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ORIGINAL PAPER

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 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 selection against rejection behaviour is likely to be very weak. 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. This result is 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.

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Introduction

The common cuckoo *Cuculus canorus* (hereafter cuckoo) and its passerine hosts experience 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 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 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; Lindström 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 (68°N, 25°E), Tana in Finnmark province, north-eastern Norway (70°N, 28°E), Ammarnäs in Västerbotten province, north-western Sweden (66°N, 16°E), and Tydal, eastern part of Sør-Trøndelag province, Central Norway (63°N, 12°E). 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 1,100 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, personal communication; 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

Fig. 1 Map of Fennoscandia showing the location of the four study populations. Kittilä is a parasitised population, whereas the other populations are not currently parasitised

[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. Heterospecific eggs were used because conspecific eggs were not always available when an experiment was about to be conducted. Because bramblings have a high interclutch variation in egg appearance (Fig. 2), conspecific eggs provide an opportunity to test responses against a wide 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). We have shown in a separate study 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). Analyses performed on datasets in which one of the two trials was randomly excluded show that conclusions based on the full data set (i.e. including all individual replicates) are very robust (see "Results").

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 3 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 5 days to determine the response. We defined the parasitic egg as

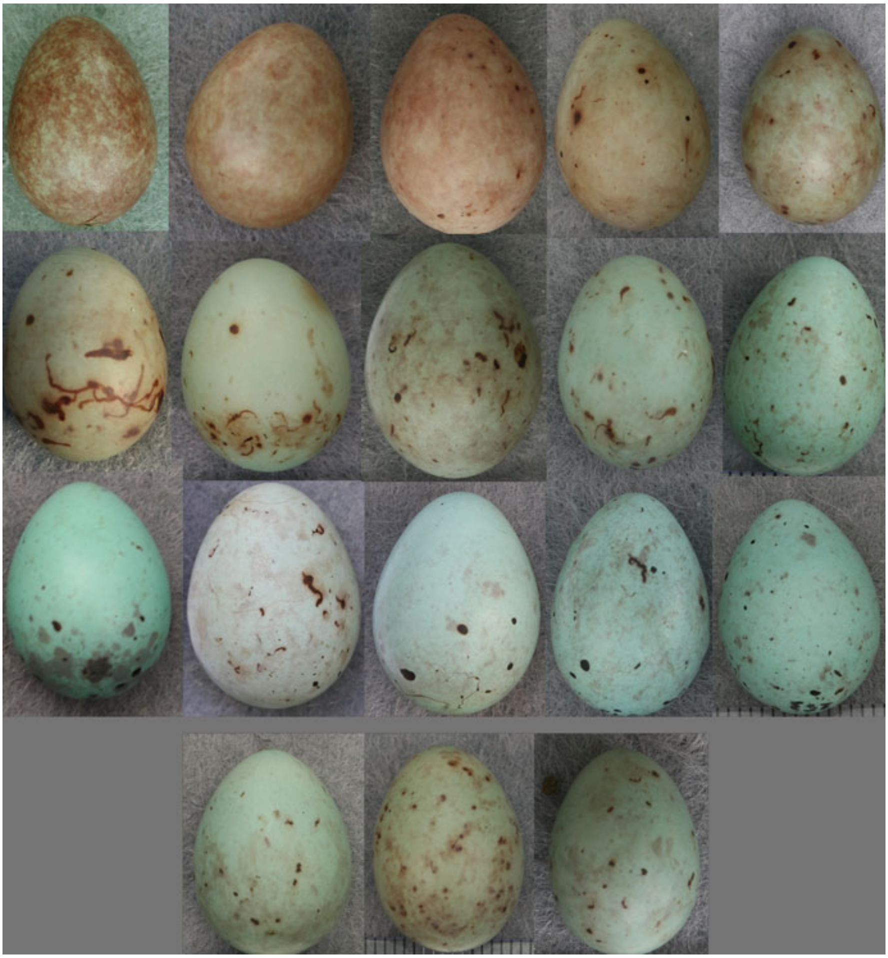

Fig. 2 Plate indicating the range of variation of brambling clutches (*rows 1–3*). Each egg represents a different clutch ($N = 15$). *Bottom row* provides examples of cuckoo eggs found in brambling nests in Kittilä. The eggs are not scaled according to relative sizes

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 5 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 parasitic egg, whereas a rejection error is defined as rejection of own egg(s) but not the parasitic 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 min 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 of the spectrum 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 since spectrophotometry-derived values measure only background colour and luminance. 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 parasitic egg, difference in volume (Hoyt (1979)) and shape (length/breadth, Picman 1989) 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 contrast and either of shape and volume ($r_s < |0.07|$), but shape and volume were significantly correlated ($r_s = 0.29$, $P < 0.0001$). Moreover, contrast, ΔT_C, and ΔT_B were strongly intercorrelated (contrast and ΔT_C: $r_s = 0.67$, $P < 0.0001$; contrast and ΔT_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 4 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 3.7% (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 nineteenth 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 24 h, 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).

Table 1 Natural parