to a brambling's eggs, only somewhat larger and heavier, precisely as detailed in the archaic recordings of the honourable (!) egg collector Ernst Wasenius. This became the only achievement of the year, which relative to the aim and effort potentially makes it the lousiest catch in the history of ornithological field work. But nevertheless; the priceless egg persuaded me to cling on to bramblings and return the next year. Reflecting on the experiences I've gained, I'm most satisfied with this decision.

The thesis could not have been produced without the invaluable assistance of a lot of persons. First and foremost, I am most grateful to Arne Moksnes, Eivin Røskaft, and Bård G. Stokke for inviting me to work on cuckoo stuff. Their friendliness, accessibility, optimism and thoughtful inputs have been greatly appreciated all the way. Frode Fossøy joined the cuckoo group as a Post doc two years ago and has been stimulating me with constructive criticism and excessive enthusiasm ever since. I have also had the pleasure of exchanging views with Anton Antonov and of joining him in his marvellous study area in Bulgaria. Although my intense side leap with the nasty corn buntings did not pay off, it was a great time.

Roger Dahl, Thomas Holm Carlsen, Pål Kvello, and Ragnar Dahle spent a lot of time together with me in the field, and I can't think of better companions: independent, easy-going, and with a strong taste for nests and skitprat. You contributed to make the field work the most memorable part of the PhD-work.

I was very lucky to get the opportunity to work together with Jarkko Rutila during my masters in Tana and have him co-authoring some of the manuscripts. Without his involvement, this work would never have been initiated. Esa Huhta initiated the work in Finland, co-authored several manuscripts, arranged facilities, and introduced me to the Finnish smoke sauna. My collaboration with Jesus Aviles was a source of inspiration at a critical moment. I'm indebted to all of you.

Fugo Takasu hosted me in Nara in 2005, where we discussed potential topics for theoretical studies. Hopefully, some of these ideas can be developed further. Thanks a lot for your hospitality and patience.

Thanks are also due to the staff at various museums for their excellent assistance: Jon Fjeldså and Jan Bolding at Zoological museum in Copenhagen, Douglas Russell at British museum in Tring, Göran Frisk at Svenska Riksmuseet in Stockholm, Torsten Stjernberg at Naturhistoriska Centralmuseet in Helsinki, and Göran Nilsson at the Museum of Natural History in Gothenburg.

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Thanks to my parents for giving me the best opportunities to develop my own interests, to my uncle Arne Vikan for encouraging me to pursue a PhD, and to Marius Eriksen for initiating my interest in birds during many fishing trips in early years.

Finally, a special thanks to my dearest: Kari for her love and support and Kåre for making me realise it was time to call it a day.

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Contents

List of papers included in thesis

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I. Avilés, J. M., Vikan, J. R., Fossøy, F., Antonov, A., Moksnes, A., Røskaft, E., Stokke, B. G. (manuscript). Avian visual perception predicts behavioural responses to experimental parasitism in chaffinches

II. Vikan, J. R., Stokke, B. G., Fossøy, F., Jackson, C., Huhta, E., Rutila, J., Moksnes, A., Røskaft, E. (2009). Fixed responses to single and multiple experimental parasitism in two *Fringilla* hosts of the common cuckoo. Ethology 115, 840-850.

III. Vikan, J. R., Stokke, B. G., Rutila, J., Huhta, E., Moksnes, A., Røskaft, E. (manuscript). Evolution of defences against cuckoo (*Cuculus canorus*) parasitism in bramblings (*Fringilla montifringilla*): A comparison of four distant populations in Fennoscandia

IV. Vikan, J. R., Stokke, B. G., Fossøy, F., Huhta, E., Moksnes, A., Røskaft, E. (manuscript). Alternative coevolutionary outcomes of brood-parasite host interactions mediated by egg mimicry

Summary

Most open nesting insectivorous passerines in Europe have a history of interaction with the brood parasitic common cuckoo. These interactions are pair-wise and strongly antagonistic, and may therefore lead to tight reciprocal evolution of adaptations and counter-adaptations in an arms race like fashion. This thesis deals with evolutionary aspects of the relationship between the cuckoo and two *Fringillidae* hosts, the brambling *Fringilla montifringilla* and chaffinch *F. coelebs*. These species are representatives of a large segment of poorly investigated hosts covering many taxa that have evolved comparatively advanced adaptations for combating the cuckoo.

We documented parasitism on bramblings in north western Finland, where average parasitism rate over three years was 6%. Historical data suggests that presence of parasitism is stable to some extent in this part of Fennoscandia. Two Norwegian and one Swedish population were not parasitised. The one chaffinch population we studied is not parasitised, and we know of no cases of regular parasitism on this species from elsewhere.

In agreement with previous studies on these two hosts, we found that egg rejection is regulated by a simple recognition system, where the acceptance threshold employed by the host, i.e. the magnitude of dissimilarity between own and parasite eggs that trigger a rejection response, is relatively fixed regardless of context. Furthermore, recognition is memory based, with no or negligible contribution of discordancy, i.e. direct comparison of eggs.

We found no noticeable variation in egg rejection behaviour between the four brambling populations. Most individuals rejected non-mimetic eggs, and the relationship between host-parasite egg dissimilarity and rejection probability was the same in all populations. Furthermore, bramblings very rarely made misstakes in rejection, suggesting that this behaviour is robust to decay. The ubiquitous presence of precise egg rejection has most likely arisen because bramblings lack breeding site fidelity, and because the average parasitism pressure has been high enough in the past to drive regional fixation of rejection alleles and evolution of clutch characteristics that facilitate cost free egg recognition.

There was no notable difference in the rejection behaviour of bramblings and chaffinches. The degree of matching in chromatic aspects of egg color, i.e. hue and chroma, was an important factor affecting rejection probability in both species. Difference in achromatic aspects (brightness) was overall less important, as expected when object discrimination takes place under the light conditions present in open, shallow nests. Given

that egg colour is a remarkably variable trait in both species, and because the heritability of egg color is known to be high, coevolution should be strongly focussed on egg colour in both species.

By combining an experimentally derived host discrimination function with the current distributions of host and cuckoo egg phenotypes, we documented a cost to commonness in bramblings, i.e. common phenotypes are more likely to be successfully parasitised. This provides indirect evidence that cuckoos in principle can drive coevolutionary cycles in natural populations. Moreover, we found that cuckoos parasitising the Finnish population layed eggs that were close to the optimal phenotype. These cuckoo eggs were also equally good matches to brambling eggs in two distant, unparasitised populations. This indicates that cuckoos and bramblings are close to a matching equilibrium in Fennoscandia, a possibility also supported by analyses of museum data covering the period 1881-1940. In the museum material, there was no variation in cuckoo or host egg appearance along latitudinal or longitudinal gradients. We suggest that high rates of brambling gene flow cools down potential coevolutionary hot spots by cancelling out much of the selection imposed by the patchily distributed cuckoo host race. This limits host evolution and allows the host race to adapt to the brambling's egg phenotype distribution, thereby possibly promoting overall persistence of this interaction. Our studies on bramblings collectively indicate that the scale of geographically structured coevolution between bramblings and cuckoos possibly encompasses the whole of Fennoscandia.

In contrast, we found that the chaffinch has evolved a markedly more bimodal egg color distribution, consistent with the direction of evolutionary change predicted for the brambling. This difference is in accordance with the observation that chaffinches are more site fidelic than bramblings, and should therefore be better able to respond to disruptive selection imposed by locally adapting cuckoos. Surprisingly, simulation of increasingly bimodal host egg color distributions did not give rise to corresponding fitness peaks for cuckoo egg color. Marked and parallel egg polymorphisms are therefore unlikely as local coevolutionary outcomes in these systems. Frequency dependent selection is expected to create a temporal pattern of matching and mismatching of phenotypes, and might be an explanation for the current lack of regular parasitism on chaffinches since cuckoo populations could face problems with persisting during the lag phase.

Introduction

Antagonistic coevolution and avian brood parasitism

Coevolution is defined as reciprocal evolutionary change in interacting species (Thompson 2005b). Most organisms have natural enemies against which they have to adapt defence mechanisms. Antagonistic coevolution, where each part in the interaction evolves to decrease the effectiveness of the others adaptations (Dawkins & Krebs 1979; Van Valen 1973), is therefore a pervasive process in natural communities (Thompson 2005b). It plays an essential role in host and parasite population dynamics (Thompson 1998), and is suggested to underlie many well known evolutionary phenomena such as sexual reproduction (Agrawal 2006; Hamilton 1980; Lively & Dybdahl 2000), the complex immune systems of vertebrates (Millinski et al. 2005), and adaptive differentiation of geographically structured populations (Benkman et al. 2003; Brodie et al. 2002; Siepielski & Benkman 2007; Soler et al. 2001; Toju & Sota 2006a).

Avian obligate brood parasites and their hosts have during the last 30 years attracted considerable attention as potential model systems of antagonistic coevolution (Rothstein 1990; Rothstein & Robinson 1998; Soler & Soler 2000) and mating and life history strategies (Krüger 2007). Interspecific brood parasites lay their eggs in the nests of other species which then rear their offspring at the expense of their own reproduction. Fitness costs are particularly high to hosts of cowbirds *Molothrus sp*, old world parasitic cuckoos *Cuculinae* and honeyguides *Indicatoridae* (Payne 1997; 2005). Brood parasitism is an obligate reproductive strategy for ~1% of living bird species distributed among five families, and has evolved independently at least seven times (Sorenson & Payne 2002; 2005). The proportion of species affected by brood parasitism is large, particularly among passerines, because several parasites utilise a wide range of hosts and may also alternate among hosts on both short and long timescales (Nakamura et al. 1998; Nuismer & Thompson 2006; Rothstein 1990). Brood parasitism can have a large impact on the fitness of host populations. This is particularly true for generalist brood parasites such as the brown headed cowbird *Molothrus ater*, where the population dynamics of host and parasite are decoupled (Robinson et al. 1995; Rothstein & Robinson 1994; Trine et al. 1998). Even in some specialist parasites like the common cuckoo, where parasitism rates tend to be low (<10%), parasitism often accounts for a large proportion of breeding failures in the host population (Barabas et al. 2004; Payne

2005; Øien et al. 1998), and can impose selection pressures similar to or larger than nest predation (Rothstein 1990).

Major adaptations in the interaction between hosts and cuckoos

Brood parasites are expected to become increasingly specialised over evolutionary time, and old world cuckoos are among the oldest and hence most specialised of the brood parasites (Rothstein 1990; Rothstein 1992; Rothstein et al. 2002). The biology of most cuckoos are poorly known, but one of the species, the common cuckoo (hereafter cuckoo), is among the most thoroughly studied of all brood parasites (Davies 2000). Evolution of cuckoo-host interactions has aptly been referred to as a coevolutionary arms race because it can involve escalation and incorporation of new "weaponry" on both sides (Davies 2000; Davies & Welbergen 2008; Rothstein 1990; Stokke et al. 2002b; Welbergen & Davies 2009; Øien et al. 1995). The young cuckoo monopolises parental care from its foster parents by evicting all host nestlings and eggs. The massive costs inflicted by the cuckoo nestling select for defences in the host, which in turn prompts a counter-adaptation by the cuckoo, which again generates selection for new or more refined host defences, and so on (Davies 2000).

Much of the coevolution between cuckoos and hosts is driven by reciprocal selection on traits that affect the likelihood that cuckoo eggs will be accepted (Rothstein 1990). The most central and widespread adaptations in this respect are rejection of dissimilar eggs by the host and egg mimicry by the cuckoo (Brooke & Davies 1988; Davies & Brooke 1989b; Langmore et al. 2005; Moksnes & Røskaft 1995; Moksnes et al. 1991; Swynnerton 1918). Egg rejection is not constrained by taxonomy and is present to some extent in hosts that have a long history as victims of brood parasites, with some notable exceptions (Davies & Brooke 1989b; Langmore et al. 2005; Rothstein 1975b). In contrast, host discrimination against parasite chicks appears to be strikingly absent, particularly in those cases where the parasite chick is raised alone in the nest (Grim 2006; Lotem 1993; Redondo 1993, but see Grim 2007 and Langmoore et al. 2003 for exceptions). Egg rejection is likely to have a strong genetic component (Martin-Galvez et al. 2006; Martín-Gálvez et al. 2007; Rothstein 1975a; Soler et al. 1999a), but many hosts show considerable individual flexibility in the expression of this ability (Stokke et al. 2005). Such flexibility may underlie many observed cases of rapid change in egg rejection rates and make a significant contribution to the marked geographic variation found in some hosts (Brooke et al. 1998; Cruz et al. 2008; Nakamura et al. 1998; Stokke et al. 2008; Zuniga & Redondo 1992). The most common mechanistic basis of egg rejection is true recognition, where host individuals obtain a cognitive image of their own eggs through an imprinting-like learning process (Moksnes 1992; Petrie et al. 2009; Rothstein 1974; 1975c; 1978). Learning has important consequences because it can facilitate establishment of novel host egg phenotypes in populations confronted with mimetic cuckoo eggs (Rothstein 1974), which in turn can set the stage for coevolution of egg polymorphisms (Takasu 2003; 2005). Prolonged learning may cause missimprinting if the parasite egg occurs among the learned set of eggs (Lotem et al. 1995; Strausberger & Rothstein 2009).

Egg mimicry in cuckoos provides some of the most arresting examples of coadaptation in vertebrates (Baker 1942; Davies 2000; Rothstein 1990; Rothstein & Robinson 1998). Individual female cuckoos lay all or most of their eggs in the nests of a single host species (Marchetti et al. 1998; Skjelseth et al. 2004). Cuckoo chicks from nests of different host species differ in mitochondrial haplotypes, showing that female lineages remain faithful to particular hosts long enough for host races (gentes) to develop specific adaptations such as mimicry (Gibbs et al. 2000). Continuity in host preference is thought to be based on host imprinting (Avilés & Moller 2004; Brooke & Davies 1991), habitat imprinting (Teuschl et al. 1998), preference for particular nest sites (Moksnes & Røskaft 1995), or a combination of these mechanisms. Males, on the other hand, show no host specificity and may sire offspring in nests of several sympatric host species (Marchetti et al. 1998; Skjelseth et al. 2004). The cuckoo therefore comprises semi-isolated female host races (Gibbs et al. 2000). Importantly, mitochondrial haplotypes are not monophyletic within each putative host race, which possibly implies that they have multiple origins (Gibbs et al. 2000). The working hypothesis for the genetics of mimicry and host race formation is that egg color coding genes are located on the W-chromosome in females (Davies 2000). At least 17-18 relatively distinct cuckoo egg morphs are known in Europe, which in appearance span almost the whole range of egg types within passerines (Alvarez 1994; Antonov et al. 2006a; Antonov et al. 2007; Moksnes & Røskaft 1995). Existing host races, as indirectly classified based on egg collections in museums, are associated with hosts that have both high and stable densities (Soler et al. 2009).

Evolution of egg mimicry has several potentially important consequences for the continuing arms race. On one hand, egg mimicry may reduce the strength of selection on egg rejection alleles (Kelly 1987), and increase the risk that hosts commit recognition errors (i.e. reject own eggs when not parasitised) by imposing cognitive constraints on detection (Rodriguez-Girones & Lotem 1999). Such costs can in turn promote evolutionary equilibra (Lotem et al. 1992; 1995; Servedio & Lande 2003; Takasu et al. 1993), favour conditional rejection strategies in the host (Alvarez 1996; Davies et al. 1996; Hauber et al. 2006; Lotem & Nakamura 1998; Moksnes et al. 1993; Øien et al. 1999), and lead to evolutionary cycles in rejection rates (Rothstein 2001; Soler et al. 1998). Evolution of mimicry is expected to generate selection for host traits that help expose the mimics (Davies & Brooke 1989a; Øien et al. 1995) or reduce the probability that the nest becomes parasitised in the first place (Welbergen & Davies 2009). Egg rejection depends on a suite of underlying traits that collectively determine the host's performance in correctly identifying and rejecting the parasite egg. Improved performance can evolve through selection on each of these traits, provided that an appropriate genetic background is present (Stokke et al. 2005). Theory predicts that the variability in egg appearance within and between clutches plays a crucial role in shaping host reaction norms, optimal acceptance thresholds, and ontogeny of egg recognition (Rodriguez-Girones & Lotem 1999; Servedio & Lande 2003; Stokke et al. 2007b). Evolution of more uniform clutches reduces the overlap between host and parasite egg phenotypes, which may promote rapid learning (imprinting on the first egg laid) and/or more precise template formation in the host (Kilner 2006; Rodriguez-Girones & Lotem 1999; Stokke et al. 2007b). There is both experimental (Moskat et al. 2008) and correlative evidence (Lahti 2005; Soler & Møller 1996; Stokke et al. 1999) for this scenario. There is also a positive correlation across species between rate of rejection of odd-looking eggs and the level of host interclutch egg variation (Kilner 2006; Soler & Møller 1996; Øien et al. 1995). Moreover, Kilner (2006) found that interclutch variation was overall more important than intraclutch variation in accounting for variation in rejection rates among species.

As the parasite evolves mimetic eggs, rare host egg phenotypes gain a selective advantage over common ones. In fact, distinctiveness of egg colors has no known function besides that of facilitating recognition of parasite eggs (Lahti 2005; 2008). Comparative studies have provided substantial support for the hypothesis that parasite egg mimicry promotes high egg phenotype diversity in hosts (Kilner 2006; Lahti 2005; Stokke et al. 2002b; Øien et al. 1995). This shows that coevolution driven by negative frequency dependent selection can be a potentially important process in many cuckoo-host interactions (Takasu 2005). Matching of phenotypes is a recurrent theme in antagonistic and mutualistic interactions, and its potential outcomes have been extensively investigated using both theoretical and empirical approaches (Benkman et al. 2001; Clayton et al. 1999; Dieckmann et al. 1995; Gavrilets 1997; Holen & Johnstone 2004; 2006; Nash et al. 2008; Nuismer et al. 2005; Nuismer et al. 1999; Servedio & Lande 2003; Takasu 2003; 2005; Zangerl & Berenbaum 2003). However, it is largely unknown if and what kind of coevolutionary dynamics is produced by local cuckoo adaptation in egg appearance (Takasu 2005). Empirical investigations have hitherto mainly addressed the host side of the interaction and long term studies of egg matching in local interactions are few (but see Avilés et al. 2006; Brooke & Davies 1987; Kilner 2006).

Diversity of outcomes within and between cuckoo-host interactions

Cuckoo-host interactions comprise a diverse set of systems regarding presence and sophistication of the major adaptations (Davies 2000; Stokke et al. 2005). At the one end are hosts such as the dunnock *Prunella modularis*, which in spite of having been parasitised for a long time in Britain, shows a baffling lack of defences (Davies & Brooke 1989b). Accordingly, cuckoos utilising dunnocks show no egg mimicry (Brooke & Davies 1988). Other hosts such as the great reed warbler *Acrocephalus arundinaceus* in Hungary (Moskát & Honza 2002) and the marsh warbler *A. palustris* in Western Bulgaria (Antonov et al. 2006b) provide examples of more advanced arms race stages, with excellent cuckoo egg mimicry and strong host egg rejection abilities. At any one point in time, local interactions are likely to reflect a mixture of systems in evolutionary equilibrium and dynamic change (Davies 1999; Stokke et al. 2005; Winfree 1999).

Community level investigations of host use and host adaptation have uncovered that far more potential host species possess defences than are regularly parasitised within a given region (Brooke & Davies 1987; Davies & Brooke 1989b; Langmore et al. 2005; Moksnes et al. 1991). As a minimum, this implies that the assembly of hosts involved in pair-wise interaction with the cuckoo changes through time (Davies & Brooke 1989a). Moreover, these currently unused hosts often show locally high rates of rejection of non-mimetic eggs (i.e. close to 100%), high interclutch and low intraclutch variation in egg appearance, suggesting that they might have outdistanced their respective gentes (Braa et al. 1992; Honza et al. 2004; Lovászi & Moskát 2004; Marchetti 2000; Moksnes & Røskaft 1992; Nakamura et al. 1998; Procházka & Honza 2003; 2004; Stokke et al. 2004). Overall, however, the dividing line between hosts that are currently parasitised and those who are not is quite fuzzy with regard to egg rejection ability (Davies & Brooke 1998). Although relevant data linking cuckoo extinction to host evolution is in short supply, extinction is expected to be a regular outcome of coevolution because of the strong link between evolutionary and ecological dynamics of specialist parasites (Boots et al. 2009; Takasu et al. 1993), and because evolutionary lag is inherent in coevolutionary arms races (Rothstein 1990).

One of the most important endeavours of cuckoo-host research is to reveal which part wins the arms race and how it does so (Stokke et al. 2005; Winfree 1999). It is through pursuing this question that arms races between natural enemies gain value as an ecological model for evolution of drug resistance by diseases and for host-pathogen interactions in general (Hanifin et al. 2008). One observation that has come to dominate much recent thinking on coevolutionary dynamics is that species interactions are often spatially structured and subject to geographical variation in factors that might affect the local coevolutionary trajectory (Thompson 1994; 2005b). Therefore, interactions normally do not coevolve as one unit across their geographic ranges. Moreover, linking together subpopulations of varying outcomes in a spatial structure may alter predictions about local coevolutionary dynamics and change the global outcome (Dybdahl & Lively 1996; Forde et al. 2004; 2007; Gandon et al. 1996; Gomulkiewicz et al. 2000; Nuismer et al. 1999; 2000; Thompson & Cunningham 2002). For example, gene flow continuously alters the spatial distribution of interacting traits, thereby interfering with local selection and potentially promoting local maladaptation (Thompson et al. 2002). Thus, the geographical complexity of interactions could make it difficult for one antagonist to get ahead of the other everywhere, thereby promoting long term persistence of the interaction (Thompson 2005a). This perspective has had a growing influence on brood parasite-host research in the last decade (Barabas et al. 2004; Lindholm 1999; Lindholm & Thomas 2000; Martín-Gálvez et al. 2007; Martinez et al. 1999; Moskát et al. 2008; Røskaft et al. 2002; Røskaft et al. 2006; Soler et al. 1999a; 2001; Stokke et al. 2007a; Stokke et al. 2008). Indeed, the most thoroughly investigated interactions show marked geographical variation in parasitism rates and egg rejection rates, showing that geographical structure is likely to be important in the coevolutionary dynamics of these interactions. Particular focus on the interplay between gene flow and selection has generated new explanations for why many old cuckoo hosts regularly accept non-mimetic eggs (Stokke et al. 2005). For example, Røskaft et al. (2002; 2006) showed that rejection rates of non-mimetic eggs are on average low and varies geographically in hosts that are naturally geographically structured in their interaction with cuckoos, and suggested that gene flow keep parasitised host populations moderately maladapted most of the time. In contrast, hosts that might have experienced more widespread parasitism (notably woodland breeding passerines) often reject non-mimetic eggs at high rates, possibly reflecting past selective sweeps (Rothstein 1975a; Røskaft et al. 2002). Similarly, Soler et al. (1999a) found that gene flow might influence the local level of egg rejection in magpies *Pica pica* interacting with great spotted cuckoos *Clamator glandarius*, and may "fuel" an ongoing coevolutionary process in this system (Soler et al. 2001).

Some important insights into the factors that promote or prevent persistence of cuckoo-host interactions can also be gained through closer investigation of the strongest putative examples of expired interactions. Our present knowledge about these "rare" interactions is limited because most studies have focussed on single populations for short time intervals (Rothstein & Robinson 1998). This means that even basic information about the current distribution of these interactions are often lacking. Extensive field surveys in geographically restricted areas have often come up with documentation of novel cuckoo-host interactions (Alvarez 1994; Antonov et al. 2006b; Antonov et al. 2007). These findings underscore our incomplete knowledge of the distribution of most cuckoo-host interactions. In theory, the same coevolutionary trajectory need not be replicated over the entire range of interaction: a cuckoo gens could go extinct in some localities, and yet be at equilibrium or ahead of its host in other localities that await examination. Another possibility is that local absence of an interaction has little to do with an arms race, but simply reflects the rate of extinction/colonisation of the host race in the particular area (Lindholm 1999). In this connection it is relevant to note that cuckoos have recently declined over a broad front in Europe with no apparent link to change in host adaptation (Brooke & Davies 1987; Glue 2006; PECBMS 2007). Thus, whereas there is strong support for the view that these hosts were formerly parasitised (Davies & Brooke 1998), the chain of events that lead to their status as rare hosts is more obscure. Comparisons across multiple local interactions or comparable systems of varying outcomes are an important step in the direction of identifying the factors that prevent or promote local (or global) persistence of these "rare" cuckoo-host interactions.

Study species, study areas, and general methods

Bramblings and chaffinches are two medium sized finches of the family *Fringillidae*. They are each others closest relatives (Sibley & Ahlquist 1990), and the only finches that feed their chicks exclusively on a protein diet (Cramp & Perrins 1994), which is a prerequisite for regularly raising cuckoo chicks to independence. Accordingly, they are the only family members that give proof of either past or present regular interaction with cuckoos (Davies & Brooke 1989b; Moksnes et al. 1991). Bramblings and chaffinches are widely distributed forest generalists in northern and southern latitudes of the western Palaearctic, respectively.

Since they are arboreal open nesting species, most nests should in principle be available for parasitism by cuckoos (Røskaft et al. 2002). The two species are also similar with regard to most other putatively important characteristics that affect their suitability as hosts. Specifically, they often breed in high densities, have wide distributions, and are among the numerically dominant hosts in their respective passerine communities. All this implies that they should have experienced high rates of parasitism throughout much of their range (Soler et al. 2009; Soler et al. 1999b). On the other hand, gene flow does not occur at comparable rates and spatial scales as inferred from ringing recoveries and subspecies structure (Cramp & Perrins 1994; Mikkonen 1983). Theoretically, this difference can have a strong influence on the outcome of antagonistic coevolution (Hoeksema & Forde 2008; Thompson 2005b), which makes the two systems interesting for comparison.

The two finches are representatives of a large segment of cuckoo hosts covering several taxa which have reached an advanced stage in their ability to counter the cuckoo, and which have retained these abilities in areas where they are currently unparasitised (Braa et al. 1992; Stokke et al. 2002a; Stokke et al. 2004). By advanced, we specifically mean high rejection rate of non-mimetic eggs (close to 100%), and high interclutch and low intraclutch variation in egg appearance (Davies & Brooke 1989a; Stokke et al. 2005; Øien et al. 1995). The same wide range of egg appearances can be found in both species (Figure 1). Importantly, no observations of conspecific parasitism have been reported for either species. Conspecific parasitism could potentially have been more frequent in the past, but the resulting selection pressure should in any case be overwhelmed by selection due to cuckoo parasitism (Stokke et al. 2004). Thus adaptations for recognising and rejecting foreign eggs should mainly be evaluated in the context of cuckoo parasitism.

A host race (gens) which mimic brambling eggs is known to occur in northern parts of Fennoscandia (Baker 1942; Moksnes & Røskaft 1995; Montell 1917; Rosenius 1929; Wasenius 1936). Here, the resemblance of cuckoo eggs to brambling eggs is in some cases so striking that Baker (1942 p. 46) regarded them as "(…) one of the most perfect examples of evolution in the eggs of the European Cuckoo (…)". In central parts of Finland, where chaffinches and bramblings overlap, *Fringilla* type cuckoo eggs have also occasionally been found in chaffinch clutches (Baker 1942; Moksnes & Røskaft 1995). Mimetic cuckoo egg types have not been reported from Britain and continental Europe, where only chaffinches breed (Baker 1942; Glue & Murray 1984; Moksnes & Røskaft 1995). Cuckoos parasitizing *Fringilla* hosts have often been lumped into one host race (Avilés 2008; Moksnes & Røskaft 1995; Soler et al. 2009). However, because the two hosts are non-overlapping throughout most of their ranges and because the abundance cline is very steep (a 100:1 ratio becomes converted within 600 km, Hogstad & Väisänen 1997), it is reasonable to assume that cuckoos parasitizing either species are able to follow independent evolutionary trajectories even if both hosts are used by the same females in the zone of overlap. Cuckoo females have been shown to be highly specific in their choice among four sympatric *Acrocephalus* warblers in Check Republic (Skjelseth et al. 2004). Thus, it is realistic that *Fringilla* cuckoos comprise two host races. Of course, these two host races may each have multiple origins (Gibbs et al. 2000).

The studies on chaffinches were carried out in three nature reserves in Stjørdal, Central Norway (63ºN, 11ºE) during May 2007-2008. The study sites are forested floodplains dominated by grey alder *Alnus incana* and hold dense breeding populations of chaffinch. These study sites have been extensively used in previous studies on chaffinches (Stokke 2001). Bramblings were studied in four geographically distant populations in Fennoscandia: Kittilä in Lapland province (May-June 2005-2008), northwestern Finland (68ºN, 25ºE), Tana in Finnmark province (June-July 2003-2004), northeastern Norway (70ºN, 28ºE), Ammarnäs in Västerbotten province (June-July 2008), north-western Sweden (66ºN, 16ºE), and Tydal in Sør-Trønderlag province (June-July 2005-2008), Central Norway (63ºN, 12ºE). The four study populations (Figure 2) span a significant part of the breeding range of bramblings in the northern Boreal zone of Fennoscandia, with distances between populations ranging from 340 to 1100 km. Tana, Tydal, and Ammarnäs are typical mountain birch *Betula* spp forests. The forest in Tana is mainly of the eutrophic type (meadow), whereas Ammarnäs and Tydal consist of both eutrophic and barren (heath) plots. Meadow forests are characterised by a rich undergrowth of herbs whereas the undergrowth of heath forests is dominated by juniper *Juniperus communis*. The Kittilä population is situated in Pallas-Ylläs national park and is an old-growth Norway spruce *Picea abies* forest interspersed with birch, goat willow *Salix caprea* and Scots pine *Pinus sylvestris*. The brambling is an abundant character species in all four study areas.

In all study populations, we obtained data on natural parasitism, conducted egg rejection experiments, and collected data on egg appearance (except Tana). Egg experiments were conduced by exchanging one host egg with a conspecific egg from another nest or, on some occasions, an egg from a different passerine species. Experiments were initiated close to clutch completion when possible, but some experiments were also initiated during incubation. The host response was defined as accepted if the foreign egg was incubated for at least 5 days, and rejected if the egg disappeared from the nest. We used a spectrophotometer to obtain objective physical measures of egg color (e.g. Avilés & Moller 2003). Measurements were taken exclusively of the ground color of eggs, which is defined as the relatively uniform background color of the egg (Lahti 2008), whereas we deliberately avoided pigmentation where spotting was obvious. The background of chaffinch and brambling eggs normally comprises more than 95% of the total surface area (Figure 1). Moreover, spots are often small and difficult to measure because the fibre width of the measurement apparatus exceeds the diameter of the spots. Spottiness was quantified for a subset of clutches using imaging software. (See the respective papers for more detailed descriptions of procedures and protocols). Data on appearance of chaffinch, brambling and cuckoo egg appearance were also obtained at egg collections held at the Zoological museum in Copenhagen, Swedish Museum of Natural History in Stockholm, British Museum in Tring, Finnish Museum of Natural History in Helsinki and Museum of Natural History in Gothenburg.

Figure 1: Range of egg colors of chaffinch (rows 1-3) and brambling clutches (rows 4-6). Each egg comes from a different clutch. The bottom row gives examples of cuckoo eggs found in brambling nests in Kittilä.

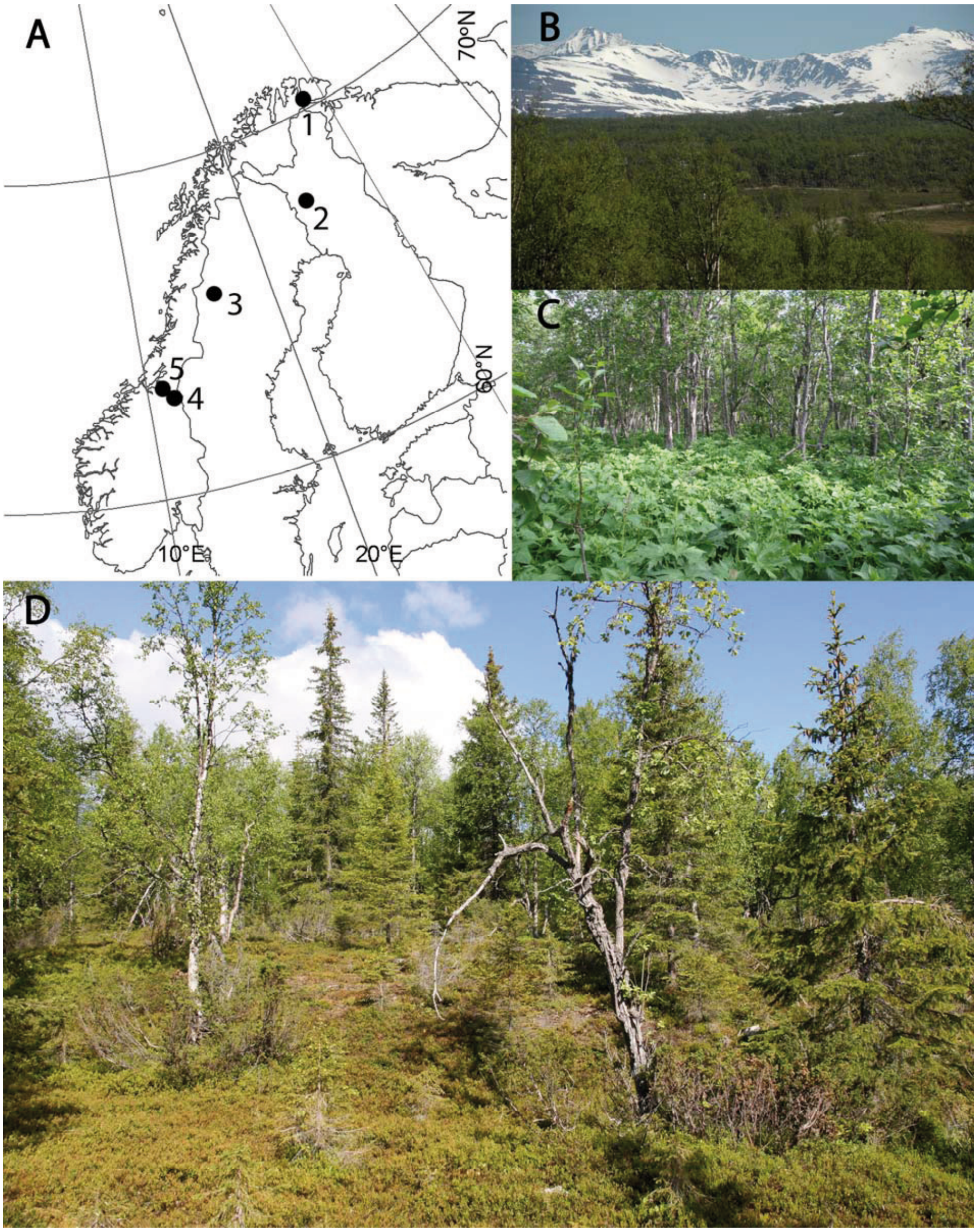

Figure 2: A). Map of Fennoscandia indicating the location of the four brambling populations (1-4) and the chaffinch population (5) that were studied in this thesis. 1: Tana, 2: Kittilä, 3: Ammarnäs, 4: Tydal, 5: Stjørdal. B). Mountain birch forest in Tydal. C). Eutrophic mountain birch forest in Ammarnäs. D). Mixed old growth forest in Kittilä.

Aims of the study and summary of papers

The overarching goal of the thesis was to gain more insight in the coevolutionary interactions between the cuckoo and its two *Fringilla* hosts. To this end we aimed to 1) study rejection of parasitic eggs from an avian visual perception perspective (paper I), 2) examine if the context of single or multiple parasitism affects rejection decisions of host individuals (paper II) 3) examine geographical variation in the occurrence of parasitism and brambling defensive traits (papers III-IV), 4) evaluate similarities and differences in the egg rejection behaviour of the two hosts (papers II, IV), 5) evaluate the opportunity for reciprocal selection on egg phenotypes and its potential consequences (paper IV).

Paper I

Birds possess perhaps the most richly endowed visual systems among vertebrates, and rely heavily on visual cues for a variety of discriminatory tasks, including recognition of parasite eggs. Realistic perceptual models of avian color discrimination provide an opportunity to relate variation in rejection behaviour to perceived dissimilarity between host and parasitic eggs, which in turn is essential for exposing the selection pressures acting on egg colors in brood-parasite host interactions. In this study, we evaluated whether color contrast values (ground color) derived from a photoreceptor noise-limited color opponent model predict behavioural levels of conspecific egg rejection in chaffinches. We used image analyses to quantify differences in aspects of spottiness. The analyses showed that rejection rates increased monotonously with differences in perceived chromatic contrast. Our results therefore support the prediction from sensory discrimination theory that the likelihood of rejection of parasite eggs should decrease the more similar the stimuli (i.e. parasite egg color) are perceived by hosts. However, rejections and acceptances did not sort exactly according to predicted color discrimination thresholds. Many individuals accepted the parasitic egg in cases where it was predicted to be discriminable, and there were also examples of the contrary. One potential interpretation is that the host's behavioural acceptance threshold is set not only by the host's perceptual abilities, but also by the need of an additional "safety margin". Neither of the spottiness variables was related to acceptance/rejection. Collectively, the results confirm that color constitutes an important part of the matching signal used by hosts to discriminate parasite eggs.

Paper II

Empirical studies have uncovered remarkable variation among hosts of avian brood parasites for tolerance of foreign eggs in their nest. Studies that examine the consistency of individual rejection decisions across different contexts are valuable because they can point to potential constraints in the recognition process. In this study, we examined to what extent chaffinches and bramblings show a different tendency to reject if they are multiply parasitised as opposed to parasitised with only one egg. Some individuals were introduced to two parasitic eggs, one partly mimetic and one non-mimetic, in the same breeding attempt. In bramblings, both eggs were introduced simultaneously whereas in chaffinches the partly mimetic egg was introduced shortly after the non-mimetic egg had been rejected. Control individuals were experimentally parasitised with one partly mimetic egg. We found no difference between the experimental and control group in the tendency to reject the partly mimetic egg. This implies that individual chaffinches and bramblings maintain a rigid acceptance threshold unaffected by multiple parasitism. In addition, the rejection rate of non-mimetic eggs was high (90-100%) regardless of whether the host was simultaneously introduced to a relatively mimetic egg. This result corroborates previous conclusions in showing that egg recognition is template based and does not involve direct pair-wise comparison of eggs in the nest (which should have lead to a lower rejection rate of the non-mimetic egg). *Fringilla* finches therefore give examples of simple, but yet advanced recognition systems. These results are discussed in light of recent studies with a different host where contrasting results were obtained in similar experimental setups.

Paper III

In this study we examined adaptations against cuckoo parasitism in bramblings on a large spatial scale in Fennoscandia. We obtained data on natural parasitism, conducted egg exchange experiments aimed to determine the potential strength of host egg rejection, and recorded behavioural responses to cuckoo dummies. One population in north western Finland was parasitised (mean annual parasitism rate was 6%), whereas we found no indication of cuckoo parasitism in one Swedish and two Norwegian populations. The mimicry of cuckoo eggs was very good, confirming the existence of a long-lasting parasitic relationship. Data from museums, literature and nest record cards suggest that geographical differences in presence/absence of *Fringilla* cuckoos could be stable to some degree. There were no differences among the four populations in the host's strength of egg rejection or in the proportion of adults behaving aggressively against cuckoo dummies. Most individuals in all populations rejected non-mimetic eggs, and the relationship between egg rejection and host-parasite egg similarity was the same in all populations. Moreover, bramblings very rarely made errors in rejection, implying that egg rejection is robust to decay. The brambling-cuckoo system therefore differs from other well studied systems which are characterised by pronounced spatial and temporal variation in egg rejection. Bramblings represent an extreme case due to their notorious lack of site fidelity, and they are in principle available to cuckoos everywhere because they build arboreal and open nests. The ubiquitous presence of precise egg rejection has most likely arisen because bramblings respond to selection as one evolutionary unit, and because the average parasitism pressures have been high enough in the past to drive regional fixation of rejection alleles and evolution of clutch characteristics that facilitate cost free egg recognition.

Paper IV

Interactions between avian-brood parasites and their hosts provide some of the most prominent examples of mimicry systems. Yet, empirical efforts to understand the trajectories of egg mimicry are in short supply. In this study, we evaluated realistic potential coevolutionary outcomes for interactions involving the chaffinch and brambling. These hosts represent a unique opportunity to address the presence and importance of egg phenotype coevolution because they are among the hosts of the cuckoo that have the highest between-clutch variation in egg appearance. At the same time, they also differ strongly in their ability to respond to local selection as indicated by subspecies structure and ringing recoveries, which leads to different predictions regarding coevolutionary outcomes. We used a tetrachromatic color space to quantify egg color distributions which we then combined with an empirical host discrimination function to determine the direction of selection on cuckoo and host eggs. We found that there is huge potential for parasite mediated disruptive selection on host egg colors, and that the cuckoo has evolved egg phenotypes that are close to the optimum color for parasitism on bramblings. This confirms that cuckoos, in principle, can drive coevolutionary cycles in natural populations. However, the cuckoo and brambling may be close to a matching equilibrium because the high rate of gene flow in the brambling interferes with selection in parasitised populations. Accordingly, we found that cuckoos are equally well adapted to one parasitised and two distant unparasitised populations. Moreover, the chaffinch, which has the largest evolutionary potential of the two hosts, has evolved a markedly more bimodal egg color distribution, consistent with the direction of evolutionary change predicted for the brambling. Somewhat surprisingly, our calculations also showed that increasing bimodality in the host does not produce corresponding adaptive peaks for cuckoo egg color. Parallel polymorphisms, as has been reported for some African and Asian cuckoos and their hosts, are therefore unlikely local outcomes in these particular interactions. Finally, we found that the cuckoo is not likely to be fundamentally constrained by between-clutch host variation in its ability to interact with the chaffinch. This result has potentially important implications because it has often been proposed without further testing that high clutch variability in the host may cause extinction of host specific cuckoo lineages, i.e. leaving little scope for coevolutionary dynamics.

Discussion

In this part, I summarise the results and discuss how they contribute to our knowledge of *Fringilla*-cuckoo interactions and cuckoo-host interactions in general. In paper I, we found that color contrast values derived from a perceptual model of avian vision predicts behavioural levels of egg rejection in chaffinches, whereas aspects of spotting are less important. In paper II, we found that egg rejection in individual chaffinches and bramblings are elicited at the same level of host parasite egg-dissimilarity, irrespective of the context being single parasitism, multiple parasitism (bramblings), or sequential parasitism within the same breeding bout (chaffinches). In paper III, we found that levels of egg rejection and behavioural aggression against cuckoo dummies do not differ between geographically distant brambling populations in Fennoscandia. In paper IV, we investigated the opportunity for reciprocal selection on egg phenotypes and its potential consequences. We found that the cuckoo may be at matching equilibrium with the brambling, and that the chaffinch has evolved a more bimodal egg color distribution, fairly consistent with the direction of evolutionary change predicted for the brambling.

I begin by briefly discussing egg rejection in light of perceptual models of avian color discrimination, and the apparently context-independent egg rejection behaviour of *Fringilla* hosts. I then move on to discuss spatial and temporal variation in host egg rejection, coevolutionary dynamics of egg appearance, and the spatial scale of brambling-cuckoo coevolution.

Proximate aspects of egg rejection in chaffinches and bramblings

Previous studies of unparasitised Central Norwegian populations have given us the following knowledge about the egg rejection behaviour of bramblings and chaffinches: egg rejection is largely determined by host-parasite egg dissimilarity, as assessed by humans (Braa et al. 1992; Stokke et al. 2004), and is based on true recognition (Moksnes 1992). Rejection costs and possible recognition errors are sparse (Stokke et al. 2002a), age or intraclutch variation does not affect egg rejection in chaffinches (Stokke et al. 2004, no age-controlled experiments excist for bramblings), and simulation of increased risk of parasitism does not stimulate increased rejection of foreign eggs (Braa et al. 1992) or erroneous ejection of own eggs from unparasitised nests (chaffinches: Stokke et al. 2002a). In this thesis, we have gone one step further and tested if perceptual models of avian color discrimination predicts rejection of foreign conspecific eggs (paper I) and if the context of simultaneous or sequential multiple experimental parasitism affects rejection behaviour (paper II).

Avian color discrimination and egg rejection

Vision is by far the most important sensory channel for detection of brood parasite eggs, although a few examples of tactile discrimination are known from hosts that build doomed nests (Marchetti 2000; Mason & Rothstein 1986). Given the indisputable differences between human and avian visual systems, it is hardly surprising that human subjective methods for describing egg similarity have repeatedly been called into question (Avilés 2008; Cherry & Bennett 2001; Starling et al. 2006). Avian and human vision differs in a number of anatomical and physiological details that are likely to lead to different perception of color and color differences: birds have a wider spectral range, four narrow-band photoreceptors instead of three broadband, and pigmented oil droplets that act as long-pass cut off filters which sharpens spectral tuning (Cuthill 2006). These differences collectively imply that birds have better colour discrimination and also perceive colours that can not be experienced by humans (Bennett & Cuthill 1994; Bennett et al. 1994; Vorobyev et al. 1998). Indeed, many of the recent advances in the study of avian plumage coloration are entirely due to the recognition that birds and humans perceive colors in different ways (Bennett & Théry 2007). The key invention has been the use of portable spectrophotometers which encompass the entire bird visible spectrum and provides objective physical measures of color. In recent years, spectral data have also been implemented in behaviourally supported perceptual models of avian color discrimination (Vorobyev & Osorio 1998), which we made use of to study egg rejection in chaffinches (paper I). Recently, this approach has generated quantitatively precise predictions of egg rejection by song thrushes *Turdus philomelos* (Cassey et al. 2008b), and illuminated the importance of nest luminosity for perception of mimetic similarity (Avilés 2008). These studies and ours (paper I) show that realistic perceptual models hold promise as a valuable tool for exposing the reciprocal selection pressures exerted on egg coloration. An important topic for future research is to reveal if and how interspecific variation in perceptual abilities influence coevolutionary arms races (Safran & Vitousek 2008).

Egg appearance is a complex visual stimulus, and we are still far from understanding how hosts integrate the various aspects of it. Thus, modelling host color discrimination is not likely to give a full account of egg rejection, even if all model assumptions are met and parameterisation is adequate. Interestingly, a simple human based index of parasite- host egg similarity (Braa et al. 1992; Stokke et al. 2004, papers II-III) explained more of the variation in egg rejection in chaffinches and bramblings than did contrast values derived from perceptual models/tetrachromatic color space (papers II-III, unpublished data, see below). It is important to stress that this finding does not devaluate the importance of realistic models of avian color perception. Behavioural tests of Vorobyev and Osorio’s (1998) model are extremely valuable and should be encouraged (Bennett & Théry 2007). Our results are important because they confirm that color as perceived by the host is an important part of the matching signal (paper I). Egg color should therefore do double duty as both target and agent of selection in chaffinch-cuckoo interactions (paper IV).

In a separate study (unpublished), I quantified three spotting variables (same as described for chaffinches in paper I) of host and parasite eggs in randomly chosen experiments with bramblings that gave a rejection (N=40) or acceptance (N=40) response. I then compared two logistic regressions on the probability of egg rejection by their AIC values (Akaike information criterion, Burnham & Anderson 2002). The first model had the subjective similarity score (described in paper II, III) as the only predictor, and had an AIC-value of 80.0. The other model had seven predictors: the contrast between host and parasite egg in each of the four spotting variables and volume and shape, and chromatic and brightness contrasts (which are strongly linearly related to values based on Vorobyev and Osorio’s (1998) model, papers I-II). The AIC value of the second model was 99.6, which shows that the first model is superior in terms of prediction. There are several additional examples where variation in rejection behaviour is accounted for by simple human-based estimates of egg similarity (Davies 2000; Rothstein & Robinson 1998). Studying village weavers *Ploceus cuculatus*, Lahti (2006) noted that "after hundreds of egg replacement experiments, I could in most cases predict a priori whether an egg would be rejected or accepted, which suggests that my methods of assessing color and spotting do not fully capture the integration of visual stimuli in a bird (or human) brain". Our experiences with chaffinches and bramblings are the same. The main drawbacks with the subjective similarity score is that 1) it does not provide any quantitative information about egg appearance, 2) it does not specify how different aspects of egg appearance are weighted to produce the total score, and 3) the scale of measurement is not transportable between studies. The range of application is therefore rather limited. Nevertheless, in light of these results and Lahti's statement, it could in some cases be wise to consult human vision rather than to discount it as entirely inappropriate (e.g. Cherry & Bennett 2001). Although bird and human vision are different with regard to color perception (but very similar with regard to how they rank color differences under bright light conditions (Håstad & Ödeen 2008; Vorobyev et al. 1998, own unpublished data)), there could be important similarities as well, for example in how the spatial configuration of colors across the egg surface is processed. A problem with the analysis in paper I is that it combines very different sorts of visual data. Whereas quantification of color differences is based upon assumptions about the physiology of the intended receiver, there are many potential ways of quantifying spottiness. However, these differ mostly by being more or less comprehensive and quantitatively precise, and at present there is no available method that fully circumvents the problem of human subjectivity (see Andersson & Prager 2006).

Interestingly, our analyses showed that many parasitic eggs were accepted in cases where they should be discriminable based on color alone. This could indicate that acceptance of parasitic eggs is not entirely due to lack of visual recognition. For example, chaffinches may also have been selected to adopt an additional "safety margin" in order to optimise the balance between acceptance and recognition errors (paper II). At the moment, however, the perceptual threshold criterion is poorly defined in birds, especially since the parameters of the model are usually approximated using data from other species. The model needs to be verified in more species and situations before the "1 JND" threshold can be trusted.

Context independent egg rejection in chaffinches and bramblings

Revealing if rejection of parasitic eggs is consistent across contexts is important because context dependence may point to constraints relevant to the process of discrimination

(Liebert & Starks 2004; Lotem & Nakamura 1998), and may affect the selection pressure for cuckoo egg mimicry (Holen & Johnstone 2006). Several experimental studies have shown that cuckoo hosts may use the presence of an adult cuckoo at the nest as cue of a high risk of parasitism (Bartol et al. 2002; Davies & Brooke 1988; Moksnes et al. 2000; Moksnes et al. 1993). Hosts have also been found to adjust their tendency to reject as parasitism risk declines during the season (Alvarez 1996; Brooke et al. 1998). Moreover, great reed warblers may change their tendency to reject within the same breeding event according to the risk of recurrent parasitism (Hauber et al. 2006). Such flexibility indicates that hosts optimise the balance between acceptance and recognition errors according to shifting risk of parasitism. In contrast, studies of egg rejection in bramblings and chaffinches did not find an effect of presenting a cuckoo dummy at the nest (Braa et al. 1992; Stokke et al. 2002a, additional unpublished results for bramblings). Our findings (paper II) add further support to the view that these two hosts adopt "rigid" acceptance thresholds. A fixed acceptance threshold may be adaptive if host and parasite clutch characteristics show little overlap (i.e. the host has low intraclutch variation and high interclutch variation). In this case, parasitism risk has little influence on the optimal acceptance threshold, and the host can afford to apply a threshold that minimizes recognition errors without simultaneously increasing the risk of acceptance errors (Rodriguez-Girones & Lotem 1999; Stokke et al. 2007b). The flexible behaviour shown by species such as the meadow pipit *Anthus pratensis*, reed warbler *Acrocephalus scirpaceus* and great reed warbler seems to be in broad agreement with the hypothesised importance of clutch characteristics, since these species tend to have both a higher intraclutch variation and a lower interclutch variation than *Fringilla* finches (Stokke et al. 2002b; Øien et al. 1995). However, the reliability and hence usefulness of conditional cues could also differ among species and populations. Future studies need to quantify and directly compare clutch characteristics between populations of species that show different degrees of flexibility. Parameterisation of perceptual models (paper I) with species-specific values is also needed to confirm that bramblings and chaffinches apply real acceptance thresholds rather than simply reject any egg that is discriminable in terms of their perceptual abilities.

Spatial and temporal variation in host egg rejection

In the interaction between cuckoos and bramblings, there is likely to be little dynamic change in the frequencies of host individuals equipped with the necessary genetic background for rejecting non-mimetic eggs (paper III). Most individuals in all four study populations reject foreign eggs if they are sufficiently odd-looking, suggesting that a genetic foundation for rejection is close to fixation in this species (paper III). Parasitism is likely to have been historically widespread in both chaffinches and bramblings, for several reasons. Both are abundant forest generalists and numerically dominant hosts in their habitats, and have distributions that overlap completely with that of the cuckoo in Europe. Colonisation of ecologically suitable hosts seems to be an inevitable process, since most hosts within a given region show defences that have no adaptive function besides in the context of brood parasitism (Davies & Brooke 1989b; Moksnes et al. 1991). Given the ubiquitous accessibility of *Fringilla* finches to cuckoos, parasitism rates may have been high enough to cause rapid fixation (or nearly so) of the genetic foundation of egg rejection (Rothstein 1975a; Røskaft et al. 2002). Due to the nomadic behaviour of bramblings, it is also in principle possible that interaction in a few geographically restricted areas could have driven evolution of defensive traits in the whole region (Gomulkiewicz et al. 2000; Lenormand 2002). It is also possible that rejection behaviour evolved before a range expansion, or was already present in a common ancestor (Bolen et al. 2000; Peer et al. 2007; Peer & Sealy 2004; Rothstein 2001).

Further studies are needed to reach a firm conclusion about geographical variation in chaffinches. Although Central Norwegian chaffinches behave very much like bramblings, chaffinches in Britain rejected only 60% (N=15) of non-mimetic model cuckoo eggs (Davies & Brooke 1989b). It is unclear if differences between protocols (e.g. use of model eggs instead of conspecific eggs and 3-day instead of 5-day criterion for acceptance) could explain some of this difference. Moksnes et al. (1991) used non-mimetic model cuckoo eggs in the same study area as we did, and measured a moderately high rejection rate (69%, N=16), which is below the rejection rate of contrasting conspecific eggs found more recently (Stokke et al. 2004, papers I, IV). This difference is likely to be an artefact because there is no reason why the chaffinch should change rejection behaviour over such a short time scale. *Fringilla* finches rarely if ever make recognition errors (Stokke et al. 2002a, paper III), and do not change rejection decisions from one context to another (Braa et al. 1992; Stokke et al. 2004, paper II), implying that egg rejection could be maintained indefinitely in the absence of any pleiotropic effects. The chaffinch has also shown to reject odd-looking eggs in Spain (Martin-Vivaldi et al. 2002) and in an introduced New Zeeland population (Hale & Briskie 2007) (although sample sizes were small in these studies). For the brambling, egg appearance is a more interesting interaction trait in terms of its larger potential for generating variable host responses. The available data suggests that this could hold true for most chaffinch populations as well.

According to the arms race view of cuckoo-host coevolution, natural selection is likely to be focussed on different sets of traits in different interactions (Davies & Brooke 1989a; Soler 2009; Stokke et al. 2002b; Welbergen & Davies 2009; Øien et al. 1995). Many hosts are likely to be similar to *Fringilla* finches in that recognition and rejection of odd-looking eggs is both ubiquitous and robust to decay (Lahti 2006; Røskaft et al. 2002; Stokke et al. 2005), although lack of significant geographic variation has yet to be confirmed for most cuckoo hosts. Because many of these hosts also have a high interclutch variation (Øien et al. 1995), which has no known explanation besides being a defence against egg mimicry (Lahti 2005; 2008), this implies that understanding the long-term outcomes of these particular interactions requires investigation of the consequences of reciprocal selection on egg appearance.

The most thoroughly investigated hosts to date show considerable geographical variation in rejection rates of experimental odd-looking eggs, both on small and large spatial scales, with parasitised populations normally showing higher rejection rates than unparasitised ones (Lindholm 2000; Lindholm & Thomas 2000; Martín-Gálvez et al. 2007; Soler et al. 1999a; Stokke et al. 2008). Furthermore, rejection rates have been observed to change rapidly in accordance with changes in parasitism rates (Brooke et al. 1998; Nakamura et al. 1998; Robert & Sorci 1999; Soler & Møller 1990). In the magpie, for example, there are indications of spatially structured evolutionary cycles in rejection rates caused by negative frequency dependent selection and recognition costs (Soler et al. 1998). These findings imply that much of the evolutionary dynamics in these hosts involve rejection alleles and/or norms that guide the conditional expression of egg rejection. Accordingly, many debates about coevolution in brood parasites-host interactions have concerned the factors that lead to varying frequencies of rejection of odd-looking eggs (Davies 1999; Rothstein & Robinson 1998; Stokke et al. 2005; Winfree 1999). Even so, the existence of cuckoo egg mimicry and egg rejection is itself a sufficient reason to explore the possibility that one or both antagonists experience variable fitness outcomes related to egg appearance (Stokke et al. 2002b; Øien et al. 1995). In general, knowledge of both egg rejection capabilities (i.e. as determined by egg experiments) and egg phenotype distributions (regardless of which factors have been shaping them) is required to reveal current selection patterns (Stokke et al. 2005), which is the basis for inquiries about how coevolution plays out on a wider temporal and spatial scale (Røskaft et al. 2002; Soler et al. 2001; Thompson 2005b). To give one example, there is no necessary direct link between the ecological intensity of an interaction (i.e. parasitism rate) and the strength of natural selection on that interaction (Hanifin et al. 2008; Thompson 2005a; Toju & Sota 2006b). Thus, it is conceivable that host and cuckoo sometimes show sufficient overlap in egg appearance to prevent selection on egg rejection alleles in heavily parasitised populations. A putative example of this situation is found in eastern Finland, where all cuckoos that specialise on redstarts *Phoenicurus phoenicurus* lay immaculate blue eggs which perfectly matches those of the redstart, and where the rejection rate of experimental odd-looking eggs is intermediate (Kelly 1987; Rothstein 1990; Rutila et al. 2002; von Haartmann 1981). In this situation, coevolution might be suspended until new rejecter individuals with distinct egg phenotypes appear through migration or mutation. Alternatively, host and parasite egg types could be so mismatched that there is no selection on either host or parasite egg types (Hanifin et al. 2008; Lyon & Eadie 2004). The advent of new methods for measuring egg phenotypes (Avilés 2008; Cassey et al. 2008a; Cassey et al. 2008b; Stoddard & Prum 2008, paper IV), and for partitioning selection based on interactions (Ridenhour 2005; Toju & Sota 2006b) offer promise in assisting more in debt descriptions of selection patterns in cuckoo-host interactions in the future.

Coevolution between host and cuckoo egg appearance

Our study demonstrated a cost to commonness for brambling hosts related to egg phenotype (paper IV). This relationship can be regarded indirect evidence that brood parasites, in principle, can drive coevolutionary cycles in natural populations (Dybdahl & Lively 1995), as suggested by theoretical work (Takasu 2003; 2005). The degree of egg mimicry varies extensively within and among cuckoo-host systems and is frequently found to be surprisingly poor (Moksnes & Røskaft 1995). Variable degrees of egg mimicry can to a large extent be explained by variation in the selection pressures imposed by hosts (Antonov et al. 2006a; b; Avilés 2008; Brooke & Davies 1988; Grim 2002; 2005). Alternative explanations for poor mimicry invoke recent or frequent host shifts (Edvardsen et al. 2001; Nakamura et al. 1998), disruption of local adaptation due to somatic inheritance of egg color and spatial overlap of hosts with different egg types (Southern 1958), opposing costs of mimicry (Holen & Johnstone 2004; Servedio & Lande 2003), fluctuating environmental effects on the evolution of underlying genes (Avilés et al. 2007), and difficulties with establishing host races due to unfavourable host demography (Soler et al. 2009). Our results point to two potential additional explanations for observed mismatch. First, as shown in paper IV, increasing diversity of host egg types can in some cases cause selection towards intermediate cuckoo egg types that do not match any of the host egg types (Takasu 2003). Second, if non-equilibrium dynamics is produced (i.e. fluctuating egg polymorphisms), this will automatically generate temporal patterns of maladaptation (Lively 1999; Nuismer et al. 2005; Thompson et al. 2002). For example, Dybdahl and Lively (1995) found that mismatch between defensive and offensive profiles of *Potamopyrgus* snails and *Microphallus* trematode parasites is expected to be observed approximately half of the time due to time lags in evolution of traits. Finally, in geographically structured interactions, a geographic mosaic may develop that can give rise to spatial patterns of match and mismatch (due to an interplay between selection mosaics, coevolutionary hot spots and gene flow, Nuismer 2006; Thompson 2005b; Thompson et al. 2002). For example, Zangerl and Berenbaum (2003) found that 8 out of 20 local interactions between parsnip *Pastinaca sativa* and parasitic parsnip webworms *Depressaria pastinacella* had mismatched phenotypes, and that mismatch was associated with proximity to localities where webworms used an alternative host.

The possibility of non-equilibrium dynamics and geographic mosaics underscores the need for both more long term studies of egg matching and/or geographical approaches similar to those that have been applied to address evolution of egg rejection (Soler et al. 1999a; 2001; Stokke et al. 2008). Long term studies of mimicry in local populations are rare (Avilés et al. 2006; Brooke & Davies 1987). One potential limitation with studies that rely on museum clutches to investigate changes in mimicry over time is that one often has little knowledge of the strength of selection associated with observed changes (Avilés et al. 2006). Another limitation is that storage and aging may distort egg colors in ways that we do not yet fully understand (paper IV). Due to the latter problem, it is difficult at present to say if cuckoos and bramblings have undergone evolutionary change in egg color in Fennoscandia during the 20th century (as could be suggested in Figure 2, paper IV). As a minimum, our results indicate that there has been no notable change in the general level of mimicry during the last 100 years. In general, frequency dependent selection has the potential to produce very rapid changes in allele frequencies (compared to directional selection, Ebert 2008), and evolutionary changes might therefore be possible to detect with detailed long term field studies of carefully chosen interactions. A complementary (transverse) approach is to compare populations across a broad range of the interaction (e.g. Hanifin et al. 2008; Kaltz et al. 1999; Lively & Dybdahl 2000; Mayhew 2006; Toju & Sota 2006b; Zangerl & Berenbaum 2003).

Previous studies have repeatedly established the adaptive value of cuckoo egg mimicry (Davies 2000; Rothstein & Robinson 1998) and provided evidence that mimicry in turn promotes increased interclutch variation in hosts (Kilner 2006; Lahti 2005; Stokke et al. 2002b). High interclutch variation places a fundamental constraint on the reproductive success of cuckoos that deposit their eggs without regard to the host individual’s egg type.

High interclutch variation has therefore understandably been implicated as a potential factor behind extinction of certain cuckoo gentes (Honza et al. 2004; Lovászi & Moskát 2004; Stokke et al. 2004). If so, this would seem to narrow the scope for coevolutionary dynamics. However, we found that the cuckoo need not be fundamentally constrained by host interclutch variation in its ability to coevolve with the chaffinch (paper IV), which is one of the most variable of all European passerines with regard to egg appearance (Øien et al. 1995). This implies that in order to address the long term persistence of gentes parasitizing hosts with variable eggs, one could benefit from focusing more on the processes that prevent/promote local adaptation by cuckoos in geographically structured interactions (Thompson et al. 2002). As an example, we suggest that a high rate of gene flow in the brambling allows the cuckoo to adapt permanently to the host egg phenotype distribution, thereby promoting overall persistence of this interaction (paper IV, see below). In contrast, local adaptation by the cuckoo prompts a stronger response to selection in the chaffinch (paper IV), and fluctuating evolution in host egg types could therefore be part of the explanation for why reports of regular parasitism on chaffinches are lacking even from areas where they are among the most abundant and available passerines (such as in Britain, Baker 1942; Brooke & Davies 1987; Glue & Murray 1984). On longer time scales, bramblings could serve as a “refugee” for cuckoos that are somewhat preadapted to resume interaction with chaffinches (see Nash et al. (2008) for an analogous example). Thus, a potential scenario is that cuckoos show stable persistence on bramblings but are involved in episodic interactions with chaffinches. The likelihood of this scenario may hinge on whether interclutch variation declines in the absence of parasitism, thereby improving the chances for future recolonisation of chaffinches. Lahti (2005) found differences in interclutch variation between populations of village weavers *Ploceus cuculatus* that were consistent with stabilising selection, but also with founder events. In a recent study Lahti (2008) showed that village weavers under relaxed selection from egg mimicking Diederick cuckoos *Chrysococcyx caprius* might adapt to solar radiation (by evolving more intense blue-green colors). Studies conducted to date suggest that nest predators are unlikely to exert strong stabilising selection on the egg appearance of arboreal open nesting species (Kilner 2006). Nevertheless, since absence/presence of alternative selection pressures has potentially important consequences for the (co)evolutionary dynamics of egg phenotypes and long-term pattern of host use, there is clearly a need for more studies designed to detect direct or correlated selection on egg appearance.

In general, we do not know if cuckoos can drive population differentiation in their hosts’ egg phenotypes and whether they are normally locally adapted (i.e. higher fitness in sympatric than allopatric host populations). Conventional wisdom holds that parasites should be locally adapted because they normally have shorter generation times, larger population sizes, and experience stronger selection than their hosts (Dawkins & Krebs 1979; Kaltz & Shykoff 1998). Cuckoos, in contrast, have smaller population sizes and longer generation times than their hosts, which might cancel out the effect of stronger selection. As long as migration rates are not too high, gene flow may be a creative force that provides new genetic variation for reciprocal selection and continued coadaptation (Gomulkiewicz et al. 2007). Theoretical and empirical studies show that the species with the relatively higher rate of gene flow normally shows local adaptation (e.g. Dybdahl & Lively 1996; Gandon 2002; Gandon et al. 1996; Hoeksema & Forde 2008). Relative gene flow rates have been estimated for great spotted cuckoos and its magpie host (Martinez et al. 1999), but not for the common cuckoo and any of its hosts. Obviously, elucidating the determinants of local cuckoo-host egg matching is a promising avenue for future research that should be of interest from the perspective of both basic and applied evolutionary ecology.

It has recently been suggested that cuckoos might tackle the problem of high host interclutch variation by actively selecting host individuals with similar egg types (Davies 2000 p. 84). There is some correlative support for this possibility (Avilés et al. 2006; Cherry et al. 2007), but there was no indication of selective laying by Diederick cuckoos parasitizing *Ploceus* weaverbirds with highly variable eggs (Davies 2000 p. 84), and matching between cuckoo and brambling eggs is not better than expectations from random laying (based on museum data, unpublished). In addition to experimental tests, it would also be useful to have more clear theoretical expectations for how non-random laying affects the distributions of egg appearance in the long run. One intuitive consequence is that selective egg laying shields otherwise unfavourable cuckoo egg types from selection, thereby possibly delaying evolution of egg types that optimise average mimetic similarity.

Geographical scale of brambling-cuckoo coevolution

Geographic mosaics in interaction traits have developed over relatively short distances in several brood parasite-host interactions (Martín-Gálvez et al. 2007; Stokke et al. 2008). Furthermore, these geographical differences have arisen at least partly because of variation in the coevolutionary interactions (i.e. as opposed to historical factors such as gene flow, Soler et al. 2001). In paper III, we documented a lack of geographical variation in egg rejection and aggression towards adult cuckoos among geographically distant brambling populations in

Fennoscandia. Since this could reflect past selective sweeps, it does not exclude the possibility that the interaction could show geographical structure with regard to other traits. However, we found that cuckoos in north western Finland (Kittilä) have egg colors that are equally close to the optimum for two distant unparasitised populations. Since there is a strong opportunity for selection on brambling egg colors, and because there are indications that presence of cuckoos might be temporally stable in this part of Fennoscandia (paper III), this suggests that bramblings show no localised response to selection in parasitised populations. In support of this interpretation, we found that the chaffinch, which is expected to show a stronger local response to selection, has evolved a markedly more bimodal egg color distribution (paper IV). Collectively, these results imply that the regional brambling population evolves as one large unit (paper III-IV), and therefore that the same cuckoo egg types are favoured by the interaction in different localities. Although it is possible that other biotic or abiotic factors may still cause spatially variable selection on cuckoo eggs, their importance is likely to be overwhelmed by selection due to the interaction with bramblings. Accordingly, preliminary analyses based on museum collections (which contain cuckoo eggs from a wider range of localities) show that there is no notable variation in the colors of cuckoo or host eggs along latitudinal or longitudinal gradients in northern Fennoscandia (unpublished). Thus, the brambling-cuckoo interaction seems to hold little of the geographical complexity found in other (probably most) brood parasite-host interactions (Lindholm & Thomas 2000; Martín-Gálvez et al. 2007; Soler et al. 1999a; 2001; Stokke et al. 2007a; Stokke et al. 2008). Nevertheless, our results still underscore that a proper understanding of this particular interaction requires attention to the spatial dynamics of the brambling. If we were studying only the parasitised area in Kittilä and treating it as a closed population, we would be able to document fitness differences related to egg phenotypes, which in turn could lead us to predict selection towards fluctuating egg polymorphisms (for example). The overall trajectory, however, may be towards a stable matching equilibrium (paper IV) because breeding nomadism impedes localised reciprocal adaptation by bramblings (Hendry et al. 2001; Nash et al. 2008; Parchman & Benkman 2008). Likewise, if we were studying unparasitised populations, documentation of strong egg rejection abilities could lead us to deduce that the interaction has evolved towards extinction of the cuckoo (Braa et al. 1992; Davies & Brooke 1989a). Yet, it is also possible that the current geographical pattern of parasitism is just a snap shot view of a gens distribution in continual change due to extinction/recolonisation dynamics (papers III-IV, Lindholm 1999).

Conclusion

In the present thesis, I have reported results which bring us one step further towards understanding the evolution of *Fringilla*-cuckoo interactions, and which has potential implications for our general understanding of who wins cuckoo-host arms races and how they do so.

Extensive experimental and observational work on bramblings in Fennoscandia revealed no differences between cold spots and a potential coevolutionary hot spot in the presence of major host adaptations such as rejection of odd-looking eggs (which is close to fixation in all populations), behavioural responses to adult cuckoos, and population level scope for rejection of cuckoo eggs. Our experimental results indicate that rejection behaviour *per se* is unlikely to show ongoing evolutionary change and is not modulated by contextual cues. Instead of representing independent replication of local evolutionary trajectories, the lack of geographical variation in brambling defences has likely arisen because the brambling evolves as one unit within Fennoscandia. Cuckoo eggs had colors that were close to the optimum for parasitism of one parasitised and two unparasitised populations. The possibility that cuckoos and bramblings are at a matching equilibrium also gains some support in analyses of museum data. Consequently, the distribution of brambling cuckoos indicated by our survey and historical data has no direct explanation in the current level of host adaptation. Instead, it could reflect differences in rates of extinction/colonisation caused by environmental conditions.

The congeneric chaffinch is similar to the brambling in that egg phenotype matching is the main factor determining the outcome of parasitic events. The two finches are also similar with regard to most ecological and demographic characteristics that affect their suitability as cuckoo hosts. Gene flow in the chaffinch is likely to occur at lower rates/shorter distances than in the brambling, which means that egg colour should respond to selection in a greater extent. Accordingly, the chaffinch has evolved an egg color distribution which matches the evolutionary trajectory predicted for the brambling. Overall, our findings suggest that focus on the factors and processes that prevent optimal cuckoo-host egg matching (i.e. relative rates of gene flow, geographical structure) is the key to understand the persistence of cuckoo gentes parasitizing *Fringilla*-like hosts with variable eggs.

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Paper I

Avian Visual Perception Predicts Behavioral Responses to Experimental Brood Parasitism in Chaffinches

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Online enhancements: table A1, Figures A1 and A2.

ABSTRACT: Species that have been involved in a coevolutionary arms-race with the European cuckoo *Cuculus canorus* have evolved anti-parasite defenses allowing them to discriminate and reject odd-looking eggs. Mechanisms of host discrimination are mostly visually mediated, and have been studied based on human vision or spectrophotometry, which does not account for what the receiver (i.e. host) actually can discriminate. Here, we apply a perceptual model of color discrimination to study whether behavioral responses to experimental parasitism in chaffinches *Fringilla coelebs* fits with model predictions of chromatic and achromatic (i.e. brightness) discrimination. Behavioral responses by chaffinches partly conformed to expectations from the model. Discrimination of parasite eggs gradually increased with increasing differences in chromatic contrasts between parasite and host eggs, whereas achromatic contrasts and differences in shape, volume and spottiness did not affect egg rejection. Our results confirm that color differences of the eggs, as quantified by realistic models of retinal function, are important integral parts of a matching signal used by chaffinch hosts.

Keywords: avian vision, cuckoo parasitism, chaffinch, egg discrimination, host perception, sensory visual discrimination

Cuckoo *Cuculus canorus* – host interactions provide some of the clearer text-book examples of coadaptation in vertebrates. Cuckoos lay their eggs in the nests of host species, and leave parental care of their offspring to unrelated foster parents (Davies 2000; Payne 2005; Stokke et al. 2005). Cuckoo parasitism is harmful for hosts since once the cuckoo egg hatches the young cuckoo readily displaces all host eggs and chicks (Davies 2000), which causes a dramatic reduction of host reproductive output (Øien et al. 1998; Krüger 2007). Cuckoo parasitism has therefore selected for effective defensive mechanisms in their hosts, which at the same time has selected for further elaborated counter-defenses in the cuckoo to overcome host defenses (Brooke and Davies 1988; Davies and Brooke 1988; Stokke et al. 2005). In this coevolutionary arms race scenario, many host species have evolved anti-parasite defenses allowing them to defend themselves against parasite exploitation by discriminating and rejecting any odd-looking egg that is added to their clutches (Rothstein 1990; Moksnes et al. 1991).

Evidence suggests that stimuli involved in cuckoo egg discrimination are mostly visually mediated (Davies 2000). A number of studies have shown that cuckoo egg rejection increases with differences in appearance between cuckoo and host eggs as judged by humans (Davies 2000). Many bird species, including cuckoo hosts, can perceive UV wavelengths, of which humans are blind, due to a fourth cone type in their retinas which is sensitive to UV light (e.g., Bennett et al. 1996; Bowmaker et al. 1997; Cuthill et al. 2000). Recent application of spectrophotometry that accounts for UV wavelength has revealed the possible existence of cuckoo gentes that appear to be cryptic to human vision (e.g., Cherry and Bennett 2001; Avilés and Møller 2004; Starling et al. 2006). However, a limitation in these studies is that egg-matching is quantified as the difference in reflectance between cuckoo and host eggs which does not account for what the hosts actually perceive (Vorobyev et al. 1998; Cuthill et al. 2000; Endler et al. 2005). Avilés (2008) recently used realistic models of hosts' perceptual physiology that also account for nest luminosity to study perception of different cuckoo egg morphs in relation to host vision. However, discrimination experiments are clearly needed to expose the evolutionary selective pressures acting on cuckoo egg coloration considering what is known about hosts' visual abilities and the light conditions of host nests.

In a recent work, Cassey et al. (2008) found that differences in quantum catches from the ultraviolet and short-wavelength sensitive cones predicted discrimination of artificial eggs in song thrushes *Turdus philomelos*. However, the colors used to paint parasite eggs in that study did not reflect ultraviolet wavelengths and displayed unnatural shades at longer wavelengths (Honza et al. 2007), which resulted in an unnaturally high discriminability of experimentally painted eggs (Cassey et al. 2008). Both intra-specific brood parasitism and cuckoo parasitism with mimetic eggs are likely to challenge hosts with difficult discriminatory tasks, and it is therefore critical to establish the limits of host sensory perception by studying host behavioral responses to natural variation in egg coloration. Furthermore, egg discrimination by hosts may rely on differences between parasite and host eggs in other characteristics than coloration (Stokke et al. 2007), such as pattern of spottiness (e.g., Lahti and Lahti 2002), shape (e.g., Underwood and Sealy 2006) or size (e.g., Marchetti 2000) that can not easily be controlled for in a visual model approach.

Here we use a visual model approach to assess the relative importance of host color discrimination for the task of parasite egg rejection in chaffinches *Fringilla coelebs.* Chaffinches are known to efficiently reject model eggs at high rates although they are not currently being parasitized by cuckoos (Braa et al. 1992; Moksnes 1992; Stokke et al. 2004). However, the existence of a *Fringilla* cuckoo egg type in egg collections dating one century back (Moksnes and Røskaft 1995; Avilés and Møller 2004) suggests that chaffinches were actively exploited by cuckoos in the recent past, and that egg rejection behavior in chaffinches has evolved in response to cuckoo parasitism (Stokke et al. 2004). Predictions emerging from sensory discrimination theory have not so far been properly tested for avian brood parasite-host systems, because previous studies have ignored how hosts actually perceive parasitism, and/or because other egg features besides coloration were not considered in the analyses. The aim of this study was therefore to test the prediction of sensory discrimination theory that the likelihood of rejecting foreign eggs should decrease the more similar the stimuli (i.e., parasite egg) are perceived by hosts.

Methods

Study Area and Experimental Procedure

The study was carried out in Stjørdal, approx. 30 km east of Trondheim in central Norway (63º10'N, 10º20'E) during April-May 2007-2008. The study area consists of three minor lowland grey alder *Almus incana* woodlands in which chaffinches breed at high densities and cuckoos are currently absent (Stokke et al. 2004).

A total of 74 successful experiments are included in this study. In order to simulate cuckoo parasitism behavior, we replaced one randomly selected chaffinch egg in each clutch with a conspecific egg from another nest on the day the fourth or fifth egg was laid. This procedure allowed the hosts to assess the appearance of their whole clutch before taking a rejection decision (see Stokke et al. 2004). The removed egg was then used in another experiment. Host and parasite eggs were photographed in the field on a neutral grey plate together with a ruler and a color reference using a Canon EOS 30D camera and a 100mm macro lens (f1/2.8). Photographs provide an easy way to assess patterns of spottiness, shape and volume (see below), although they do not capture the variation in coloration in the entire bird-visible waveband. There are remarkable differences in egg appearance among different chaffinch females in our population (fig.1A,B; Stokke et al. 2004). Therefore, our egg-exchange experiment produces a smooth gradient of color matching between parasite and host eggs from the host's perspective. The host's response was recorded as either rejection (parasite egg ejected) or acceptance if the parasite egg had been incubated for at least five days.

Spectral Measurements of Eggs and Nest Luminosity

We estimated coloration (i.e., spectral reflectance at the 300-700 nm waveband) of host and all experimentally exchanged chaffinch eggs with an Ocean Optics spectrometer equipment [S2000 spectrometer connected to a deuterium-halogen light (D2-W, mini) by a coaxial reflectance probe (QR-400-7-UV-vis) and the OOIBase32^{TM} operating software (Ocean Optics, Inc. Dunedin, FL, USA)]. A stratified random sample of spectra from all regions of the eggs was obtained by dividing each egg in three bands around the long axis (e.g., Cherry and Bennett 2001; Avilés et al. 2004; 2006a, 2006b; Starling et al. 2006). Color was measured in each of these three bands (twice in the central band and once in each of the distal bands) deliberately avoiding scans within spots. Chaffinch eggs are not densely spotted and huge spot-free portions of the background are always predominant over spotted egg-shell areas (see fig 1A,B). Therefore, for this particular species, and, given low spot density and size, our approach reliably captures most of the variance in egg color. Reflectance was measured with the probe placed at a constant distance and at a 45º angle. Measurements were relative to a standard white (WS-2) and to the dark, which was calibrated before the measurement of each clutch. All the measurements were performed in a dark room indoors to avoid an effect of ambient light on spectro-measurements. We estimated average coloration of chaffinch eggs in a clutch by sampling one single host egg per clutch, which is justified by an extraordinary high consistency in coloration among eggs within a clutch in this species (fig.1A,B; Stokke et al. 2002; 2004). Therefore, the four measurements from each egg were averaged to give a mean host spectrum for each clutch. The average spectral distribution of sampled chaffinch eggs is shown in fig. 1C.

Ambient light measurements were collected in the morning between 10.00 h and 12.00 h on May 16th and 17 th 2008 at six deserted nests which each were mounted in five randomly selected nest sites in our study area. To get representative irradiance we collected two different sets of measurements in one hour at every nest. We do not have information on the time of day when chaffinches recognize the eggs, but video recordings have shown that a significant proportion of parasite eggs are rejected in the morning among other cuckoo hosts (Martín-Vivaldi M., Com. Pers.). Briefly, we used a cosine-corrected fiber-optic probe (P400-2-UV-VIS; Ocean Optics) with a 180º angle of acceptance and a measurement surface of 6 mm in diameter (CC-3-UV; Ocean Optics). The spectrometer was calibrated with a light source of known color temperature (LS-1-CAL; Ocean Optics). We measured the ambient light (three readings per nest) close to the nest floor (i.e. where parasite and host eggs were placed) with the measurement surface oriented to the sky, and the probe held perpendicular to the ground. We transformed irradiance readings into photon units, as described by Endler (1990), and calculated the average irradiance spectrum in chaffinch nests in our population for model calculations (fig. 1D).

Fig. 1 about here

Avian Color Space Modeling

Chromatic Contrasts. We calculated discriminability of parasite eggs for each experiment using the model of Vorobyev and Osorio (1998) developed for the tetrachromatic visual system of birds in its log form (Vorobyev et al. 1998). This model establishes a color distance ΔS which describes the color contrasts between two eggs as:

$$\Delta S^2 = [(e_1e_2)^2 (\Delta f_4 - \Delta f_3)^2 + (e_1e_3)^2 (\Delta f_4 - \Delta f_2)^2 + (e_1e_4)^2 (\Delta f_2 - \Delta f_3)^2 + (e_2e_3)^2 (\Delta f_4 - \Delta f_1)^2 + (e_2e_4)^2 (\Delta f_3 - \Delta f_1)^2 + (e_3e_4)^2 (\Delta f_2 - \Delta f_1)^2] / [(e_1e_2e_3)^2 + (e_1e_2e_4)^2 + (e_1e_3e_4)^2 + (e_2e_3e_4)^2] \quad (1)$$

where Δf_i is the log ratio of the quantum catches of each class of single cones (long-wavelength sensitive [LWS], medium-wavelength sensitive [MWS], short-wavelength sensitive [SWS], ultraviolet wavelength sensitive [UVS]) denoted by the subscript for cone *i*, for host (H) and parasitic (P) eggs.

$$\Delta f_i = \log \frac{\int_{300}^{700} R_H(\lambda) I(\lambda) S(\lambda) d\lambda}{\int_{300}^{700} R_P(\lambda) I(\lambda) S(\lambda) d\lambda} \quad (2)$$

where $R_H(\lambda)$ represents the average reflectance of the host eggs, $R_P(\lambda)$ is the average reflectance of the parasite egg in a given chaffinch clutch, $I(\lambda)$ is the spectral irradiance at the nest, and $S(\lambda)$ is the spectral sensitivity of host *i*. Results of calculations using equation (1) provide the chromatic distance ΔS separating the perceptual value of two eggs in host receptor space. The units for ΔS are JNDs (just noticeable differences). Essentially, colors that appear similar to a signal receiver (either because of the nature of their visual system or an absolutely small difference in the reflectance spectra of the colors) result in small Δ*S* values, while those that have high chromatic contrast have large Δ*S* values (Osorio and Vorobyev 1996). Spectral sensitivity has not been measured in the chaffinch. Therefore, following recently published literature (e.g., Håstad et al. 2005; Gómez and Théry 2007; Avilés et al. 2008; Avilés 2008; Håstad and Ödeen 2008) we used spectral sensitivity data from the blue tit *Cyanistes caeruleus* with SWS1 : SWS2 : MWS : LWS cone proportions of 1: 1.92: 2.68: 2.7 (Hart et al. 2000) as representative of a UVS system, and assumed that the signaling noise e_i for each cone was independent of light intensity.

$$e_i = \omega / \sqrt{\eta_i} \qquad (3)$$

where ω is the Weber fraction (taken as 0.05 (Vorobyev et al. 1998)) and η_i is the relative density of the cone class i on the retina. The version of the Vorobyev-Osorio model used here assumes daylight conditions, which is justified because parasite egg rejection seems to always occurs under daylight conditions (Martín-Vivaldi M., Com. Pers.), and because the chaffinch build open and shallow nests (Cramp 1998).

Spectral sensitivity is affected by the relative cone proportions in the bird retina, which may vary from one species to another (Hart 2001). We therefore assessed the sensitivity of our analysis to variation in cone proportions by repeating color contrast calculations for all the six UVS species found by Hart (2001). Estimations of differences in chromatic contrasts between parasite and hosts eggs were strongly correlated ($r^2 > 0.99$, $P < 0.00001$ for all the 15 possible combinations). Furthermore, the averaged estimate of chromatic contrast based on blue tit cone proportion fell within 1 SD of the means calculated using all known cone proportions for UVS species in Hart (2001) (mean/SD: blue tit: 2.77/1.19; blue-faced honeyeater *Entomyzon cyanotis*: 2.76/1.19; noisy miner *Manorina melanocephala*: 2.63/1.13; satin bowerbird *Ptilonorhynchus* *violaceus*: 3.02/1.31; european starling *Sturnus vulgaris*: 2.89/1.24; blackbird *Turdus merula*: 2.47/1.05). Thus our results were robust to variations in the relative cone proportions of the bird retina.

Achromatic Contrasts. Evidence suggests that birds may use achromatic signals in discriminatory tasks (reviewed in Kelber et al. 2003). In this vein, it has been recently suggested that achromatic mechanisms could play a key role in the discrimination of cuckoo eggs at low-light levels (Avilés 2008). In birds, double cones are assumed to be responsible of achromatic visual detection (e.g., Osorio et al. 1999a; 1999b). We thus applied equations 1 to 3 to sensitivity data for double cones of blue tits (Hart et al. 2000). We estimated the Weber fraction as 0.05 (at threshold) for the double cone in birds and calculated achromatic (brightness) contrasts similar to the chromatic analysis. For every experimentally parasitized clutch we therefore calculated chromatic and achromatic contrasts between the averaged host spectrum and the averaged spectrum for the parasite egg.

Egg Volume and Shape

The maximum length and breadth of one host and the parasite eggs were estimated to the nearest 0.1 mm based on the photographs using digital imaging software (NIS Elements BR 3.0, Nikon, Amstelveen, The Netherlands). To ensure consistency all measurements were done by one person (JRV). Egg volume index (EV) was calculated from the length (EL) and breadth (EB) using the formula $EV=0.5\times EL\times EB^2$ (Hoyt 1979). In addition, we used Picman's (1989) simple shape index (shape = EL/EB) to determine egg shape. For every experimentally parasitized clutch we calculated the absolute value of the difference between volume and shape between the host and the parasite eggs.

Patterns of Spottiness

Based on the photographs, spot measurements of one host and the parasite egg were carried out using NIS-Elements BR 3.0. Measurements were delimited to a rectangle of the egg surface covering 90% of the longitudinal axis and the respective width (see figure A1 in appendix). Spots were marked with the threshold tool (analogous to the magic wand tool in Photoshop) in the binary editor of NIS, and three different variables were extracted: Spot coverage as the total spot area relative to the background in the rectangle; Perimeter/Area ratio (P/A hereafter) defined as the sum of the perimeter of all spots divided by the sum of the total spotted area. This measure allows us to differentiate between patterns of a few but large versus many but small spots having the same spot coverage. Finally, we used Mean circularity as a measure of spot shape. Circularity is a derived measure which equals $4*\pi*\text{Area}/\text{Perimeter}^2$. Perfect circles have circularity 1 while non-circular spots have circularity values between 0 and 1. We estimated repeatability for the three variables in a set of 20 randomly selected eggs sampled in two different days. Repeatability proved to be very high for the three variables ($r = 0.94$-0.98, $F_{19,20} > 23.7$, $P < 0.00001$, N = 20). For every experimentally parasitized clutch we calculated the absolute value of the difference between the three descriptors of spottiness between the host and the parasite eggs.

Statistical methods

In chaffinches, the female is the sex responsible for rejection of parasite eggs (Moksnes et al. 1994). Previous intensive catching and ringing of breeding chaffinches in this population has revealed a negligible chance of sampling the same female in two consecutive years (Stokke et al. 2004). We therefore counted every experiment as an independent data point in our analyses. Also, previous studies revealed no age-specific patterns of recognition and laying in chaffinches (Stokke et al. 2004). Chromatic and achromatic contrasts as well as contrasts in volume, shape and spottiness between parasitic and host eggs were not significantly different from a normal distribution (Kolmogorov-Smirnov tests, $P > 0.05$).

In a first analysis, we used logistic regression models (GENMOD procedure in SAS, SAS Institute, 1996) to test whether rejection of parasite eggs in chaffinches (i.e., rejection *vs* acceptance) was explained by differences in matching (i.e. chromatic and achromatic contrasts, volume, shape, spot coverage, spot P/A ratio and spot circularity) between host and parasite eggs. Year was entered as a fixed factor to control for annual variation. From this global model, we constructed candidate models using the main effects of each predictor. Due to limited sample size we discarded those subsets including interactions. The best-fit model was determined using Akaike's information criterion (Burnham and Anderson 1998). Because the number of datapoints in the global model divided by K (the number of parameters in the model) is less than 40, AIC was corrected for small sample sizes (known as AICc) following Burnham and Anderson (1998). The model with the lowest value of AICc is the most parsimonious one in the sense that it provides the best balance between overfitting (hence loss of precision) and underfitting (hence bias) and is the selected model. The Akaike weights give the relative support for a given model compared to the other models in the set (all information in Burnham and Anderson 1998). Furthermore, we also employed model averaging (Burnham and Anderson 1998; Symonds and Johnson 2008) to identify more accurately the relative importance of each model term in predicting rejection of parasite eggs. This involved taking the subset of the most likely models (cumulative Akaike weight ≤ 0.95), adjusting the Akaike weight for each model accordingly, and then calculating Akaike weights for each model term by summing the Akaike weights for each model in which the term features. These scores range from 0 (the term appears in none of the most likely models) to 1 (the term appears in all of the most likely models) (Symonds and Johnson 2008).

According to Green (1979) any correlation less than 0.70 eliminate serious problems of collinearity in multivariate analyses. None of the predictors had r_p values larger than 0.7 (see table A1 in appendix).

Results

Egg rejection in relation to parasite-host egg matching.

54 out of 74 (72.98 %) experimental parasite eggs were rejected by the chaffinch. There were eight different models that provided substantial support (i.e., $\Delta_i \leq 2$) for egg rejection (table 1). The best model describing the average rejection rate of parasite eggs included chromatic contrast as the only term, and this term appeared in all models providing substantial support for egg rejection (table 1). Model averaging showed that chromatic contrast was clearly the most important predictor of parasite egg discrimination, with an Akaike weight of 0.84, indicating that it featured in 117 out of the 139 most likely models (table 2). Achromatic contrasts and shape contrasts were the second and third most important predictors of parasite egg rejection by chaffinches (Akaike weights of 0.51 and 0.43, respectively, table 2). The remaining predictors of rejection had low Akaike weights (table 2).

Table 1 about here

Inspection of model average estimates showed that chromatic contrast was the only term for which the 95% CI did not include zero (table 2). Rejection probability of parasite eggs increased with chromatic differences between parasite and host eggs (range: from 25.0 % for pairs tested against parasite eggs differing 0-1 JND to 92.3 % for pairs tested against parasite eggs differing > 4 JND; table 2; fig 2). The model averaged estimates of remaining predictors of rejection had 95% CI's that included zero values (table 2).

Table 2 about here

Figure 2 about here

Discussion

To our knowledge, this is the first study in which realistic models of the hosts' perceptual physiology have been applied to investigate host behavioral responses to natural variation in egg coloration. The behavioral responses by chaffinches to experimental parasitism using conspecific eggs partly conformed to expectations from the discrimination model based on host perception of chromatic differences. The higher the value of chromatic contrasts between the parasite and the host eggs, the higher was the probability of the parasite egg being rejected. Our findings confirm the adaptive value of matching as perceived by hosts for a parasite egg, which was previously known intuitively based on more indirect methods for the assessment of mimicry such as those based on human vision (e.g., Davies and Brooke 1988; Moksnes and Røskaft 1992; Davies 2000) and spectrophotometry (e.g., Avilés et al. 2006c; Honza et al. 2007; Polaciková et al. 2007; Cherry et al. 2007). In addition, our results provide experimental support to previous findings in other animal taxa (e.g., bees, mice and humans) suggesting that sensory discrimination improves with the intensity of the perceived stimulus (e.g., Wolfe 2000; Abraham et al. 2004; Chittka et al. 2003; Dyer and Chittka 2004).

Although we found that the probability of egg rejection gradually increased with intensity of the visual stimulus (i.e., ΔS), chaffinches discriminated between eggs whose visual stimulus according to the perceptual model would appear similar to a bird receiver (i.e., small ΔS values). In the other direction, chaffinches also accepted a considerable proportion of clearly contrasting parasite eggs (fig.2). Previous studies have shown that for some bird species, predicted thresholds for chromatic discrimination are matched by behavioral data on discrimination of colors against a background under photopic conditions (e.g., Vorobyev and Osorio 1998; Kelber et al. 2003; Goldsmith and Butler 2005). The JND threshold should be treated as a guideline in this study since we parameterized the model using data from other species. A certain level of mismatching between model predictions and behavioral data has been reported for dim light conditions, probably due to a higher relative importance of the achromatic mechanism (Vorobyev and Osorio 1998). One explanation for the discrepancy between the predictions of the color discrimination model and the test results in chaffinches is that parasite egg discrimination may somehow depend on specific aspects of egg appearance (i.e., shape, volume, spottiness) that are not accounted for by avian chromatic and achromatic contrasts as measured in this study. Here we have quantitatively assessed differences between parasite and host eggs in other characteristics than coloration, such as pattern of spottiness, shape or size. However, it cannot be discarded that our way of quantifying spottiness did not capture how the host processes the spatial configuration of colors across the egg surface. Nonetheless, our results confirm that color difference of the eggs is an integral part of the host matching signal. Finally, although our results were robust to reported cone proportion variations among UVS species (see methods), spectral sensitivity data for chaffinch were not available in the literature, and therefore we parameterized the model with blue tit data as representative of typical ultraviolet sensitive birds.

Previous empirical data for humans and other animals have shown that photopic discrimination is based on predominantly color opponent channels (Vorobyev and Osorio 1998; Schaefer et al. 2007). In addition, it has been shown that cuckoo hosts would better perceive chromatic differences with cuckoo eggs in bright than in dim nest environments (Avilés 2008). Chaffinches are typical open nesters and, therefore, discriminatory tasks should be photopic. In agreement, we have found that chromatic difference as would be perceived by hosts was by far the best predictor of egg rejection. However, our experiment did not break the correlation between differences in color and brightness between host and experimental eggs ($r_p = 0.62$, $P < 0.00001$, N = 74 nests). Only future experiments in which the chromatic and achromatic parts of the compound visual stimulus are manipulated would allow disentangling the role of chromatic and achromatic signals in parasite egg discrimination.

In conclusion, we have documented that difficult discriminatory tasks in terms of visual discrimination, as predicted by physiological models of host perception, are solved less frequently by chaffinches than easier discriminatory tasks. Physiological models both under- and overestimated chaffinch acuity for discriminating parasite eggs. Two previous papers (Cassey et al. 2008; Avilés 2008) concluded that the use of retinal models was necessary for quantitatively describing the strength of the selection pressures acting on parasite egg coloration. The findings of this study highlighted the importance of incorporating realistic models of the host' perceptual color physiology in conjunction with other candidate components of matching signal (e.g., shape, volume and spottiness) to the study of egg discrimination by host of avian brood parasites.

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Table 1: Most likely models in descending order explaining variation in rejection behavior in chaffinches. The table shows the factors included in the model and model estimates (slopes) from logistic regression model that assesses the relationship between frequency of experimental egg rejection and the differences between host and parasite eggs in ΔS, ΔQ, shape, volume, spot coverage, spot circularity and spot spot P/A ratio. Model selection was based on AICc, and ΔAICc is the difference between a particular model and the best one within each subanalysis. *K* is the number of estimated parameters. Akaike weights show the relative support a given model has from the data compared with the other models in the set. ΔS and ΔQ correspond to avian color and achromatic contrasts, respectively.

Model	ΔS	ΔQ	Shape	Volume	Spot coverage	Spot circularity	Spot P/A ratio	Year	*K*	AICc	ΔAICc	Akaike
	Estimate (s.e.)	Estimate (s.e.)	Estimate (s.e.)	Estimate (s.e.)	Estimate (s.e.)	Estimate (s.e.)	Estimate (s.e.)	Estimate (s.e.)				Weights
Rejection behavior												
ΔS	0.79 (0.27)								3	80.4	0.0	0.051
ΔS, ΔQ	0.61 (0.32)	0.28 (0.28)							4	81.5	1.1	0.028
ΔS, shape	0.82 (0.28)		-4.43 (4.33)						4	81.6	1.2	0.028
ΔS, year	0.83 (0.28)							0.53 (0.57)	4	81.7	1.4	0.025
ΔS, volume	0.83 (0.28)			-0.001 (0.002)					4	81.9	1.5	0.024
ΔS, spot circularity	0.82 (0.28)					3.53 (4.59)			4	82.0	1.6	0.024
ΔS, spot P/A ratio	0.82 (0.28)						0.04 (0.06)		4	82.1	1.7	0.022
ΔS, ΔQ, shape	0.58 (0.33)	0.37 (0.29)	-5.76 (4.49)						5	82.2	1.8	0.020
ΔS, spot coverage	0.80 (0.28)				2.05 (7.16)				4	82.5	2.1	0.017

Table 2: Akaike weights for each factor in the most likely models predicting parasite egg rejection. ΔS and ΔQ correspond to avian color and achromatic contrasts, respectively. Estimates in bold indicate that 0 is excluded from 95% confidence interval and that variable influences rejection of parasite eggs.

Term	Akaike Weight (95 %)	Model averaged estimate (± 95 % CI)
ΔS	**0.84**	**0.74** **(0.13 to 1.35)**
ΔQ	0.51	0.47 (-0.08 to 1.02)
shape	0.43	-6.42 (-15.47 to 2.63)
volume	0.36	-0.002 (-0.005 to 0.002)
spot circularity	0.35	5.25 (-4.16 to 14.66)
year	0.28	-0.16 (-0.81 to 0.49)
spot P/A ratio	0.23	0.04 (-0.09 to 0.16)
spot coverage	0.22	2.03 (-12.39 to 16.45)

Note: 139 models were identified as most likely (i.e., accounting for a summed Akaike weight of 0.95) for parasite egg rejection.

LEGEND FOR FIGURES

Figure 1: Sample photographs of experimentally parasitized chaffinch clutches showing moderate (A) and high (B) contrast, with the parasite egg on the right in the bottom row. Average reflectance spectrum (C) of chaffinch eggs and average spectral irradiance at chaffinch nests (D). Curves are the mean of individual means of four measurements taken at every egg for reflectance and the mean of individual means of four measurements taken at every nest for irradiance, respectively. Bars are standard deviations.

Figure 2: Percent of parasite eggs rejected (grey bars) and accepted (white bars) in relation to chromatic matching estimated under the Vorobyev-Osorio model. Numbers of nests in which the parasite egg was rejected or accepted or in which means are calculated are denoted on top of the bars.

Figure 1: Avilés et al.

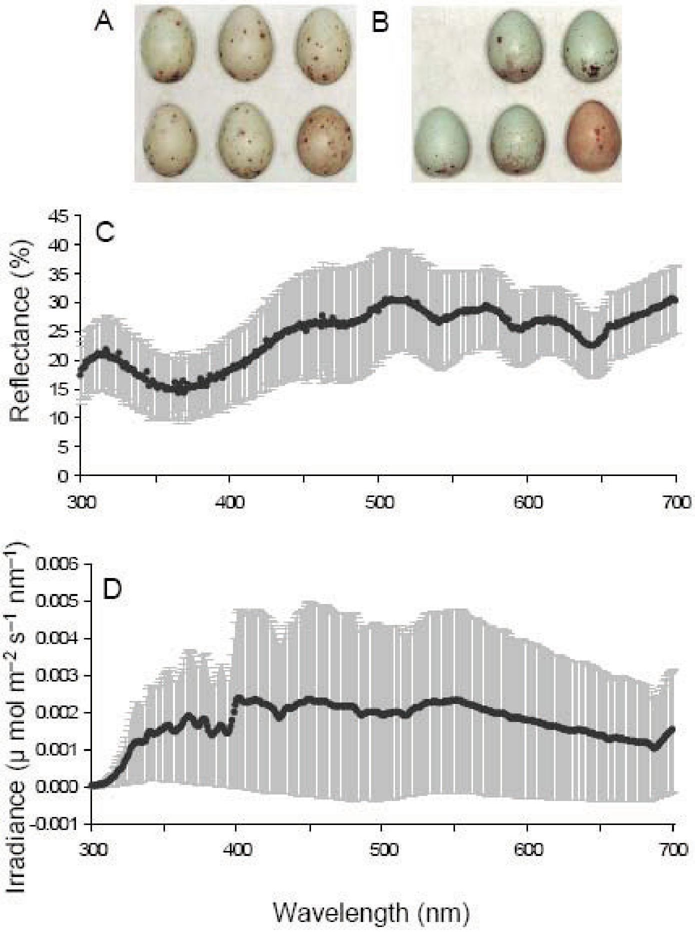

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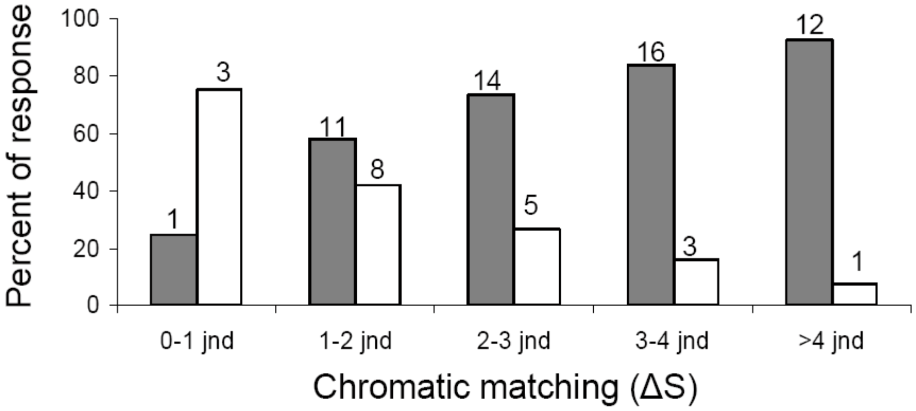
Figure 2: Avilés et al.



APPENDIX

Table A1. Pearson's correlations among predictors of rejection and latency to rejection of parasitic eggs (N =74). ΔS= differences in chromatic contrast between parasite and host eggs as estimated by Vorobyev & Osorio model, ΔQ= differences in achromatic contrast between parasite and host eggs as estimated by Vorobyev & Osorio model, volume= differences in egg volume between parasite and host eggs; shape= differences in egg shape between parasite and host eggs; spot coverage=differences in coverage of spottiness between parasite and host eggs; spot P/A ratio=differences in P/A ratio of spottiness between parasite and host eggs; spot circularity=differences in circularity of spots between parasite and host eggs. See methods for further details.

	ΔS	ΔQ	volume	shape	spot coverage	spot P/A ratio
ΔQ	.6172 p=.000					
volume	.1319 p=.263	.2599 p=.025				
shape	-.0505 p=.669	.1639 p=.163	-.0978 p=.407			
spot coverage	-.0359 p=.761	-.1894 p=.106	-.1784 p=.128	-.2229 p=.056		
spot P/A ratio	-.0918 p=.437	-.0081 p=.946	-.2729 p=.019	-.0880 p=.456	.2097 p=.073	
spot circularity	-.0431 p=.715	-.1983 p=.090	.0492 p=.677	-.0068 p=.954	.0562 p=.635	-.1173 p=.320

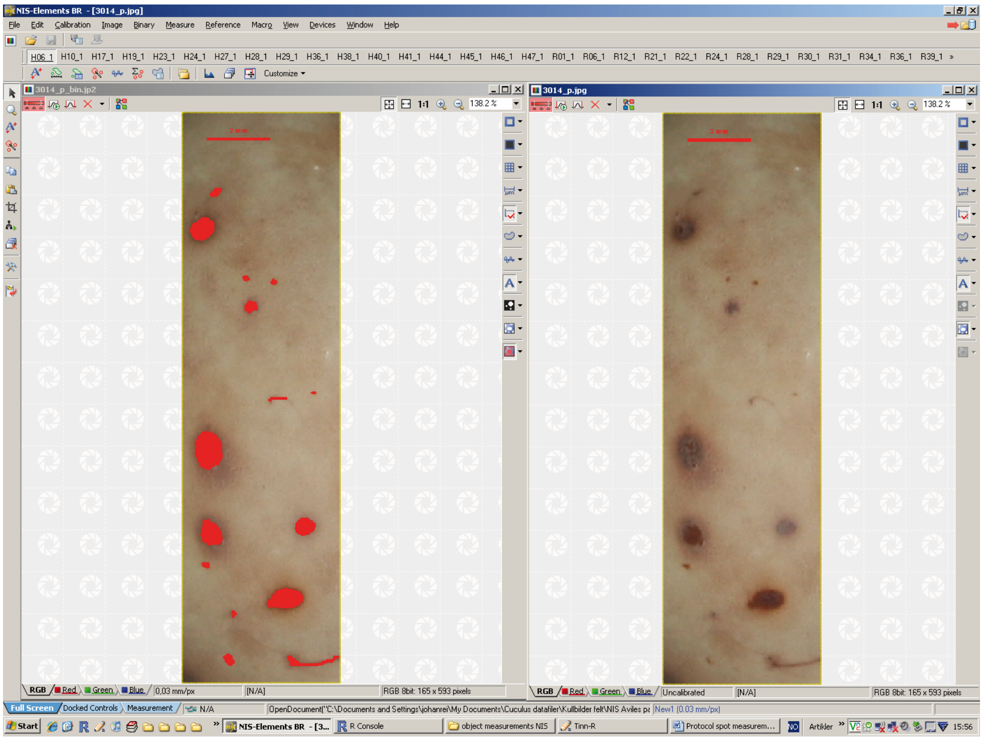


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Figure A1. Spot data acquisition. Spots were marked with threshold tools in the binary editor of NIS (NIS-Elements BR 3.0, Nikon Corporation, Amstelveen, The Netherlands). Measurements were delimited to a rectangle of the egg surface. The sample rectangular area was set in such a way as to cover as much as possible of the egg area. However, because we cannot optimize both sides of the rectangle at the same time, we gave priority to the axis along which spotting pattern varies more. In general, passerine eggs vary more along their long axis. The sample rectangle's length was fixed to 90% of the egg length. Once the length of the rectangle was set, the width was adjusted by the enforcement that the sample rectangle must lay within the egg surface.

Paper II

Is not included due to copyright

Paper III

EVOLUTION OF DEFENCES AGAINST CUCKOO (*CUCULUS CANORUS*) PARASITISM IN BRAMBLINGS (*FRINGILLA MONTIFRINGILLA*): A COMPARISON OF FOUR POPULATIONS IN FENNOSCANDIA

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ABSTRACT

The brood parasitic common cuckoo *Cuculus canorus* has a history of coevolution that involves numerous passerine hosts, but today only a subset is known to be regularly parasitised in any area. In some potential hosts, there is significant variation in the occurrence of parasitism between populations, but still individuals in non-parasitised populations show strong antiparasite defences. In the present study we compared the strength of egg rejection of four distant Fennoscandian brambling *Fringilla montifringilla* populations experiencing different levels of cuckoo parasitism (0-6%). Egg rejection ability was in general very well developed and we did not find any population differences in the relationship between egg rejection probability and similarity between host and experimental parasitic eggs. Furthermore, bramblings very rarely made errors in rejection, indicating that rejection behaviour is robust to decay. The brambling-cuckoo system therefore differs from other well studied systems which are characterised by pronounced spatial and temporal variation in the host's level of defence. Furthermore, the proportions of adults behaving aggressively towards cuckoo dummies did not differ significantly between populations. These results are unlikely to reflect independent replication of the same evolutionary trajectory because the weak breeding site tenacity of bramblings should result in an extreme amount of gene flow within the distribution area and thus strongly impede localised responses to selection. Instead, lack of geographic variation has more likely arisen because bramblings respond to selection as one evolutionary unit, and because the average parasitism pressures have been high enough in the past to cause regional fixation of rejection alleles and evolution of clutch characteristics that facilitate cost free egg recognition.

INTRODUCTION

The common cuckoo *Cuculus canorus* (hereafter cuckoo) and its passerine hosts comprise a diverse set of interactions regarding the existence and sophistication of coevolved traits (Rothstein and Robinson 1998; Davies 2000). An intriguing trend uncovered by broad community level investigations is that suitable but non-parasitised hosts tend to discriminate more strongly against parasitic eggs than do regularly parasitised hosts (Davies and Brooke 1989b; Moksnes et al. 1991). This suggests that the subset of hosts involved in pair-wise interactions with the cuckoo changes through time, and that local evolution of host defence is a potentially important factor in this process by promoting host switches and/or local extinction of specialist parasite tribes (gentes) (Davies and Brooke 1998; Nakamura et al. 1998; Nuismer and Thompson 2006).

A limitation in most of these studies is that they cover geographically restricted areas and short time spans (Rothstein and Robinson 1998). This is problematic because the state of interacting populations can be influenced by a multitude of ecological, historical and geographical factors (Thompson 1994; 2005). For example, selection pressures acting upon host and parasites for interaction traits may vary significantly in intensity between areas according to the prevailing ecological settings (e.g. Brodie et al. 2002; Siepielski and Benkman 2004; Toju and Sota 2006; Martín-Gálvez et al. 2007; Stokke et al. 2007a; Parchman and Benkman 2008). Moreover, the interaction in one locality may be influenced by the interaction in others through gene flow (e.g. Dybdahl and Lively 1996; Nuismer et al. 1999; Soler et al. 1999; Gomulkiewicz et al. 2000; Røskaft et al. 2006; Moskát et al. 2008b). Consequently, inferring the processes behind local trait patterns requires extensive geographical sampling and consideration of the spatial dynamics of the interacting parties (Thompson 2005).

The potential importance of spatial dynamics in host-parasite coevolution has had a growing influence on empirical studies of brood parasite-host interactions in the last decade (Stokke et al. 2005). So far, however, only a small and biased subset of hosts has been thoroughly examined. For example, most of the hosts examined show low defence levels in populations allopatric with the cuckoo (e.g. Stokke et al. 2008), whereas population comparisons are scarce for hosts that show high defence levels in non-parasitised populations. In general, investigation of a more diverse set of systems would add useful bricks to the edifice of our understanding of cuckoo-host coevolution and its diverse outcomes.

The present study concerns the interaction between bramblings *Fringilla montifringilla* and cuckoos in Fennoscandia. Among potential cuckoo hosts in Europe, the brambling represents an extreme case with regard to population genetic structure. It is a northern boreal species which employs an opportunistic breeding strategy for exploitation of favourable but unpredictable breeding opportunities (Hogstad 2000; 2005; Lindstrom et al. 2005). It has therefore very low breeding site tenacity (Mikkonen 1983; Lindström 1987; Fransson and Hall-Karlson 2008), and ringing recoveries indicate that bramblings may breed at sites up to 600 km apart in different years (Lindström 1987). This pervasive aspect of brambling ecology should strongly impede any localised responses to selection (e.g. Hendry et al. 2001; Lenormand 2002; Nash et al. 2008; Parchman and Benkman 2008). Accordingly, in spite of having a wide breeding distribution, implying that it has been subject to a vast array of environmental selection pressures, no subspecies are recognised (Cramp and Perrins 1994; Hogstad and Väisänen 1997). The brambling has long been known as a cuckoo host in northern Finland and north-western Russia, where there are several accounts of cuckoo eggs that mimic brambling eggs (Montell 1917; Wasenius 1936; Baker 1942; Malchevsky 1987; Numerov 2003), whereas records from other parts of Fennoscandia are sparse. Nevertheless, in Central Norway, where parasitism has never been recorded, bramblings were observed to reject 90 % of artificial cuckoo eggs (both non-mimetic eggs and eggs painted to resemble brambling eggs), which makes it a candidate example of an expired cuckoo-host interaction as suggested by Braa et al. (1992). The aim of the present study was to examine geographical variation in brambling defences to cuckoo parasitism (egg rejection and aggression to cuckoo dummies), including both parasitised and non-parasitised populations, and to discuss evolution of these defences in light of the distribution of current/historical selection and the spatial dynamics of the brambling.

METHODS

Study areas

The four study areas included in this study are situated in Kittilä in Lapland province, north-western Finland (68ºN, 25ºE), Tana in Finnmark province, north-eastern Norway (70ºN, 28ºE), Ammarnäs in Västerbotten province, north-western Sweden (66ºN, 16ºE), and Tydal, eastern part of Sør-Trøndelag province, Central Norway (63ºN, 12ºE). The four study populations span a significant part of the breeding range of bramblings in Fennoscandia (Fig. 1), with distances between populations ranging from 340 to 1100 km. The brambling is a numerically dominant species in all four study areas. Tydal is the same area as was studied by Braa et al. (1992). Tana, Tydal, and Ammarnäs are mountain birch *Betula* spp. forests (see Moksnes and Røskaft (1987) for a general description of the Tydal area), whereas Kittilä, which lies within Pallas-Ylläs national park, is a mixed old growth forest of birch, goat willow *Salix caprea*, Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. The cuckoo is currently present in all four study areas. In Kittilä, we have recorded no other hosts than the brambling. In the other three localities, the meadow pipit *Anthus pratensis* is the main host (Tydal: Moksnes and Røskaft 1987; Ammarnäs: Roland Sandberg pers. com; Tana: own observations).

The data material was collected during the breeding seasons 2003-2008 (Tana in June-July 2003-2004, Kittilä in May-June 2005-2008, Tydal in June-July 2005-2007, and Ammarnäs in June-July 2008). Most nests were visited daily during egg laying, and each egg in a clutch was marked with waterproof ink in sequence as laid. If necessary, laying dates were estimated from floating tests of the eggs (Hays and Lecroy 1971) and, if available, hatching dates.

Experiments

In this study, we analyse the responses of bramblings to 296 cases of experimental parasitism and 6 cases of natural parasitism. Of these cases, 112 are from Tana, 65 from Kittilä (including all the cases of natural parasitism), 77 from Ammarnäs, and 48 from Tydal. Experimental parasitism was carried out by replacing one random host egg with a fresh conspecific egg. In 26 experiments, an egg from a different passerine species was used (chaffinch *Fringilla coelebs* (12), reed bunting *Emberiza schoeniclus* (5), tree pipit *Anthus trivialis* (3) greenfinch *Carduelis chloris* (3), yellowhammer *Emberiza citrinella* (2), dunnock *Prunella modularis* (1)). Such eggs were used for eight experiments in Ammarnäs, thirteen in Kittilä, and six in Tydal. Because bramblings have a high interclutch variation in egg appearance (Fig. 2), conspecific eggs provide an opportunity to test responses against a range of contrasts, enabling detailed comparison of egg rejection between populations. Fifty-eight experiments (20 from Kittilä, 16 from Tydal, and 22 from Ammarnäs), are replicates at the individual level. These experiments always involved parasitic eggs with different degree of similarity to the host's eggs (one highly contrasting egg and one low-intermediate contrasting egg. The use of both these experiments is justified in a separate study, where we show that rejection of the highly contrasting egg does not affect the probability that the host rejects the low-intermediate contrasting egg (compared to control individuals that were presented to only one low-intermediate contrasting egg) (Vikan et al. 2009). Hence, both experiments can safely be used for a comparison of the strength of egg rejection between populations. In the one case where both parasitic eggs were accepted, acceptance of the highly contrasting egg was counted as a response whereas acceptance of the less contrasting egg was ignored. Experiments were carried out close to clutch completion when possible. However, we also include experiments (N=34) that were initiated later (i.e. after the clutch had been incubated for three days) because rejection probability does not change with advancing incubation in this species (own data). The length and breadth of the parasitic egg and one random host egg was measured with a digital calliper or estimated from pictures by use of imaging software (NIS-Elements 2.20, Nikon). Host eggs were photographed together with the parasitic egg and a ruler on a neutral grey plate using a Canon EOS 350D/EOS 30 camera and a 100 mm macro lens (f1/2.8).

Host responses to foreign eggs

After the experiment had been initiated, most of the nests were revisited every day or every second day for at least five days to determine the response. We defined the parasitic egg as accepted if it was still incubated on the fifth day. If the foreign egg was ejected, the response was classified as a rejection. Nests associated with a rejection response had to survive at least five days after initiation of the experiment in order to be included in the analyses. This removes any bias due to population differences in survival probabilities of experimental nests. In this study, nest desertions after experimental treatment are not considered to be genuine responses to parasitism because they occurred at frequencies that were highly correlated with background frequencies of desertions, which shows considerable variation between years (own data). In each experiment, we recorded ejection costs and rejection errors. An ejection costs is defined as ejection of own eggs in addition to the parasite egg, whereas a rejection error is defined as rejection of own egg(s) but not the parasite egg (Røskaft et al. 2002a; Stokke et al. 2002).

Presentation of cuckoo dummies

We had three cuckoo dummies at our disposal from which we chose one at random for each exposure. The dummy was attached to a branch at 0.5 m distance from the nest with its beak pointing towards it. The nest owners' reactions were then recorded for a period of 5 minutes after they had showed up in the vicinity of the nest, and their behaviours were ranked as either aggressive (mobbing or attack, see Røskaft et al. (2002b)) or not aggressive (either no reaction or distress calling). In total, 126 nests were used for cuckoo dummy exposures (93 in Tana, 10 in Kittilä, and 23 in Tydal). The number for Tydal includes 17 presentations that were carried out as part of a previous study (Moksnes et al. 1991).

Assessing differences between host and parasitic eggs

The difference in appearance between host and parasitic eggs (hereafter contrast) was scored from pictures by four experienced persons according to an established protocol (1 = low contrast, 2 = medium contrast, 3 = high contrast (Braa et al. 1992; Stokke et al. 2004)). The repeatability (Lessells and Boag 1987) of the assessments was high (all experiments: 0.79, $F_{301,906} = 15.4, p < 0.0001$; natural parasitism and experiments with conspecific parasitic eggs: 0.76, $F_{281,846} = 13.7, p < 0.0001$), and we therefore used the means of the four persons' scores in the analyses.

Methods of subjective assessment of clutch characteristics based on human vision have been repeatedly criticised, particularly because they do not account for colour variations in the UV part to which birds are sensitive (Cherry and Bennett 2001). On the other hand, the suitability of methods using UV-VIS spectrophotometry can be questioned when it comes to describing differences in overall egg appearance. Spectrophotometric measurements are available for 144 experiments from three populations, and we choose to present results from both approaches for complementarity. We calculated chromatic contrasts ΔT_C and achromatic (brightness) contrasts ΔT_B for each experiment using reflectance spectra from eggs and spectral sensitivity functions of typical passerine cones (Endler and Mielke 2005). For a detailed description of measurement procedures and derivation of ΔT_C and ΔT_B, see Vikan et al. (2009). For most clutches, one random egg was measured and taken as representative of the whole clutch. For a random subset of clutches (N=35) two eggs were measured. The repeatability of idealised quantum catch values (equation 1 in Stoddard and Prum 2008) of eggs from the same clutch was high (0.73-0.77, $F_{34,35} < 6.4, p < 0.0001$), which justifies the use of one egg as representative for most clutches.

Statistical analyses

We used generalised linear models with binomial distribution (logit link) to compare the strength of egg rejection between the populations. A first global model included contrast in appearance between host and parasite egg, relative difference in volume (calculated according to Hoyt (1979)) and absolute difference in shape (length/breadth) as predictors, and their two-way interactions with a factor denoting the population affiliation of the tested pair. Using the reduced data set of eggs with data for spectra (144 experiments, three populations), we analysed a second model with ΔT_C and ΔT_B as predictors, and their respective interactions with the population term. The interaction terms were included because they capture potential differences between populations for each host-parasite egg similarity measure. Significance of parameters was addressed with log likelihood-ratio tests in a stepwise backward deletion procedure (Crawley 2007). There was no correlation between shape, volume and contrast ($|r_s| < 0.11$), whereas contrast, ΔT_C, and ΔT_B were strongly intercorrelated (contrast and

ΔT_C: $r_S = 0.67, p < 0.0001$; contrast and $\Delta T_B : r_S = 0.43, p < 0.0001$; ΔT_C and ΔT_B: $r_S = 0.40, p < 0.0001$). Lastly, we ran a model with contrast, ΔT_C, and ΔT_B as predictors in order to examine how much variation each variable explains when the others are accounted for.

We applied a generalised linear model with quasipoisson distribution (log link) and contrast as covariate to test if there was a difference in the latency to reject parasitic eggs between Kittilä, Tana, and Tydal. For this analysis, we included only nests that were visited at least every second day after initiation of the experiment (only a few nests were visited often enough to determine the day of rejection in Ammarnäs). For those cases where the exact day of rejection was not known, day of rejection was defined as mid between the day rejection was confirmed and the day of the preceding nest visit.

All analyses were conducted using the software R version 2.7.1 (R Development Core Team 2008).

RESULTS

Natural parasitism

Occurrences of natural parasitism events are summarized in Table 1. No cuckoo parasitism was observed in Tydal, Tana or Ammarnäs. To date, no records have been made in Tydal among more than 280 brambling nests that have been checked regularly. However, in museum collections, we have found three clutches containing mimetic cuckoo eggs which were collected in an area 40 km northeast of Tydal in the 1940s. For Ammarnäs, there were no records of either cuckoo eggs or chicks in more than 500 nest record cards covering 1963-1996 (more than 400 of the nests were checked at least once close to clutch completion or later). In Tana, there were no cases among 250 nests checked daily in 2003-2004. In Kittilä, parasitised nests were found in all four years of study. Parasitism rates were 3.4% (1/29) in

2005, 9.8% (5/51) in 2006, 3.9% (2/51) in 2007 and 3.2% (1/27) in 2008. These numbers most likely underestimate the real parasitism rate because the complete nest history is known only for a minority of the nests. Furthermore, several older parasitism records from Kittilä and neighbouring municipalities are known, dating back to the late 19th century (Montell 1917; Wasenius 1936; Baker 1942, and observations based on museum collections), which suggests that parasitism is temporally stable to some degree in this specific part of Fennoscandia. The cuckoo eggs were generally very good mimics of the hosts' eggs (Fig. 2).

Conspecific parasitism

No incidents of conspecific parasitism were detected among more than 400 nests that were checked daily. There were neither cases where two eggs appeared on the same day, nor cases where eggs appeared outside the laying sequence. Because only 20% of ejections of experimentally added conspecific eggs happened within the first 24hrs, we should have a high probability of detecting conspecific parasitism if it occurred. To our knowledge, conspecific parasitism has never been recorded in the brambling (Yom-Tov 2001).

Spatial variation in egg rejection

Logistic ANCOVA analyses detected no differences between populations in the overall probability of acceptance when controlling for differences in distribution of host-parasite egg similarities (Table 2). Moreover, contrast, ΔT_C, and ΔT_B were significant predictors on their own (Table 1, Table 2) whereas shape or volume did not explain a significant proportion of the variation in the response. More importantly, the effects of contrast and ΔT_C on rejection probability were consistent across populations (Table 1, Table 2, Fig. 3). However, there was a tendency for a steeper relationship between ΔT_B and acceptance probability in Tydal compared to Ammarnäs and Kittilä (Table 1, Table 2, Fig. 3). When analysing the model containing contrast, ΔT_C, and ΔT_B as predictors, only contrast explained significant additional variation to that already explained by the other variables (Table 2). The rate of rejection of highly contrasting eggs (i.e. eggs that were given the highest contrast score by all four persons who assessed pictures) was high in all populations (Kittilä: 95%, N = 19; Tana: 85%, N = 13; Tydal: 100%, N = 14, Ammarnäs: 100%, N=22).

There was no difference in the latency to reject between individuals in Kittilä (N=35), Tana (N=54), and Tydal (N=15) ($\chi^2 = 2.7, df = 2, p = 0.13$) when controlling for the effect of contrast (β (*SE*) = -0.29 (0.08), t = -3.7, df = 1, p < 0.0003).

Ejection costs and rejection errors

The frequency of possible rejection costs and possible rejection errors was low in all four populations (Table 1). Considering all ejections, costs were registered in 3.3% (7/210) of the cases. Out of all experiments where the parasitic egg was accepted, rejection errors occurred in only 0.8% (1/199) of the cases. True recognition costs (i.e. ejection of own egg(s) from non-parasitised nests) are notoriously difficult to estimate (Rothstein and Robinson 1998; Røskaft et al. 2002a), and since nearly all of the nests we found were used for experiments, we have no estimate of such errors. However, it is reasonable to consider the frequency of rejection errors (i.e. 0.8%) to be an upper limit to the true frequency of recognition costs.

Aggressive behaviour against cuckoo dummies

There were no differences between Tydal and Tana in the proportion of host pairs that behaved aggressively against the cuckoo dummy (19/23 and 77/93 Fisher's Exact Probabilities test, $P = 1$). Although few pairs were tested in Kittilä, a similar proportion of the pairs responded aggressively (8/10).

DISCUSSION

We have shown that there are no notable geographical differences in the overall tendency to reject parasitic eggs in bramblings. Moreover, the slope of the relationship between host-parasite egg similarity and acceptance probability was similar in all four study populations, irrespective of whether the similarity measure was based on subjective indexing or colour contrasts derived from a combination of reflectance spectra and cone sensitivity functions. There was a tendency for a steeper relationship between brightness contrast and acceptance probability in Tydal compared to Kittilä and Ammarnäs. Overall, however, our results show that the geographical component related to variation in egg rejection behaviour is negligible in the brambling. It is reasonable to expect that lack of variation extends to any arbitrary pair of brambling populations within the area spanned by the four study populations. Since rejection rate of non-mimetic eggs by bramblings is high (85-100%), allele(s) responsible for egg rejection (Martin-Galvez et al. 2006, 2007) is likely to be fixed (or nearly so) in all four populations. This result would be highly unlikely if there are both small-scale geographical variation in the trait and potential for remixing among local populations. Our four geographically distant samples therefore strongly suggest that a genetic basis for rejection is close to fixation also at the species level. Furthermore, the level of aggression against cuckoo dummies was similar based on a dichotomous “aggressive/not aggressive” category, suggesting that, at the population level, bramblings also perceive the cuckoo as a threat to the same extent.

Cuckoo hosts subject to geographical variation in parasitism rates tend to show considerable variation in rejection rates of non-mimetic model eggs, both on small and large spatial scales, with parasitised populations normally exhibiting stronger defences than non-parasitised ones (Davies and Brooke 1989a; Nakamura et al. 1998; Soler et al. 1999; Lindholm 2000; Lindholm and Thomas 2000; Stokke et al. 2008, but see Rutila et al. 2006, Moskat et al. 2002, 2008b). These variations have been explained as reflecting local host evolution (Soler and Møller 1990; Soler et al. 2001; Røskaft et al. 2002c; Stokke et al. 2008), flexible adjustments to shifting risks of parasitism (Zuniga and Redondo 1992; Brooke et al. 1998; Lindholm 2000; Lindholm and Thomas 2000), or as variation in reaction norms (Stokke et al. 2008). The spatial consistency of bramblings' responses clearly breaks with this pattern. In general, this result could have at least three potential explanations: 1) the populations have traced the same evolutionary trajectory independently; 2) the breeding populations do not constitute independent evolutionary units; 3) the traits are inherited from an ancestral species (Bolen et al. 2000; Rothstein 2001; Peer and Sealy 2004; Peer et al. 2007) or evolved before the host underwent a range expansion (Thompson 2005).

Widespread historical parasitism is a precondition for the first scenario, and since bramblings build open arboreal nests they should in principle be available to cuckoos everywhere (Røskaft et al. 2002c). Nevertheless, any widespread interaction is likely to show some clinal or mosaic variation in the intensity of selection that can give rise to geographical variation in coevolved traits (Thompson 2005). In addition, even if parasitism was widespread initially, our survey indicates that there are consistent geographical differences in recent distribution of parasitism, with Finnish Lapland constituting a potential coevolutionary hot spot. Thus, under the first scenario, bramblings in Kittilä should eventually evolve stronger defences than bramblings in now non-parasitised populations.

The pervasive lack of breeding site fidelity implies that lack of geographic variation has arisen because the regional brambling population approaches one single evolutionary unit (scenario 2 above). An examination of egg characteristics also supports that local adaptations do not develop in bramblings because they show that cuckoo eggs found in Kittilä would have equal acceptance probability in non-parasitised populations (in preparation, see e.g. Lahti 2006). In this situation, widespread historical parasitism is not an absolute prerequisite for evolution of widespread defence (Gomulkiewicz et al. 2000; Lenormand 2002). For the same reason, maintenance of intense egg rejection in non-parasitised populations does not necessarily imply that negative selection is irrelevant (Rothstein 2001; Stokke et al. 2002). However, rejection errors were recorded in only 0.8% of the experiments where the parasitic egg was accepted (0.5% of the experiments where any egg(s) where ejected). Because it is prudent to consider the frequency of rejection errors as an upper bound to the frequency of recognition costs (i.e. rejection of own eggs from non-parasitised nests), our experiments indicate that fitness costs associated with rejection behaviour are currently close to being evolutionary insignificant. Another indication of this (Lotem and Nakamura 1998) is that egg rejection is not conditionally expressed according to current risks and costs of parasitism (Braa et al. 1992; Vikan et al. 2009). Importantly, bramblings have both low intraclutch and high interclutch variation in egg appearance (Øien et al. 1995, Fig. 2). These traits have likely evolved because they facilitate efficient and cost free egg recognition (Kilner 2006; Lahti 2006; Stokke et al. 2007b; Moskát et al. 2008a).

Although past episodes of parasitism is not a strict requirement for explaining current defence levels in allopatric brambling populations, a high average parasitism pressure across all populations could be required to drive the regional level of host defence to the high level found in this species (Rothstein 1975; Røskaft et al. 2006). The extensively studied reed warbler *Acrocephalus scirpaceus* shows a weak isolation by distance in Europe (P Procházka, pers. com.), implying significant amounts of homogenizing gene flow among populations. In contrast to the brambling, the reed warbler shows spatially and temporally variable egg rejection (Brooke et al. 1998; Lindholm and Thomas 2000; Stokke et al. 2008). It has also relatively high intraclutch and low intraclutch egg variation (Øien et al. 1995; Stokke et al. 1999), and the phenotypically flexible component to variation in egg rejection can be significant, implying that recognition errors are a potent cost in this host (Davies and Brooke

1988; Davies et al. 1996; Brooke et al. 1998; Lindholm 2000; Moksnes et al. 2000; but see Røskaft et al. 2002a). The reed warbler-cuckoo interaction involves many structural cold spots where the vast proportion of reed warblers breeds far from trees and are therefore inaccessible to cuckoos. This suggests that differences in historical selection pressures could be part of the explanation for why the brambling and reed warbler came to evolve markedly different patterns of egg rejection (Røskaft et al. 2002c).

Since the brambling represents an extreme case due to its notorious lack of breeding site fidelity, it provides a clear example of how a proper understanding of a local interaction requires attention to the spatial dynamics of the host. Documentation of strong host defence levels in non-parasitised host populations could often mean that the interaction has evolved towards extinction of the cuckoo in these localities (Davies and Brooke 1998). The cuckoo could also be at evolutionary equilibrium with its host but go extinct for other reasons. In this regard, it is relevant to note that the cuckoo has declined in Britain without any apparent link to change in host adaptation (Brooke and Davies 1987; Glue 2006). A plausible scenario for the highly mobile brambling is that the geographical pattern of parasitism reflects variation in the cuckoo's probability of extinction/recolonisation due to ecological conditions.

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TABLE 1: Natural parasitism, responses against cuckoo dummies and parasitic eggs in four brambling populations in Fennoscandia. Parameter estimates from logistic regressions on the probability of acceptance (0 = reject, 1 = accept) for measures of similarity between host and parasitic egg (parameter estimates are taken from univariate regressions). Ejection costs are the proportions of ejections where host egg(s) disappeared in addition to the parasitic one. Rejection errors are the proportion of experiments where the parasitic egg was accepted but where own egg(s) disappeared.

Population	**Parasitism rate (# nests)**[1]	**Historical records of parasitism (mimetic egg type)**	**Mean (SD) contrast of experimental parasitic eggs**	**Contrast β (SE) 95%CI N**	**ΔT_C β (SE) 95%CI N**	**ΔT_B β (SE) 95%CI N**	**Mean (SD) nr of days taken to respond**[6]	**Ejection costs (# nests) Rejection errors (# nests)**	**Aggression against cuckoo dummies (# nests)**
Tana	0 (0/250)		1.90 (0.68)	-1.68 (0.36) [-2.95,-0.41] 112			2.96 (1.42)	0.07 (4/61) 0.02 (1/58)	0.83 (77/93)
Kittilä	0.06 (9/158)	Several records from Kittilä and neighbouring municipalities 1890's-1930's[2,5]	2.20 (0.72)	-2.91 (0.74) [-4.36,-1.46] 65	-38.2 (16.2) [-70.0,-6.5] 42	-0.17 (0.10) [-0.37,0.03] 42	2.14 (1.22)	0.02 (1/61) 0.00 (0/19)	0.8 (8/10)
Ammarnäs	0 (0/90)	0 of +500 nests 1963-1996[3]	2.14 (0.65)	-2.48 (0.65) [-3.75,-1.21] 77	-34.7 (11.8) [-57.8,-11.6] 77	-0.23 (0.09) [-0.41,-0.05] 77		0.02 (1/51) 0.00 (0/26)	
Tydal	0 (0/100)	0 of +250 nests 1967-1986[4], 3 records 40km northeast of study area 1948-1949[5]	2.19 (0.70)	-2.27 (0.67) [-3.58,-0.96] 48	-68.9 (27.6) [-126.0,-11.8] 25	-0.74 (0.32) [-1.40,-0.08] 25	2.33 (1.65)	0.03 (1/37) 0.00 (0/16)	0.83 (19/23)

1) Calculated using nests that were checked at least once close to clutch completion or later. 2) Rosenius (1926), Montell (1917), Wasenius (1936). 3) Cards available at Gothenburg Natural History Museum. 4) Moksnes and Røskaft (1987), Braa et al. (1992). 5) Data from Swedish Museum of Natural History in Stockholm, Zoological Museum in Copenhagen, British Museum in Tring, Finnish Museum of Natural History in Helsinki, and Museum of Natural History in Gothenburg.

TABLE 2: Generalised linear models of the probability of accepting parasitic eggs (0 = reject, 1 = accept) in bramblings. Stepwise backward deletion was used to simplify global models, and significance of parameters was evaluated by the change in deviance between models with and without the parameter in question. Minimal adequate models are in bold. ΔT_C and ΔT_B are the chromatic and achromatic contrast, respectively, between the colours of host and parasitic eggs. See Methods for further details.

Variable	N	df	Deviance	p
Model 1				
Contrast	**302**	**1**	**106.9**	**<0.0001**
Population		3	4.3	0.23
Volume		1	0.02	0.89
Shape		1	0.01	0.93
Contrast × Population		3	3.16	0.37
Shape × Population		3	2.85	0.42
Volume × Population		3	1.09	0.78
Model 2				
ΔT_C	**144**	**1**	**29**	**<0.0001**
ΔT_B		**1**	**9.05**	**0.003**
Population		2	0.41	0.81
ΔT_B ×Population		**2**	**6**	**0.05**
ΔT_C ×Population		2	3.76	0.15
Model 3				
Contrast	**144**	**1**	**25.2**	**<0.0001**
ΔT_B		1	3.71	0.06
ΔT_C		1	0.09	0.77

FIGURE LEGENDS

Figure 1: Map of Fennoscandia showing the location of the four study populations. 1 = Tana, 2 = Kittilä, 3 = Ammarnäs, 4 = Tydal.

Figure 2: Plate indicating the range of variation of brambling clutches (rows 1-3). Each egg represents a different clutch (N=15). Bottom row provides examples of cuckoo eggs found in brambling nests in Kittilä. The eggs are not scaled to size.

Figure 3: Rates of rejection of parasitic eggs in four brambling populations for different extents of similarity between host and parasitic egg as measured by a) Contrast, b) ΔT_C c) ΔT_B (see Methods). Sample sizes above the bars. ΔT_C and ΔT_B are the chromatic and achromatic contrast, respectively, between the colors of host and parasitic eggs.

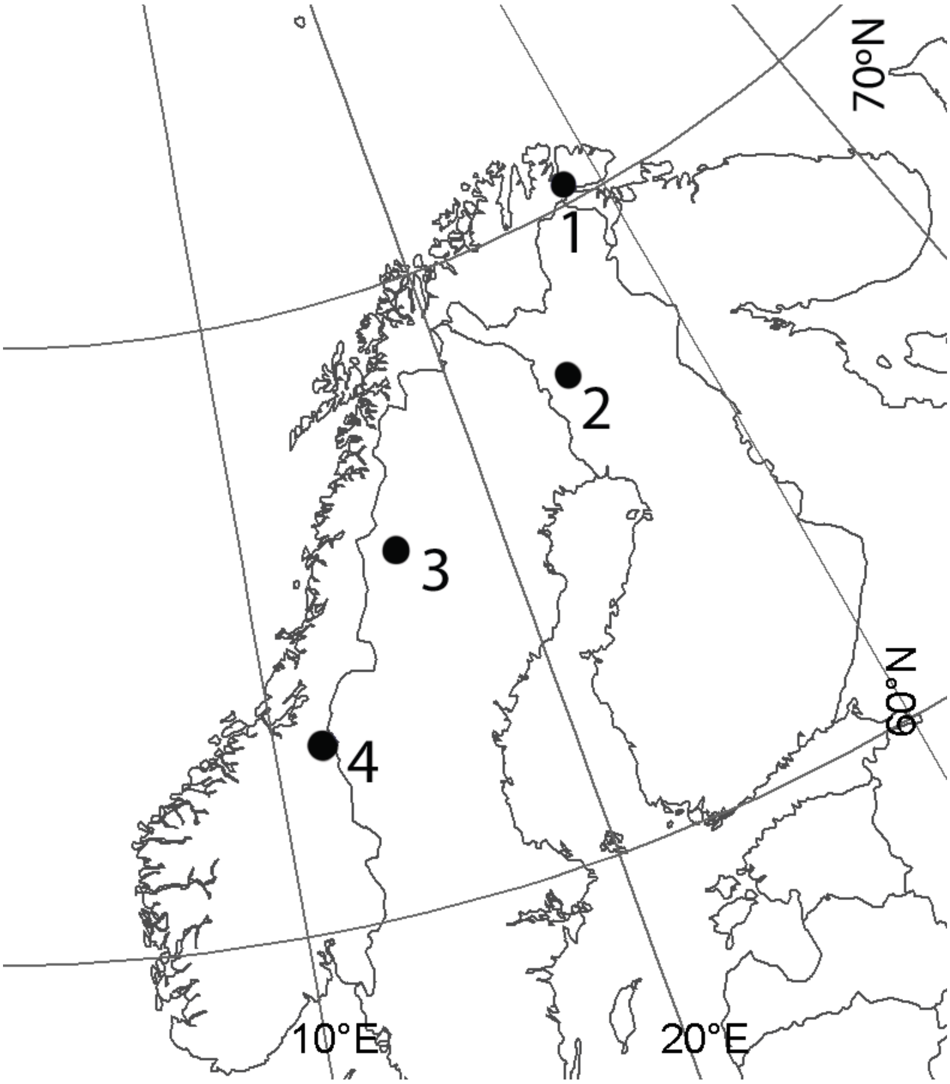

FIGURE 1

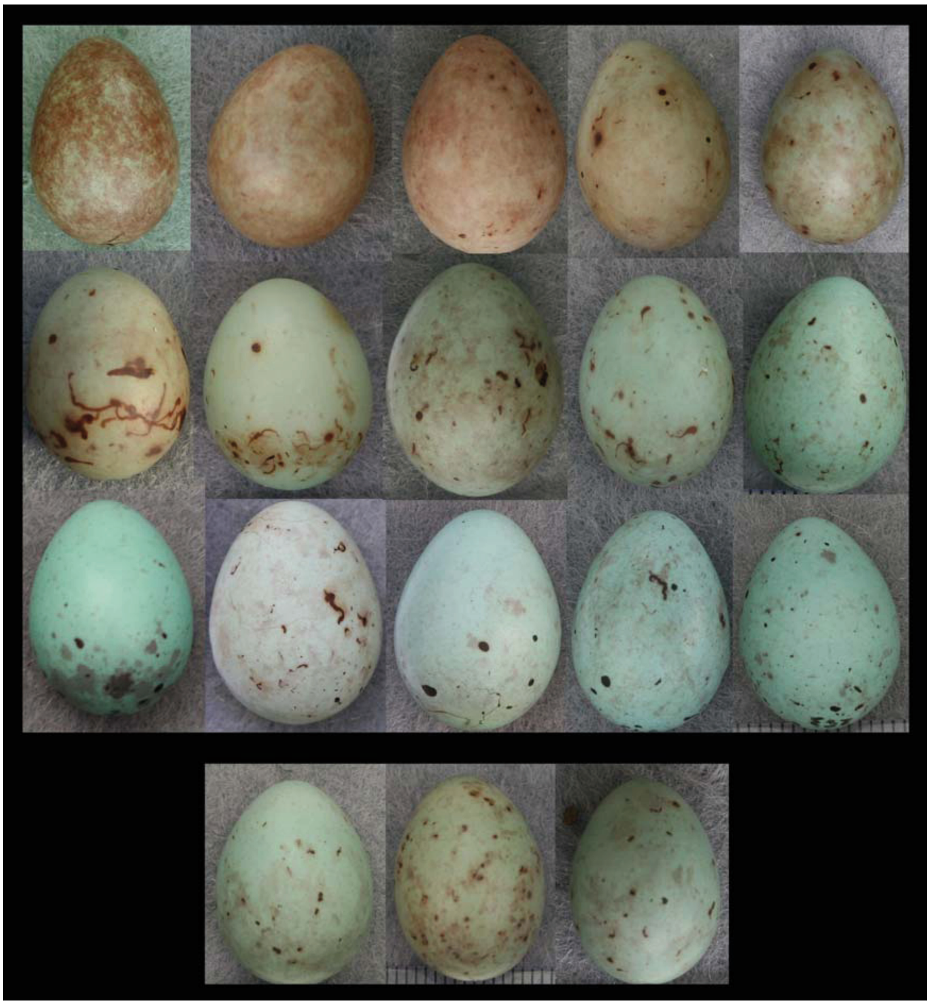

FIGURE 2

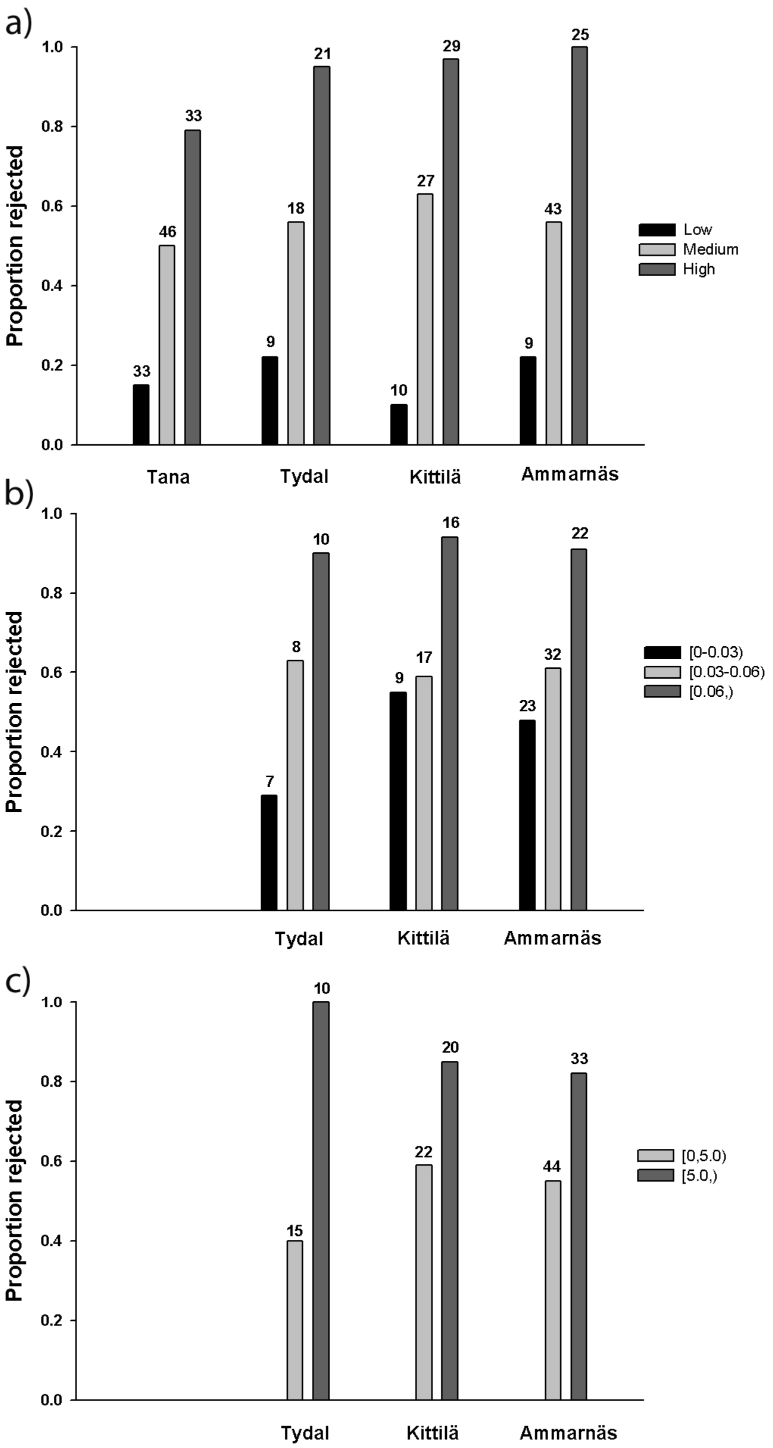
a)
Proportion rejected
1.0
0.8
0.6
0.4
0.2
0.0
33
46
33
9
18
21
10
27
29
9
43
25
Tana
Tydal
Kittilä
Ammarnäs
Low
Medium
High
b)
Proportion rejected
1.0
0.8
0.6
0.4
0.2
0.0
7
8
10
9
17
16
23
32
22
Tydal
Kittilä
Ammarnäs
[0-0.03)
[0.03-0.06)
[0.06,)
c)
Proportion rejected
1.0
0.8
0.6
0.4
0.2
0.0
15
10
22
20
44
33
Tydal
Kittilä
Ammarnäs
[0,5.0)
[5.0,)

FIGURE 3

Paper IV

ALTERNATIVE COEVOLUTIONARY OUTCOMES OF BROOD PARASITE-HOST INTERACTIONS MEDIATED BY EGG MIMICRY

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Figures to be printed in color: Figure 2, Figure 3

Additional keywords: egg color, tetrahedral color space, cuculus canorus, Fringilla montifringilla, Fringilla coelebs

ABSTRACT: Coevolution of egg phenotypes is likely to be a key process affecting interactions between avian brood parasites and their hosts. To gain more insight into the range of realistic potential coevolutionary outcomes, we used a tetrahedral color space to study the egg color distributions of two closely related common cuckoo *Cuculus canorus* hosts, the brambling *Fringilla montifringilla* and chaffinch *F. coelebs*. Whereas the brambling and cuckoo are close to a matching equilibrium, the chaffinch has evolved towards a more bimodal egg color distribution (hue) consistent with the direction of evolutionary change predicted for the brambling. This difference can be explained by the chaffinch having a markedly higher evolutionary potential than the brambling. Surprisingly, the chaffinch's egg color distribution does not produce distinct fitness peaks for cuckoo egg color, even when the bimodal pattern is strengthened. Parallel and marked egg color polymorphisms in host and cuckoo are therefore unlikely to evolve in these systems. Our results also indicate that the cuckoo is not fundamentally constrained by the variation in host clutch appearance in its ability to successfully parasitize the chaffinch. Several coevolutionary scenarios are therefore possible, including fluctuations in host and parasite egg phenotypes driven by negative frequency dependent selection.

Numerous antagonistic species interact via matching of phenotypes (e.g. Benkman et al. 2003; Clayton et al. 1999; Matsuura et al. 2009; Nash et al. 2008; Zangerl and Berenbaum 2003). Some of the prime examples of this kind are found among avian brood parasites, such as the common cuckoo *Cuculus canorus* (hereafter cuckoo), and their hosts. In these interactions, the outcome of a parasitic event is often to a large extent determined by the ability of cuckoos to mimic the eggs of their hosts (Davies 2000). Since this situation can give rise to strong associations between fitness and egg phenotype in both species, and because the heritabilities involved are usually very high (Blow et al. 1950; Collias 1993; Wei et al. 1992), a disproportionate share of the coevolutionary dynamics of these interactions is likely to concern variation in egg phenotypes. Indeed, substantial comparative evidence now implicates coevolution as the main driver behind the high egg phenotype diversity found in some hosts of specialized brood parasites (Kilner 2006). However, our present insight in the specific dynamics and outcomes of egg phenotype coevolution rests almost exclusively on mathematical models and theoretical arguments (Dieckmann et al. 1995; Gavrilets 1997; Gavrilets and Hastings 1998; Nuismer et al. 2005; Servedio and Lande 2003; Stokke et al. 2007; Takasu 2003; 2005). Theoretical predictions cover a wide range of scenarios, from stable matching equilibriums (equal mean phenotypes) to persistent coevolutionary cycles and stable point polymorphisms, depending on the specific assumptions made about the structure of genetic variance, the details of inheritance, and the presence of stabilizing selection. This diversity of theoretical outcomes clearly warrants empirical investigations of the potential for reciprocal selection and its consequences in different host-parasite systems (Takasu 2005).

The main aim of this study is to examine possible coevolutionary scenarios by comparing patterns of variation in host egg distributions within and between two closely related cuckoo hosts, the brambling *Fringilla montifringilla* and the chaffinch *F. coelebs*. The cuckoo is known to comprise specialized female lineages (called gentes) which in many cases have evolved eggs that tend to mimic those of their respective hosts, resulting in an astonishing diversity of egg types (Baker 1942; Brooke and Davies 1988; Gibbs et al. 2000; Moksnes and Røskaft 1995). The two *Fringilla* finches are apt for comparison because they are similar with regard to most of the basic ecological features that affect their suitability as hosts, but differ markedly in one respect that is likely to affect coevolution (Table 1). Since they are each others closest living relatives (Sibley and Ahlquist 1990), we can assume that their respective arms races have had similar starting conditions with regard to egg appearance. Moreover, both hosts build open arboreal nests of similar dimensions (Cramp and Perrins 1994), suggesting that alternative selection pressures related to nest site selection and nest architecture (Kilner 2006) should be of minor importance in accounting for eventual differences. Indeed, the same wide range of egg colors can be found in both species, including pure blue, green, reddish-grey and dark olive-brown clutches (Cramp and Perrins 1994). Therefore, both species should show enough variation between clutches to generate significant fitness differences among individuals in parasitized populations, provided that the cuckoo has at least partially mimetic eggs.

A central tenet of coevolutionary theory is that the outcome of reciprocal selection depends crucially on the evolutionary potential of the interacting species (Dawkins and Krebs 1979; Thompson 2005). That is, their relative ability to respond to changing adaptive landscapes (Garant et al. 2007; Hoeksema and Forde 2008). For example, a stable matching equilibrium (perfect mimicry) is likely to be reached only if the response to selection is stronger in the parasite than in the host. If, on the other hand, the host has the stronger response to selection, the parasite falls increasingly behind or coevolutionary cycles may evolve (Dieckmann et al. 1995; Gavrilets 1997; Nuismer et al. 2005). In this context, the brambling and chaffinch makes an interesting pair precisely because it is likely that they hold very different evolutionary potentials. The brambling is the northern boreal ecological counterpart of the chaffinch (Hagemeijer and Blair 1997). It employs an opportunistic breeding strategy for exploitation of favorable but unpredictable breeding opportunities (Hogstad 2000; 2005), and therefore has a very low breeding site fidelity (Fransson and Hall-Karlson 2008; Lindström 1987; Mikkonen 1983) that is likely to cause high amounts of gene flow which can swamp the effects of selection (Lenormand 2002). The chaffinch, in contrast, exhibits modest breeding site fidelity (Fransson and Hall-Karlson 2008; Mikkonen 1983), possibly reflecting the more predictable ecological conditions of a southern distributional range (Andersson 1980). The potential evolutionary consequences of these differences are manifested in the subspecies-structure of the two species. While the chaffinch has a marked geographical variation comprising several subspecies (7 in the *coelebs* group), no subspecies has so far been described for the brambling (Cramp and Perrins 1994; Hagemeijer and Blair 1997). Thus, theoretical considerations prescribe that the pace of egg phenotype coevolution should differ significantly between the two systems because, all else being equal, the ability to respond to selection should be markedly stronger in the chaffinch. At any point in time, therefore, the two species are expected to occupy different positions along the coevolutionary trajectory for egg phenotypes. As such, the species comparison can be regarded complementary to studies that cover the broader scale of time during which coevolution takes place (Davies and Brooke 1989a).

The early transient stages of any chase between egg phenotypes are likely to involve evolution of an increasingly bimodal host egg distribution as a response to disruptive selection imposed by mimetic parasite eggs (Niusmer et al. 2005). We should therefore expect to find a stronger bimodality in the chaffinch than in the brambling. The first aim of this study is to investigate the possible occurrence of such differences and evaluate their causal link to the parasitic interaction. In order to achieve this, we use a tetrahedral color space to compare the egg color distributions of the two species, evaluate the opportunity for disruptive selection on brambling egg colors, and visualize the direction of predicted evolutionary change in color space.

A second aim of this study is to examine if the range of the coevolutionary trajectory is likely to extend beyond the early stages of increasing host variance. One essential step in this direction is to reveal if evolution on part of the host can give rise to several distinct adaptive peaks for cuckoo egg appearance (Takasu, 2003). We use an experimentally derived host discrimination function to estimate average rejection probabilities for a wide range of potential cuckoo egg phenotypes. We then use these probabilities to sketch the forms of selection imposed by the hosts' egg distributions and relevant subsets of these distributions.

Unfortunately, many of the hosts that have both high interclutch variation in egg appearance and strong egg discrimination abilities, and thereby potential to set in motion more strong dynamics, are rarely parasitized at present (Davies and Brooke 1998; Honza et al. 2004; Lovaszi and Moskát 2004; Procházka and Honza 2004; Røskaft et al. 2002b; Øien et al. 1995). This fact does of course limit the reach of any empirical approach. The furthest we can get is to clarify whether there are any fundamental restrictions on parasite coevolution in these cases. Obviously, evolution of a high interclutch variation can cause non-recoverable reductions in cuckoo fitness. At worst, the level of interclutch variation attained by the host might reduce the mean acceptance probability of any potential cuckoo egg type to the extent that extinction becomes deterministic. Thus, in addition to revealing the selective pressures on cuckoo eggs, it is important to evaluate whether such restrictions are absolute. The *Fringilla* finches are very suitable in this respect since their levels of interclutch variation are among the highest found for potential European hosts of the cuckoo (Stokke et al. 2002b; Øien et al. 1995). Moreover, the brambling has long been known as a regular host (Baker 1942; Rosenius 1929; Wasenius 1936) whereas reports of regular parasitism on chaffinches are lacking even from areas where they are among the most abundant passerines (Baker 1942; Glue and

Murray 1984; Malchevsky 1987; Moksnes and Røskaft 1995; Røskaft et al. 2002b). Thus, by comparing the scope for egg discrimination in the two hosts, we can also assess whether current absence of parasitism in chaffinches is likely to be explained solely by a fundamental inability to cope with a static host distribution with large variance.

Methods

Field Data

The brambling was studied in three areas in Fennoscandia: Tydal in Central Norway (63ºN, 12ºE, 2006-2008), Ammarnäs in Northern Sweden (66ºN, 16ºE, 2008), and Kittilä in Northern Finland (68ºN, 25ºE, 2005-2008). The Kittilä population is the only one currently parasitized. Data on host egg coloration were obtained from 47 clutches in Tydal, 97 clutches in Ammarnäs, and 88 clutches in Kittilä. Five cuckoo eggs which were all found in Kittilä were also measured. The chaffinch was studied in an unparasitized population in Stjørdal, Central Norway (63ºN, 11ºE, 2007-2008), where data from 157 clutches was obtained.

Museum Data

In addition to field data, we also collected data on chaffinch, brambling, and cuckoo egg appearance from clutches held in the collections of British Museum (Natural History), Tring, Great Britain; Museum of Natural History, Gothenburg, Sweden; Museum of Natural History, Copenhagen, Denmark; Finnish Museum of Natural History, Helsinki, Finland, and Swedish Museum of Natural History, Stockholm, Sweden. Data on 262 brambling and 483 chaffinch clutches that were all collected during the period 1881-1940 were used in the analyses. There were no temporal trends in tetrachromatic egg color parameters (see below) within this period. The brambling clutches were distributed throughout northern Fennoscandia, most of them originating from Northern Finland (N=136) and Northern Sweden (N=108), whereas the chaffinch clutches had been collected in Great Britain (N=207), Denmark (N=105), Sweden (N=94), Finland (N=62), Russian Karelia (N=5), and Northern Estonia (N=10). For some analyses, Denmark and Sweden are pooled into one region and Finland together with Russian Karelia and Northern Estonia are pooled into one region.

Based on visual inspection, cuckoo eggs were classified to belong to a *Fringilla* morph (Moksnes and Røskaft 1995) if the egg was clearly within the range of variation of brambling and chaffinch eggs (N = 68). These cuckoo eggs were laid in clutches of brambling (N=43), chaffinch (N=10), willow warbler *Phylloscopus trochilus* (N=5), robin *Erithacus rubecula* (N=2), spotted flycatcher *Muscicapa striata* (N=2), reed bunting *Emberiza schoeniclus* (N=1), tree pipit *Anthus trivialis* (N=1), rustic bunting *Emberiza rustica* (N=1), chiffchaff *Phylloscopus collybita* (N=1), yellow wagtail *Motacilla flava* (N=1), and one unknown. In all of the non-*Fringilla* hosts, the sampling locality was within Northern Fennoscandia and indicated sympatry with either chaffinch or brambling. Conversely, the cuckoo egg was discarded if it obviously belonged to a different cuckoo egg morph (such as *Anthus* or *Motacilla*, Moksnes and Røskaft 1995). There are two main reasons for this delimitation. Firstly, in the context of egg phenotype coevolution, cuckoo eggs that are outside the trait space of the host are likely to contribute little to selection on host egg appearance, because such eggs are nearly always rejected by both hosts, irrespective of the host's own egg type. We have conducted a total of 66 egg rejection experiments where the parasitic egg came from a non-*Fringilla* species, and 92% of those eggs were rejected (19/19 experiments with bramblings and 42/47 experiments with chaffinches). Consequently, even if such egg types are occasionally accepted they would survive for few generations at most. Secondly, the occurrence of such cuckoo eggs may differ between the two *Fringilla* hosts for reasons that are completely unrelated to a coevolutionary process, for example because of differences in host community composition (host specific gentes may lay eggs in other hosts accidentally (Moksnes and Røskaft 1995)). Including such cuckoo eggs in the analyses could therefore introduce non-essential variation that might obscure relevant differences or similarities. Finally, it is important to note that this is a conservative approach from a visual perception perspective because, while cuckoo eggs may frequently appear less mimetic to a bird than to a human observer, the opposite is false for most conceivable situations (Håstad and Ödeen 2008; Vorobyev et al. 1998, own unpublished data). “Hidden” coevolved egg morphs (i.e. eggs that match host eggs in the UV-part of the spectrum but are otherwise contrasting) (Cherry and Bennett 2001; Starling et al. 2006) are therefore no more than a remote possibility in these two systems. Field and museum clutches are treated separately throughout because the color distributions of museum eggs differed markedly from fresh eggs (see Results).

Egg Experiments

We carried out numerous egg exchange experiments across all study populations in order to obtain the precise relationship between the difference in coloration between host and parasitic eggs and the corresponding probability of egg rejection. We also analyzed egg rejection in relation to relative difference in egg volume (Hoyt 1979; Marchetti 2000) and shape (length/breadth, Picman 1989). As parasitic eggs, we used real brambling and chaffinch eggs. Hence, the host discrimination function obtained applies to differences that occur within the boundaries of the trait space of the two hosts. A total of 288 successful experiments were recorded (137 with bramblings (14 of the parasitic eggs where chaffinch eggs) and 151 with chaffinches (all parasitic eggs were chaffinch eggs)). The result of each experiment was classified as either rejection (parasitic egg ejected) or acceptance (parasitic egg incubated for at least five days). We have shown in two separate studies that previous experimental parasitism does not affect the probability of rejection of a parasitic egg added later in the same breeding attempt and that there are no differences in strength of egg discrimination among the brambling populations (Vikan et al., unpublished manuscripts). We therefore included seventy-four experiments that were replicates at the individual level. In all cases where two experiments were carried out on the same individual, two different parasitic eggs were used.

The egg experiments serve three main functions in this article. Firstly, they establish a ground for comparison of the strength of egg color discrimination in bramblings and chaffinches. Secondly, they make a standard of reference for assessing the biological significance of differences in mimicry. Thirdly, we use the host discrimination function to predict average acceptance probabilities for alternative cuckoo egg types.

Quantification of Egg Color and Color Contrasts

Reflectance spectra of eggs were obtained with a USB2000 spectrophotometer from surfaces illuminated with a deuterium halogen light source. Measurements were taken at a 45degree angle to the egg surface, with the spectrophotometer and the light source connected with a coaxial reflectance probe (QR-400-7-UV-vis). Four (N=1080) or eight (N=126) measurements were taken from each egg by dividing the egg into three regions along the long axis of the egg and measuring the background (i.e. avoiding pigmentation where spotting was obvious) in each region (one (two) measurements in the pointed and blunt parts and two (four) measurements in the middle part. Eggs that were collected in the field were all fresh when measured. One random egg was measured in each clutch, which is justified by the extraordinary low intraclutch variation found in these two species (Stokke et al. 2004; Øien et al. 1995). To establish whether four spectra per egg are enough to describe egg coloration adequately, we obtained 20 measurements from each of a total of 20 eggs (4 chaffinch and 16 brambling eggs), each originating from a different clutch. Firstly, we calculated quantum catch values (see below) for each of these eggs based on the mean of all the 20 spectra. Secondly, for each egg, we randomly selected four reflectance spectra out of the 20 available spectra (no replacement) and repeated this procedure 10000 times. At each step, we calculated a quantum catch value based on the mean of the four spectra. More than 97% of the simulated quantum catch values laid within 1 SD of the grand quantum catch value in all 20 eggs, indicating that four measurements are sufficient to describe background color adequately.

We calculated an average spectrum from the four (eight) measurements, and used these spectra for the subsequent analyses. For each egg we then calculated idealized quantum catches for each of the four classes of passerine cone (Goldsmith 1990; Stoddard and Prum 2008a):

$$Q_i = \sum_{i=300}^{700} R(\lambda)S_i(\lambda) \qquad (1)$$

where $R(\lambda)$ is the mean reflectance spectrum for an egg interpolated to a step with of 1nm between 300nm and 700nm, and $S_i(\lambda)$ is the spectral sensitivity function for cone *i*. Both S_i and R were normalized to have integrals of 1. We used the average of spectral sensitivity curves for UVS – type retinas from Endler and Mielke (2005, available in their supplementary online material). Q_i-values for each egg were normalized to sum to 1. Formula 1 sets the irradiance spectrum constant at all wavelengths with integral 1. Given that von Kries color constancy is a fundamental feature of avian color vision (Vorobyev 2003; Vorobyev et al. 1998), the opportunities for natural variations in the composition of ambient light to affect color discrimination should be rather limited (Stoddard and Prum 2008a). Accordingly, when von Kries transformation for color constancy is applied, quantitative estimates of color values differ only marginally for different illumination regimes (Siddiqi et al. 2004; Stoddard and Prum 2008a, own unpublished data). Bramblings and chaffinches build open, shallow nests, and it is therefore reasonable to assume that light conditions do not limit color discrimination.

The normalized quantum catch values for an egg constitutes a vector $\{u,s,m,l\}$ in a color tetrahedron whose vertices correspond to exclusive stimulation of each of the four cone types respectively. The $\{u, s, m, l\}$- values were mapped into Cartesian coordinates $\{x, y, z\}$ using the transformation of Endler and Mielke (2005). The tetrahedron places the achromatic point of equal cone stimulation at the origin and the uv-vertex along the z-axis.

All calculations in this study are based on this simple color space, which has been strongly advocated by others for use in analyses of color evolution (Stoddard and Prum 2008a). The color space has the important property that discriminability of two colors can be assumed to be proportional to the Euclidean distance between their corresponding color vectors (Endler and Mielke 2005):

$$\Delta T_C = \sqrt{(x_a - x_b)^2 + (y_a - y_b)^2 + (z_a - z_b)^2} \qquad (2)$$

ΔT_C is related to discriminability values calculated by the non-logarithmic version of Vorobyev and Osorio's (1998) noise-limited color opponent model, but does not specify a threshold criterion for when a pair of points is discriminable (Endler and Mielke 2005).

Using non-normalized reflectance spectra, we also calculated idealized quantum catches Q_B for double cones which are assumed to be involved in achromatic discrimination (Osorio and Vorobyev 2005). The spectral sensitivity of double cones was obtained by combining the absorbance spectra of the medium- and long-wavelength-sensitive cones (Gomez and Thery 2007). Achromatic (brightness) contrasts were then calculated as the Euclidean distance between quantum catches of double cones for host and parasitic egg:

$$\Delta T_B = | Q_{B,H} - Q_{B,P} | \qquad (3)$$

We checked the explanatory power of color contrasts calculated using equation 1-2 against contrast values calculated using the logarithmic version of Vorobyev and Osorio's (1998) model. In the latter calculations, we disregarded irradiance and assumed that the noise-to-signal ratio is independent of light intensity. We further used Vorobyev's (1998) estimate of the Weber fraction for the LWS cone. Remaining Weber fractions were calculated according to the relative proportions of the different cone types in the retina of the blue tit *Cyanistes caeruleus* (Hart et al. 2000). We then sat up two alternative logistic regression models on the probability of rejection of parasitic eggs, and compared them by their relative AIC-values (Burnham and Anderson 2002). As might be expected, the AIC-values were very similar (331.2 for the model containing ΔT_C and 331.8 for the alternative model), implying that the two models do not differ in their ability to predict host behavior.

Characteristics of Egg Color Distributions.

Color contrast. We obtained the population distribution of color contrast values (equation 2) by calculating the color contrast for all pair-wise combinations of clutches. The average color contrast is a measure of the overall contrast between the clutches in a population, whereas the variance is a measure of the uniformity of the color contrasts. If the distribution of color contrasts has a large mean this would indicate ample scope for discrimination against any parasite egg type. As such, average color contrast can be regarded as a measure of interclutch variation.

Color volume. The volume occupied by a sample of clutches in color space can be regarded a measure of color diversity, or alternatively, as the magnitude of space presently available for egg color coevolution. Color volume complements the distribution of color distances since a population of egg colors can have a large mean color distance but a low color volume, and vice versa. Color volumes were estimated by applying the *convhulln-*

function in the geometry package for R.2.8.1 (Grasman and Gramacy 2008; R Development Core Team 2008). The volume thus obtained equals the volume of the minimal convex polygon that encloses all colors in the specified sample.

Hue contrasts. The hue of a color in tetrahedral color space is defined as the direction of the color vector. A given hue is therefore jointly defined by the angular displacement of the color vector from the positive x-axis ($\theta \in [-\pi, +\pi]$), which runs between the m (green) and l (red) vertices of the tetrahedron, and the angular displacement from the horizontal xy-plane ($\phi \in [-\frac{\pi}{2}, +\frac{\pi}{2}]$), which equals the uv-component of hue (Stoddard and Prum 2008a). θ and ϕ are analogous to longitude and latitude, respectively. The contrast in hue between two eggs equals the magnitude of the angle that separates their color vectors (Stoddard and Prum 2008a; b, equation 3 in their online appendix). This measure of contrast in hue is independent of chroma (saturation). In order to visualize the distribution of hues for a sample of clutches, we mapped the hues onto a unit sphere centered at the achromatic origin and derived their two-dimensional Robinson projections (*sensu* Endler et al., 2005).

Chroma (saturation). The chroma of a color equals the Euclidean norm of the color vector. Colors that differ only in chroma are therefore positive scalar multiples of the same color vector. Because the maximum chroma varies with hue, we also calculated an alternative measure of chroma by dividing chroma by the maximum chroma for the given hue (achieved chroma, sensu Stoddard & Prum, 2008a). A regression of achieved chroma on chroma reveals a strong linear relationship ($b=2.81$, $R^2=0.75$, $p<0.001$), and the two measures give qualitatively identical results. We therefore report values of chroma only.

Estimating the Form of Selection on Cuckoo and Host Egg Color

In order to evaluate the direction of selection on brambling egg phenotypes we calculated the average color contrast for each clutch based on pairings with real cuckoo eggs. For brambling clutches measured in the field we used five cuckoo eggs found in brambling nests in Kittilä. For museum clutches we used 68 *Fringilla* type cuckoo eggs (see above). In order to evaluate the potential forms of selection imposed on cuckoo eggs by the hosts, we sampled 3000 potential cuckoo egg colors from within the tetrachromatic color space of each host that were evenly distributed for hue and chroma and then calculated the average acceptance probability of each of these eggs. In order to assess the potential effects of an increasing bimodality in the host, we also simulated that the potential cuckoo eggs were facing appropriate subsets of the host's current distribution.

Statistical Analyses

All calculations and analyses were carried out in R2.8.1. We used the Euclidean distance version of a multi-response permutation procedure (MRPP, Mielke and Berry 2007) to test for differences in the egg color distributions among bramblings and chaffinches. We tested for differences in both the general location of clutches in color space (as given by xyz coordinates) and for differences in the location of hue values alone (as given by θ and Φ). P-values were obtained by approximation based on 10000 resamplings. We used a binomial logistic regression (logit link) to obtain parameter estimates for prediction of egg rejection probability.

Results

The Host Discrimination Function

The results of egg exchange experiments revealed no significant interactions between species and any of the four measures of difference between eggs (ΔT_C, ΔT_B, volume contrast, shape contrast). Furthermore, ΔT_C was the only term that was retained after model simplification (Table 2). Hence, equal values of ΔT_C gives equal probabilities of rejection in both species. Moreover, since contrast in volume or shape does not seem to affect rejection probability, this indicates that the host response curve (Figure 1) approximates the hosts' responses to real cuckoo eggs. Figure 1 shows the relationship between rejection probability and ΔT_C for the pooled data, and may serve as a standard of reference for addressing the biological significance of differences in ΔT_C.

General Characteristics of Host Egg Color Distributions

Color space volumes. The color space volumes tended to be larger for bramblings than for chaffinches (Table 3). For example, the volumes of each of the three brambling populations were all larger than the volume of the chaffinch population (Stjørdal), even though the latter had the largest sample size. The degree of overlap in volume provides an indication of the extent of sharing of egg colors among populations and species. For each comparison, we estimated the proportion of the total color space that was shared among the populations. We then obtained a permutation distribution (10 000 shufflings, original data structure) of the test statistic for the null hypothesis that all clutches come from same population. For the fresh eggs collected in the field, there was no significant difference between the three brambling populations (proportion of shared color space = 0.65, 2.5-97.5th percentiles = 0.47-0.71). However, there was a significant difference between the two species (proportion of shared color space = 0.08, 2.5-97.5th percentiles: 0.38-0.55). For the museum data, there was a significant difference between the eggs originating from different regions (proportion of shared color space = 0.52, 2.5-97.5th percentiles: 0.71-0.94), but not between the two species (proportion of shared color space = 0.50, 2.5-97.5th percentiles = 0.48-0.65). Hence, when comparing museum and field data, more of the egg colors measured in museums is found in both species. For each species, the volume occupied by fresh clutches tended to be higher than for museum clutches (Table 3), even though the latter were collected over a larger area and a longer time span and were also represented with larger sample sizes.

Color contrasts and optimal mimicry. The distribution of pair wise color contrasts (ΔT_C) were similar in all populations studied (Table 3), meaning that interclutch variation in egg coloration is of same magnitude. The average mimicry (ΔT_C) of the best achievable mimics was also similar. Accordingly, the average acceptance probabilities of optimal cuckoo egg types are of the same magnitude across populations and species (i.e. around 50%, Table 3). Although ΔT_B is a comparably weak predictor of rejection probability (Table 2), a strong negative correlation with ΔT_C could imply a constraint on minimization of average ΔT_C. We therefore calculated correlations between average color contrast and average achromatic contrast (ΔT_B). The correlation coefficients were either significantly positive (meaning that the best potential mimics with regard to average ΔT_C are also the best with regard to average ΔT_B) or not significantly different from zero (Kittilä: r_s=0.02, p=0.87; Ammarnäs: r_s=0.27, p=0.01; Tydal: r_s=-0.01, p=0.92; Stjørdal: r_s=0.48, p<0.0001; Kittilä, Ammarnäs and Tydal pooled: r_s=0.17, p=0.01; Great Britain: r_s=0.31,p<0.001; Denmark and Sweden: r_s=0.48,p<0.001; Finland: r_s=0.19, p=0.10; All museum chaffinch clutches: r_s=0.35, p<0.001: All museum brambling clutches: r_s=0.19, p=0.002).

The distribution of clutches in the color tetrahedron differed significantly between the chaffinch and brambling, considering both field data (Euclidean distance MRPP on xyz-coordinates, $p < 0.001$) and museum data (Euclidean distance MRPP on xyz coordinates, $p < 0.001$)

Hue distribution and hue contrasts. Whereas the distributions of color contrasts were largely similar across populations and species, a different pattern emerged for hue contrasts. When viewing field and museum data separately, chaffinch clutches tended to have larger contrasts in hue than brambling clutches (Table 3). Chaffinch clutches also tended to be more densely distributed around bluish-green and reddish-brown colors, whereas brambling eggs were more often of a pure greenish type (Figure 2). The variance of hue contrasts also reflects this since a more bimodal distribution would have a higher variance than a uniform or unimodal distribution (Table 3).

The Robinson projections of hues illustrate the patterns of variation in hue independent of chroma (Figure 2). The projections show that a large proportion of the hues are found in both species, except from the most pure blue hues which were not found among brambling clutches collected in the field (Figure 2B-C). Therefore, the higher average hue contrast of chaffinch clutches is not merely a consequence of a broader range of hues (Table 3). The important differences are instead related to the frequency distributions of clutches with similar hues (Figure 2 B-E).

As for color volumes, average contrast in hue was markedly lower for museum clutches than for fresh clutches in both species (Table 3). Compared to fresh clutches, hue distributions of museum clutches were more skewed towards the l (red) vertice, and clutches in the blue and blue-green segment had markedly reduced values for the ultraviolet component (Φ) of hue (Figure 2 B-E). Since these differences were evident in both species, they are likely to reflect effects of storage on egg shell reflectance.

The distribution of hues differed significantly between clutches of chaffinch and brambling, considering both field data (Euclidean distance MRPP on θ, Φ, $p < 0.001$) and museum data (Euclidean distance MRPP on θ, Φ, $p < 0.001$)

Chroma (saturation). Chaffinch clutches had on average less saturated colors than brambling clutches (Figure 4, Table 3), both when comparing fresh clutches data (t-test: $t=18.2$, $df=387$, $p<0.0001$, $N=157$, $N=232$) and museum data (Welch t-test on log transformed values: $t=11.6$, $df=644.04$, $p<0.0001$, $N=483$, $N=262$).

Natural Parasitism and Appearance of Cuckoo Eggs in Relation to Optimum Color

Among the museum cuckoo eggs found in chaffinch clutches, 22% (N=45) had a *Fringilla* type cuckoo egg. In comparison, 78% (N=55) cuckoo eggs found in brambling clutches were *Fringilla* type. These numbers are in close agreement with Moksnes and Røskaft (1995), who classified 12% (N=76) of cuckoo eggs in chaffinch clutches as *Fringilla* type compared to only 77% (N=53) of cuckoo eggs in brambling clutches. This difference might reflect a qualitative difference in the nature of the two cuckoo-host interactions, i.e. the brambling is a main host whereas the chaffinch is a secondary host. Eight of the nine *Fringilla* type cuckoo eggs found in chaffinch clutches in our survey were from the zone of overlap between chaffinch and brambling breeding range (locality unknown in one case). In contrast, among 32 parasitized chaffinch clutches from Great Britain and continental Europe, only one was classified as *Fringilla* type.

The cuckoo eggs measured in the field in Kittilä were close to the optimum for that population, and were also close to the optimum for the regional distribution (Figure 3). *Fringilla*-type cuckoo eggs in museums were also close to the optimum for parasitism of bramblings (Figure 3, 4). Moreover, the *Fringilla*-type cuckoo eggs achieved lower average color contrast in brambling clutches than in chaffinch clutches (Paired Wilcoxon test, $V =$

113, $p < 0.001$, $N = 68$). This result holds whether we calculate average color contrast for only the 10 cuckoo eggs that were found in chaffinch clutches (median brambling = 0.032, median chaffinch = 0.045, Paired Wilcoxon test, $p = 0.002$, $V = 0$), the 43 cuckoo eggs that were found in brambling clutches (median brambling = 0.035, median chaffinch = 0.043, Paired Wilcoxon test, $p < 0.001$, $V = 67$), or the 15 cuckoo eggs that were found in clutches of other passerines (median brambling = 0.034, median chaffinch = 0.041, Paired Wilcoxon test, $p < 0.001$, $V = 2$). These tests do not take into account that the minimal achievable color contrast differ between the two species (Table 3). When we corrected for these differences (i.e. by subtracting the average color contrast of the optimal egg type for each species (Table 3) from the average color contrast of each cuckoo egg) cuckoo eggs were still better matches to brambling clutches than to chaffinch clutches (Paired Wilcoxon test*, $V = 605$, $p < 0.001$*). Thus, we conclude that the cuckoo eggs that were identified as *Fringilla*-type in museum collections are closer to the optimal phenotype for bramblings than for chaffinches.

Form of Selection Imposed on Brambling Clutches by Cuckoo Eggs

We calculated the average ΔT_C of each brambling clutch in order to determine the direction of selection on hue. We assumed that the cuckoo egg distribution was given by the *Fringilla* cuckoo egg types measured in this study (treating field and museum data separately), which are close to their optimum color (Figure 3, 4). The calculations indicate that there should be huge opportunities for disruptive selection on hue (Figure 2 B, D). An evolutionary response in the brambling would transiently change the hue distribution in the direction of stronger bimodality, which in turn would cause the distribution to converge on the chaffinch distribution.

Form of Selection Imposed on Cuckoo Eggs by Host Clutches

We first compared the average color contrast of each brambling and host clutch measured in the field when calculated using the local host clutch distribution with the value obtained using the pooled distribution of the two other populations. The correlations between average color contrasts were very high in all three comparisons ($r_s>0.82$, $p<0.0001$), indicating that cuckoo egg phenotypes that are optimal in one population would also tend to be optimal in the remote populations (see also Figure 3). The same conclusion can be drawn with respect to the three chaffinch regions based on museum data ($r_s>0.63$, $p<0.0001$). The rest of the calculations were therefore based on the pooled sets of clutches.

To resolve if there are any fine details in the form of selection, we calculated the mean acceptance probability of a large number of hypothetical cuckoo egg colors selected from within the tetrahedral color spaces occupied by the two hosts, respectively. Figure 5 (A-B) shows the forms of selection imposed on the longitudinal (θ) component of hue by the two host distributions (selection on the latitudinal component is always directional, and selection on chroma is stabilizing towards the same value for all θ). The results show that selection on cuckoo egg colors would be mainly stabilizing, but with a wider plateau in the chaffinch case. To see if distinct adaptive peaks could evolve, i.e. giving rise to two distinct cuckoo egg phenotypes, we defined subsets of the chaffinch distribution that had stronger bimodality and re-calculated the curves. Although increasing bimodality had the expected effect of reducing the average acceptance probability, it did not give rise to distinct peaks (Figure 5 C-E).

Ecological, Life History, and Defensive Characteristics of Hosts

Table 1 summarizes characteristics of chaffinches and bramblings that are likely to have direct or indirect relevance in egg phenotype coevolution. At present, bramblings and chaffinches are very similar with regard to the overall importance of egg phenotypes for the outcome of parasitic events. Both species are single trajectory species and possess few, if any, conditional responses (Braa et al. 1992; Rothstein 2001; Stokke et al. 2004), meaning that there is little dynamic change in the proportion of individuals capable of rejecting contrasting parasitic eggs. Likewise, both species are equally suitable hosts judging by their adult body weight, general abundance, ecological dominance, chick diet and availability to cuckoos. Some important differences stand out, however. Most obvious and important is the difference in site fidelity which affects the response to selection in the host and local adaptation by the parasite. Bramblings might also impose stronger limitation on cuckoo recruitment because of a shorter breeding season and larger fluctuations in abundance and breeding success. Therefore, all else being equal chaffinches might have been subject to higher historical parasitism pressures. On the other hand, the brambling has larger clutch sizes than the chaffinch, which in isolation leads to a stronger opportunity for selection in the former species. Finally, the brambling breeds in larger tracts of homogenous habitats than the chaffinch (compare, for example, the degrees of forest fragmentation in Great Britain and Continental Europe with northern boreal forests). According to Southern (1958), this should make it easier for the cuckoo to evolve good mimicry to the brambling provided that genes for egg color segregates through both sexes. The conventional view, however, is that cuckoo egg color is under maternal control (Davies 2000).

Discussion

Coevolution is driven by reciprocal selection at an interphase of phenotypic traits which mediate the outcome of interactions among individuals (Brodie and Ridenhour 2003). Any study dealing with questions about coevolution must therefore identify the traits that are most strongly associated with variation in fitness. Although cuckoo-host interactions are famously known as mimicry systems (Baker 1942; Brooke and Davies 1988; Chance 1940; Stokke et al. 2002b; Swynnerton 1918), most of the attention to date has been on the coevolutionary trajectories of egg recognition, whereas the dynamic aspects of mimicry have been largely neglected in the major discussions (Krüger 2007; Rothstein and Robinson 1998, but see Rothstein 1990 p 498). The potential importance of mimicry evolution for the occurrence and spread of rejection behavior is widely approved (Kelly 1987; Lotem et al. 1995; Rodriguez-Girones and Lotem 1999; Rothstein 1990; Servedio and Lande 2003; Stokke et al. 2007). However, many hosts like the brambling and chaffinch are unconditional rejecters of non-mimetic eggs with little geographical variation, even after long periods without parasitism (Lahti 2006; Stokke et al. 2005; Stokke et al. 2004). In these hosts, coevolutionary change is particularly likely to be manifested in egg phenotype distributions.

We found that cuckoos which parasitize bramblings are subject to strong stabilizing selection for egg color and that they have evolved egg phenotypes that are close to the optimal value. The results concerning museum clutches are somewhat tentative, however, because of the possible homogenizing effect of storage on egg shell reflectance. The high variability among brambling clutches does in turn create ample opportunity for disruptive selection. One important question that arises from these results is whether the brambling and cuckoo could be at a stable matching equilibrium. Theoretically, coevolution leads to a stable matching equilibrium if the response to selection, which is proportional to the additive genetic variance for the trait and the intensity of selection acting on it, is stronger for the parasite than the host

(Dieckmann et al. 1995; Gavrilets 1997; Takasu 2005). Although it is possible that parasitism rates can reach high rates locally, the intensity of selection is likely to be considerably reduced as a consequence of the nomadic behavior of the brambling. In the limit, the evolutionary unit might approach the regional population, in which case the average parasitism rate for the region as whole would determine the selection pressure on host egg phenotypes (i.e. a panmictic model of coevolution would be appropriate). Similarly, in the interaction between the parasitic *Maculinea* butterfly and its ant host *Myrmica ruginodis*, a high level of gene flow in *M. ruginodis* produces coevolutionary cold spots by canceling out any selection imposed by the patchily distributed *Maculinea* (Nash et al. 2008). This perspective leads to the prediction that there should be little potential for local parasite adaptation, or that local adaptation occurs on a large spatial scale (Laine 2005), which is supported by our finding that cuckoo eggs appear to be equally well adapted to each of three distant brambling populations. The bottom line is that the prevailing intensity of selection on brambling and cuckoo egg colors could differ by orders of magnitude. If there in addition is direct stabilizing selection towards an optimal egg color, the brambling and cuckoo could currently be at equilibrium. Whether certain egg colors are favored over others in absence of parasitism is an open question regarding arboreal open nesting birds (Kilner 2006; but see Lahti 2005; Lahti 2008). An equilibrium state could be maintained indefinitely if parasitism rates remain low when the cuckoo is at its fitness optimum.

The current egg color distribution of the chaffinch seems to be a good prediction for how an evolutionary response to parasitism would initially affect the distribution of the brambling. Somewhat counter to intuition, the bimodal tendency in the chaffinch's distribution does not create distinct adaptive peaks for cuckoo egg color, even if the tendency is strengthened. This result is a consequence of the egg discrimination abilities being too weak and/or the color distance between the most common host clutches being too small. The evolution of cuckoo egg color polymorphism is therefore an unlikely outcome in these systems. Instead, polymorphism could be realized in the broad sense that a continuous segment of cuckoo egg colors simultaneously enjoy equal fitness. Therefore, if the brambling-cuckoo system was perturbed from an equilibrium state (i.e. because of a sudden increase in parasitism rate), we would expect evolution of stronger bimodality in the brambling accompanied by a wide diversity of cuckoo egg types distributed in between. Although a large fraction of the cuckoo eggs might not resemble any host clutch in this situation, it would not reflect a true evolutionary lag on part of the cuckoo.

Several outcomes may arise from this situation, and we suggest a few intuitive possibilities. First, if we assume that direct stabilizing selection is at work, the system might be attracted to a new equilibrium where the host's clutches are concentrated around two main optima created by the joint effect of disruptive and stabilizing selection and where the cuckoo is loosely distributed around the midpoint of the trait space. Interestingly, such an outcome resembles the theoretical conclusion by Takasu (2003) that host and parasite can converge on discrete non-overlapping polymorphisms from continuous initial egg phenotype distributions. The stability of the polymorphisms was in this case achieved without stabilizing selection because it was assumed that egg color was maternally inherited. Although discrete morphs were eventually fixed, the proportions themselves were not stable and changed continuously because of fluctuating selection.

Alternatively, if the host continues to be pushed towards the boundaries of the trait space, further increasing the width as more extreme phenotypes are introduced by mutation or immigration, then distinct cuckoo egg morphs might eventually be favored. However, our results indicate that before this stage can be reached, the cuckoo population must go through a period where probability of acceptance is markedly reduced for all egg phenotypes (as shown in Figure 5F). Extinction may therefore take place before this stage is reached, depending on the sensitivity of cuckoo growth rate to a decrease in recruitment rate. Extreme and parallel egg polymorphisms are purportedly found in some African and Asian cuckoos and their hosts (Baker 1942; Fry et al. 1988). It would be interesting to examine what ecological and behavioral conditions underlie these outcomes.

Even if the host was responding to selection mainly by an increase in variance, the distribution would sooner or later become skewed (for example towards reddish-brown clutches as shown in Figure 5E), leading to a corresponding shift in the optimum for cuckoo eggs. It therefore seems more likely that selection on cuckoo egg color becomes directional towards one new optimal egg type than disruptive towards two egg types. The stage could then be set for a scenario where negative frequency dependent selection drives continuous cycling in the frequencies of different phenotypes (Rothstein 1990, p 498). Theoretical studies have shown that this can take place if the host has the strongest response to selection and there is direct stabilizing selection (Dieckmann et al. 1995; Gavrilets 1997; Gavrilets and Hastings 1998; Servedio and Lande 2003; Takasu 2005). One limitation in these studies is that they make the unrealistic assumption that genetic variances are constant or absent. This means that if one ignores stabilizing selection, coevolution can lead to one of only two outcomes (Nuismer et al. 2005): 1) a stable matching equilibrium (the parasite has the strongest response to selection) or 2) the parasite falls increasingly behind (the host has the strongest response to selection). However, Nuismer et al. (2005) showed that this is an oversimplification and that cycling can take place without stabilizing selection if the genetic variances are themselves allowed to evolve. In this model, any matching equilibrium is eventually destabilized because selection erodes additive genetic variance in the parasite which in turn allows the host to escape temporarily.

Since we have no information about the egg appearance of cuckoos that have coevolved with chaffinches, it is impossible at present to critically evaluate the relative likelihood of the hypothetical scenarios. Our results only go so far as to indicate that the cuckoo is not fundamentally constrained by host interclutch variation in its ability to coevolve with the chaffinch. Our estimates of the rate of rejection of optimal cuckoo egg types do not differ between brambling and chaffinch. Also, judging from the comparison of putatively important ecological features (Table 1), the chaffinch should be an equally (if not more) suitable host. Although conjectural, these observations are important because they imply that if the cuckoo regularly goes extinct in the process of egg phenotype coevolution, it may do so because of evolutionary lags created by directional host evolution and not because host interclutch variation inflicts low success on all potential cuckoo egg types, as has been suggested (Honza et al. 2004; Lovaszi and Moskát 2004; Stokke et al. 2004). Our analyses show that even moderate deviations from optimum bring considerable reductions in average acceptance probabilities.

It is not straightforward to predict the prevalence and magnitude of evolutionary lags in the process of egg phenotype coevolution. On the one hand, it is commonly assumed that cuckoos have an evolutionary advantage over their hosts due to the inbuilt inequality that all cuckoos face a host whereas not all hosts face a cuckoo (Dawkins and Krebs 1979). On the other hand, the effect of unequal selection pressures could possibly be cancelled out by differences in population size, generation time and genetic variance, which also affect the potential rate of evolution. A minimum of migration might be important for introducing new variation to cuckoo populations because selection is stabilizing on average, whereas migration might be less important for the host because selection is on average disruptive in form and therefore normally acts to maintain or increase variation (Nuismer et al. 2005). Our study indicates that the degree of overlap in clutch colors between areas is quite high for both chaffinch and brambling, suggesting that variation would not be a limiting factor for the host.

In summary, our study portrays two closely related cuckoo host species that have evolved different clutch color characteristics from presumably similar starting points most likely because differences in ecological features have promoted different coevolutionary outcomes. We have discussed how the nomadic behavior of the brambling may contribute to tilt the outcome in favor of the cuckoo. It might also be that the chaffinch has been subject to higher historical selection pressures because it fluctuates less in abundance and breeding success, and also has a longer breeding season (Table 1). Future studies need to clarify the potential importance of stabilizing selection. Identification of functional genes for egg color could also provide an opportunity to test for ongoing coevolution in other cuckoo-host systems (Nuismer et al. 2005). Future studies also need to take more fully into account the potential ramifications of population structure (Thompson 2005). Broad geographical comparisons that control for historical population relationships represent a complementary approach to multigenerational studies since they allow us to sample across a range of histories and conditions (Hanifin et al. 2008). Such approaches have made important contributions to our understanding of evolution of egg recognition (Soler et al. 1999; 2001), and should now be applied to ongoing interactions in order to clarify whether coevolution drives population differentiation in egg phenotypes and whether cuckoos are normally locally adapted to their hosts.

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Table 1: Comparison of bramblings and chaffinches with regard to behavioral and basic ecological and life history characteristics that might influence on the process of egg phenotype coevolution either indirectly or directly. The fourth column contains an assessment of how the characteristic exert its importance. Host suitability can have indirect importance through limitation effects on cuckoo abundance which in turn determines parasitism rate and also evolutionary potential to some extent. Intensity of reciprocal selection refers to the correlation between egg appearance and fitness (for a given parasitism rate). Note that our categorization does not take into consideration how selection might change as a consequence of the ecological feedbacks intrinsic to the interaction.

Characteristic	Chaffinch	Brambling	Importance of characteristic	References, notes
Overall strength of discrimination against unlike eggs, proportion of individuals capable of rejection (species level)	High	High	Intensity of reciprocal selection	(Braa et al. 1992; Davies and Brooke 1989b; Hale and Briskie 2007; Stokke et al. 2004)
Conditional rejection of parasitic eggs owing to factors other than mimetic similarity	No evidence	No evidence	Intensity of reciprocal selection	(Braa et al. 1992; Stokke et al. 2002a; Stokke et al. 2004, Vikan et al., unpublished manuscript)
Aggression against cuckoo dummies	60-90%	80%	Host suitability	(Røskaft et al. 2002a, Vikan et al., unpublished manuscript)
Abundance, distribution, habitat selection	Abundant, widespread, forest generalist	Abundant, widespread, forest generalist	Host suitability	(Cramp and Perrins 1994; Hagemeijer and Blair 1997)
Proportion of bird community	20-40%	20-50%	Host suitability	(Enemar et al. 2004; Hagemeijer and Blair 1997; Hogstad 2000; Virkkala 1989)
Maximum local density	150 bp/km2	150 bp/km2	Host suitability	(Enemar et al. 2004; Hagemeijer and Blair 1997)
Population fluctuations	No cycles	Both cycling and stable	Host suitability	(Enemar et al. 2004; Hagemeijer and Blair 1997; Hogstad 2000; Virkkala 1989)
Spatio-temporal variation in host breeding success	Comparably low	Comparably high	Host suitability Intensity of reciprocal selection	(Hilden et al. 1982; Hogstad 2000; Lindstrom et al. 2005)
Modal host clutch size	5	7	Response to selection by host	(Cramp and Perrins 1994, own data)
Generation time	Lack accurate estimates	Lack accurate estimates	Potential speed of host evolution	Host and cuckoo generation time differ by the same magnitude in both hosts

Chick diet	Invertebrates	Invertebrates	Host suitability	(Cramp and Perrins 1994)
Adult body weight (summer months)	21.7-23.1	22.6-23.8	Host suitability	(Cramp and Perrins 1994)
Length of breeding season (months where nests are found with eggs)	~2 (own population) ~2.6 (Sweden)	~ 1 (own populations) ~1.8 (Finland)	Host suitability	(Cramp and Perrins 1994, own data)
Fragmentation of breeding habitat	Comparably high	Comparably low	Constraint on mimicry under asexual inheritance of egg color (Southern, 1958)	Correlates with human population density
Nest site selection and nest architecture	Arboreal, open nest cup	Arboreal, open nest cup	Host suitability, importance of alternative selective pressures	(Cramp and Perrins 1994)
Site fidelity	Modest	Weak	Response to selection by host	(Cramp and Perrins 1994; Lindström 1987; Mikkonen 1983)

Table 2: Generalized linear models of the probability of accepting congeneric parasitic eggs in chaffinches and bramblings. Stepwise backward deletion was used to simplify the global model including all parameters, and significance of parameters was evaluated by the change in deviance between models with and without the parameter in question. ΔT_C is the only term included in the minimal adequate model. Rejection rates were 0.60 (N=151) for the chaffinch and 0.66 (N=137) for the brambling. Mean (SD) of ΔT_C and ΔT_B, respectively, was 0.044 (0.023) and 6.48 (4.20) for the chaffinch and 0.051 (0.031) and 5.52 (4.01) for the brambling

Parameter	DF	Deviance	P-value
ΔT_C	1	52.8	< 0.0001
ΔT_B	1	3.48	0.06
Species	1	0.43	0.51
Shape	1	0.36	0.55
Volume	1	0.05	0.82
ΔT_B × Species	1	2.52	0.11
Volume × Species	1	1.1	0.29
ΔT_C × Species	1	0.45	0.5
$\Delta T_B \times \Delta T_C$	1	0.15	0.7
Shape × Species	1	0.01	0.94

Table 3: Summary statistics describing important aspects of clutch color distributions of bramblings and chaffinches. Optimal cuckoo egg types equal the host egg type which achieves the lowest ΔT_C value/rejection probability when averaged over all possible pair wise combinations in which the egg features. Rejection rates are predicted from a univariate logistic regression of ΔT_C on the probability of rejecting a parasitic egg (Figure 1)

Population/Sample	N	Color space volume (volume*1000)	Color contrast (ΔT_C) max, mean (SD)	Hue contrast max, mean (SD)	Chroma mean (SD)	Average color contrast of optimal cuckoo egg type (SD)	Average rejection rate of optimal cuckoo egg type (SD)
Brambling							
Field data (2007-2008)							
Tydal	47	0.065	0.136, 0.047 (0.025)	1.01, 0.35 (0.23)	0.109 (0.019)	0.034 (0.017)	0.53 (0.16)
Kittilä	88	0.101	0.177, 0.044 (0.025)	1.41, 0.37 (0.25)	0.100 (0.018)	0.031 (0.018)	0.50 (0.16)
Ammarnäs	97	0.110	0.159, 0.043 (0.025)	1.55, 0.36 (0.25)	0.102 (0.016)	0.031 (0.017)	0.50 (0.16)
Fennoscandia	232	0.167	0.180, 0.045 (0.025)	1.58, 0.37 (0.26)	0.103 (0.018)	0.032 (0.018)	0.51 (0.16)
Museum data (1881-1940)							
Fennoscandia	262	0.091	0.157, 0.039 (0.023)	1.23, 0.30 (0.22)	0.106 (0.017)	0.028 (0.016)	0.47 (0.15)
Chaffinch							
Field data (2007-2008)							
Stjørdal	157	0.060	0.152, 0.045 (0.027)	1.38, 0.48 (0.34)	0.070 (0.016)	0.033 (0.018)	0.52 (0.17)
Museum data (1881-1940)							
Great Britain	207	0.063	0.150, 0.044 (0.025)	1.20, 0.35 (0.26)	0.095 (0.022)	0.032 (0.017)	0.51 (0.16)
Sweden & Denmark	199	0.040	0.124, 0.039 (0.023)	1.24, 0.38 (0.27)	0.089 (0.015)	0.029 (0.014)	0.49 (0.13)
Finland, Karelen (Russia) & Estonia	77	0.039	0.120, 0.042 (0.024)	1.26, 0.40 (0.27)	0.089 (0.017)	0.031 (0.014)	0.50 (0.14)
Great Britain and Fennoscandia	483	0.093	0.161, 0.042 (0.025)	1.36, 0.38 (0.27)	0.091 (0.019)	0.031 (0.016)	0.50 (0.15)

FIGURE LEGENDS

Figure 1: Bar plot showing the empirical relationship between rejection rate and color contrast (ΔT_C) between host and parasitic eggs. Superimposed is the host discrimination function obtained from a univariate logistic regression on the probability of rejection (95% confidence interval indicated by dotted lines). For plotting purposes the width of the bars for some groups were adjusted to obtain similar sample sizes across groups. Sample sizes for each group depicted above the bars. Total N = 288.

Figure 2: Robinson projection (see main text for explanation) of hues for chaffinch and brambling clutches. Figure A shows the entire projected tetrachromatic hue-space for reference. Red triangles indicate the projections of the ultraviolet (uv), short (s), medium (m) and long wavelength (l) vertices of the tetrahedron. Solid lines indicate the projections of the four edges connecting the different vertices. Figure B and C show the distribution of hues for 232 brambling (pooled clutches from Kittilä, Ammarnäs and Tydal), and 157 chaffinch clutches (Stjørdal), respectively. Figure D and E show the distribution of hues for 262 brambling (Fennoscandia) and 483 chaffinch clutches (Great Britain and Fennoscandia) collected in the period 1881-1940 and now held in various museum collections. Figure F show the distribution of hues for 68 museum cuckoo eggs classified as *Fringilla* egg morphs (blue color) and five fresh cuckoo eggs found in brambling nests in Kittilä in the period 2005-2008 (red color). Note the overlap between the hue-spaces occupied by the two hosts (Fig. B-E). The circles in Figure B and D have different colors to illustrate the direction of selection on hue under the assumption that cuckoo egg color distributions are given by the five and 68 cuckoo eggs in figure F, respectively. Different colors indicate differences in the average color distance (ΔT_C) between host and cuckoo eggs. Parasitism clearly imposes disruptive selection, and an eventual evolutionary response is therefore predicted to change the distribution towards stronger bimodality, whereupon it would converge with the chaffinch's hue distribution (Figure C and E).

Figure 3: Distribution of average color contrasts (ΔT_C) for brambling clutches calculated from pairing each clutch with all other clutches in the population. Black triangles (A-D) and black bars (E) indicate the mean color distance of cuckoo eggs resulting from comparison with all brambling clutches in a population. A. Kittilä (N=88), B. Ammarnäs (N=97), C. Tydal (N=47), D. Kittilä, Ammarnäs and Tydal pooled (N=232). E. Museum clutches

collected in the period 1881-1940 (N=262). F. A brambling clutch with three host eggs and one cuckoo egg (top). The cuckoo eggs in A-D were all found in brambling nests in Kittilä in 2005-2008. Cuckoo eggs in E (N=68) were subjectively classified to belong to a *Fringilla* cuckoo egg morph. The figure indicates that the color of the cuckoo eggs are close to their optimum in Kittilä, and also that local adaptation by the cuckoo is either absent or occurs at the larger geographic scale.

Figure 4: Distribution of chroma (saturation) of brambling (A, C) and chaffinch clutches (B, D). Left column (A, B) gives the distribution of chroma for fresh brambling and chaffinch clutches. Black triangles indicate the chroma of five cuckoo eggs found in brambling nests in Kittilä in 2005-2008. Right column (C, D) gives the distribution of chroma for brambling and chaffinch clutches collected in the period 1881-1940. Black superimposed columns in C-D show the distribution of chroma for 68 cuckoo eggs from the same period which were classified to belong to a *Fringilla* cuckoo egg morph.

Figure 5: Forms of selection on the longitudinal (θ) hue component of hypothetical cuckoo eggs imposed by brambling (A) and chaffinch (B-F) egg distributions. The curves are drawn by cubic spline interpolation and are based on 3000 egg colors that were drawn from within the tetrachromatic color space of each of the hosts to obtain a uniform distribution of θ-values. The mean acceptance probability of each cuckoo egg is based on matching with 232 brambling clutches (A), 157 chaffinch clutches (B), and various subsets of the 157 chaffinch clutches (C-F). Insets show the hue distribution (Robinson projection) of the host clutches in each case. C-F indicates the effect of an increase in the bimodality or skew of the chaffinch's hue distribution. C: Chaffinch clutches with θ-values between 30th and 50th percentiles excluded. D: Clutches with θ-values between 40th and 60th percentiles excluded. E: Clutches with θ-values between 50th and 70th percentiles excluded. F: Clutches with θ-values between 30th and 70th percentiles excluded.

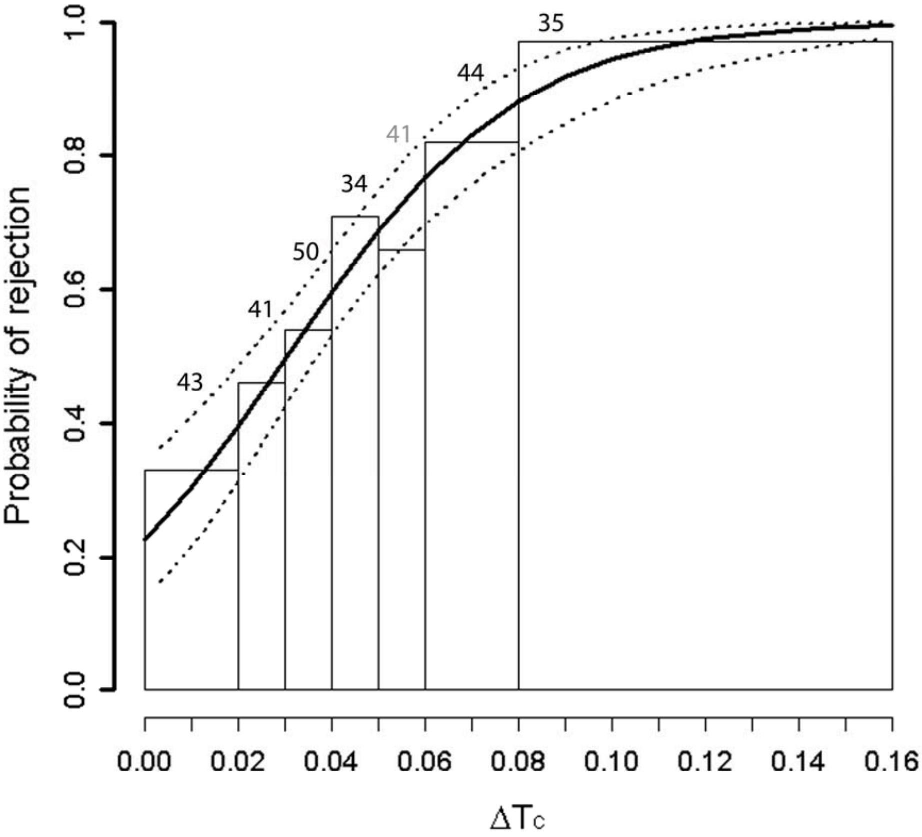

Probability of rejection
0.0
0.2
0.4
0.6
0.8
1.0
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
ΔTc
43
41
50
34
41
44
35

FIGURE 1

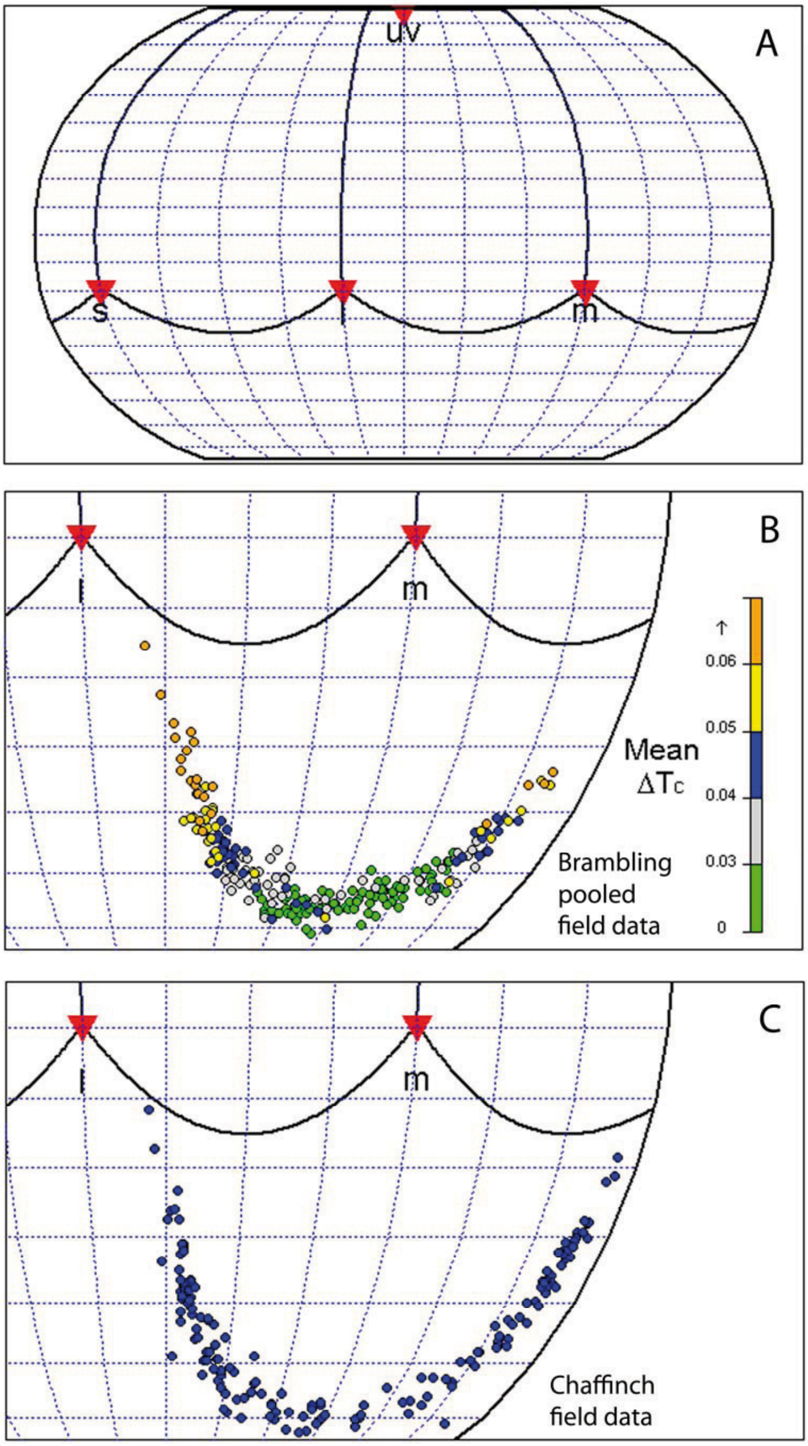
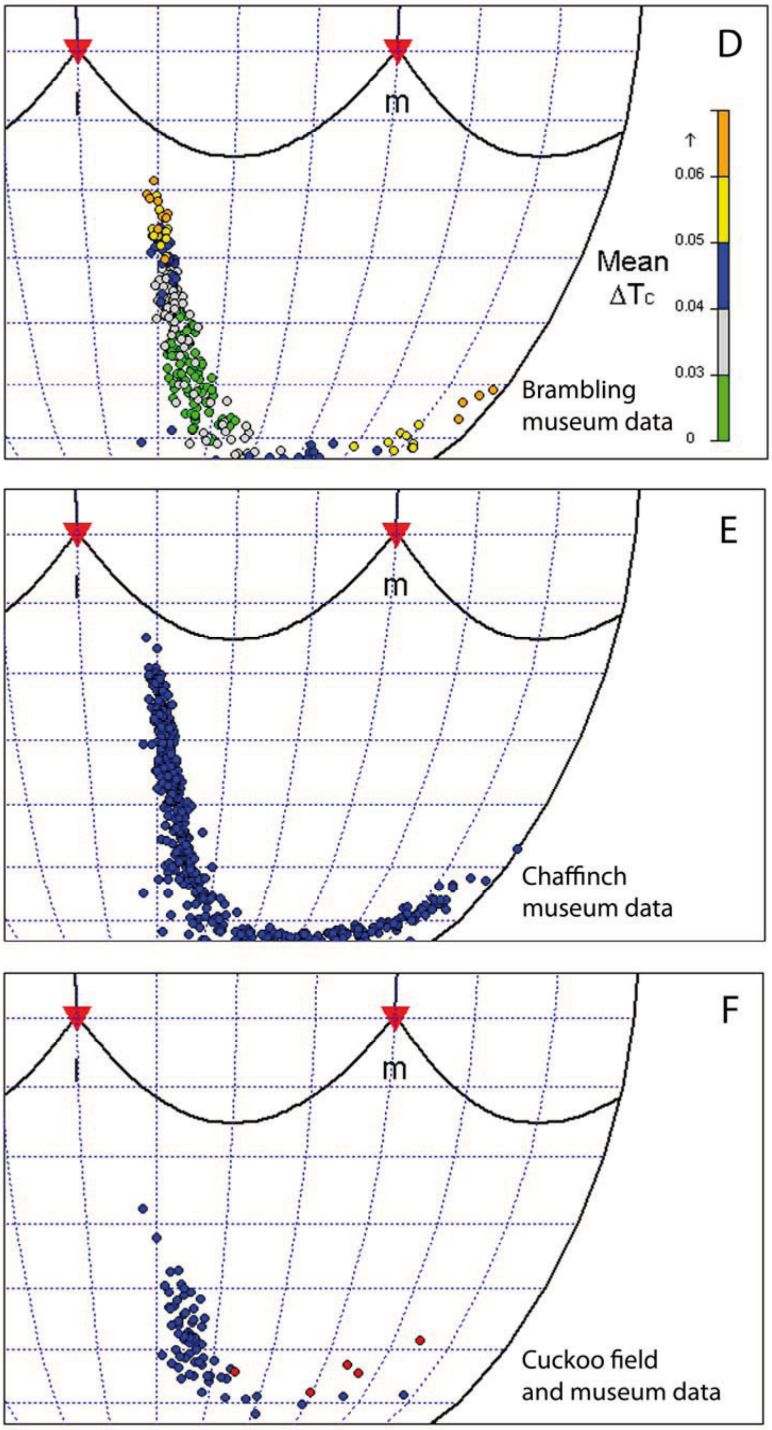

uv
A
s
l
m
B
l
m
↑
0.06
0.05
Mean
ΔTc
0.04
0.03
0
Brambling
pooled
field data
C
l
m
Chaffinch
field data

FIGURE 2, A-C


D
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0.06
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0
Mean
ΔTc
Brambling
museum data
E
l
m
Chaffinch
museum data
F
l
m
Cuckoo field
and museum data

FIGURE 2, D-F

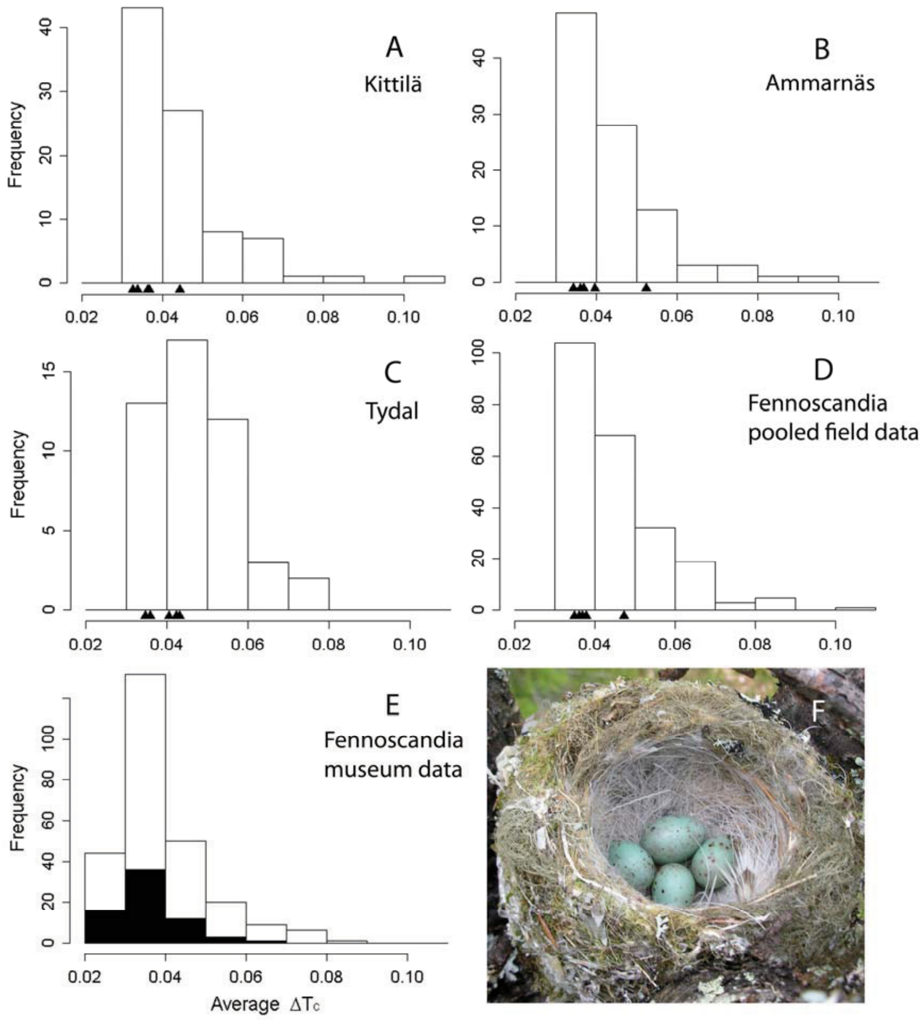
A
Kittilä
Frequency
0
10
20
30
40
0.02
0.04
0.06
0.08
0.10
B
Ammarnäs
0
10
20
30
40
0.02
0.04
0.06
0.08
0.10
C
Tydal
Frequency
0
5
10
15
0.02
0.04
0.06
0.08
0.10
D
Fennoscandia
pooled field data
0
20
40
60
80
100
0.02
0.04
0.06
0.08
0.10
E
Fennoscandia
museum data
Frequency
0
20
40
60
80
100
0.02
0.04
0.06
0.08
0.10
Average ΔTc
F

FIGURE 3

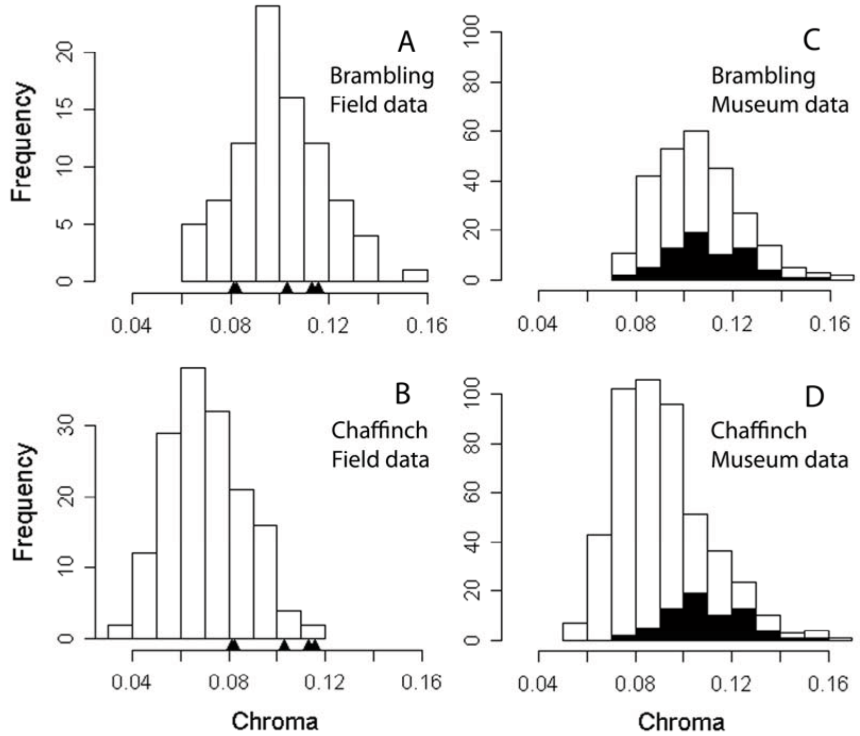
A
Brambling
Field data
B
Chaffinch
Field data
C
Brambling
Museum data
D
Chaffinch
Museum data
Frequency
Chroma
0.04
0.08
0.12
0.16
0
5
10
15
20
30
40
60
80
100

FIGURE 4

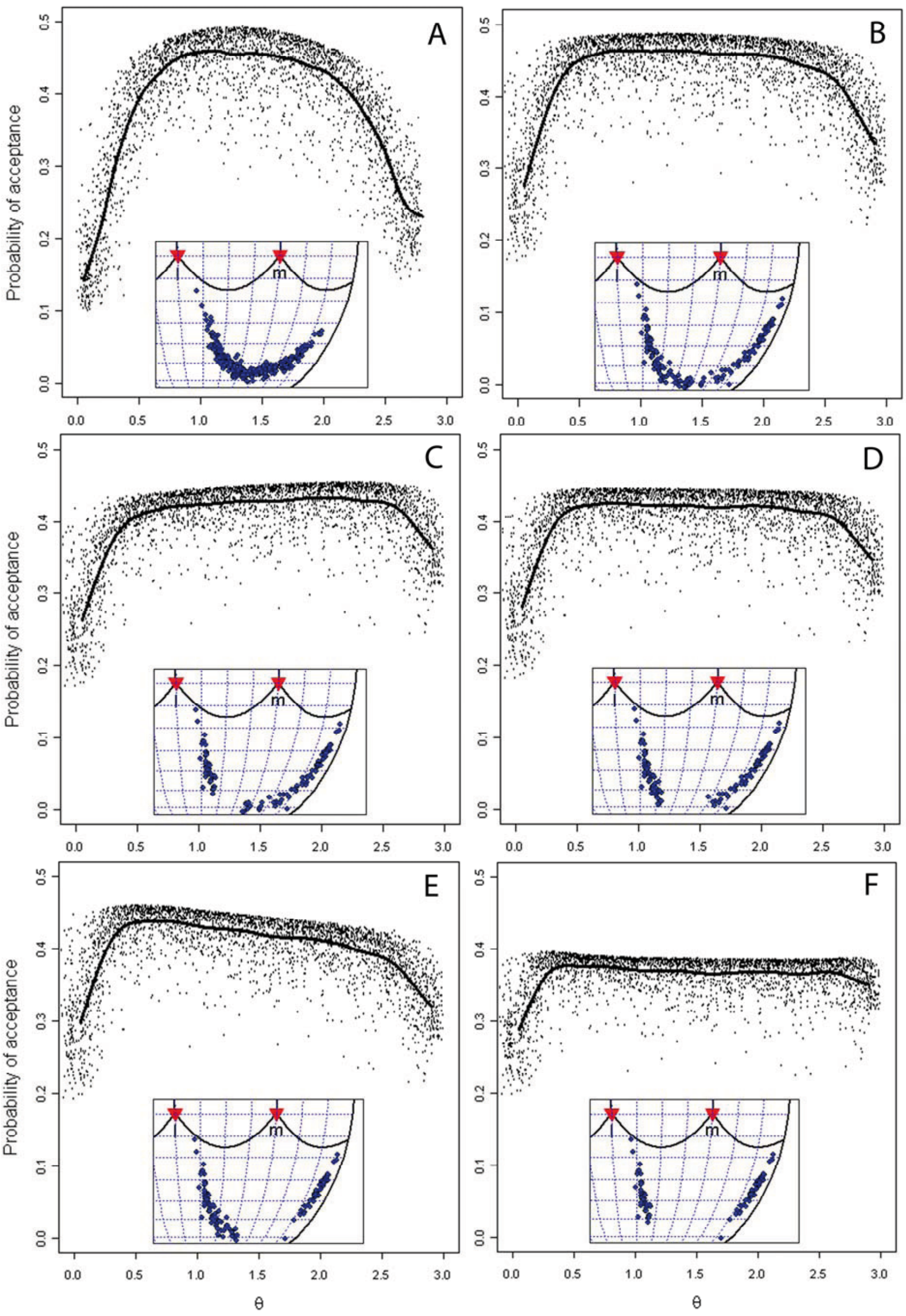
A
B
C
D
E
F
Probability of acceptance
0.0
0.1
0.2
0.3
0.4
0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
θ
l
m

FIGURE 5

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

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

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

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

1994 Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994 Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994 Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995 Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995 Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995 Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995 Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995 Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996 Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996 Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996 Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
1996 Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997 Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.

1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.
1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)

1999 Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999 Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999 Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999 Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999 Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999 Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999 Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999 Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999 Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999 Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999 Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999 Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999 Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999 Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000 Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000 Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000 Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000 Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000 Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000 Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway

2000 Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001 Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001 Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001 Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001 Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002 Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002 Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002 Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002 Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002 Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002 Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002 Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002 Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002 Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002 Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003 Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003 Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003 Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003 Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003 Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003 Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003 Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003 David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003 Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective

2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia

2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	Ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, */Mamestra Brassicae/* L. (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry

2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, */Taeniopygia guttata/*
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhu/*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania

2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers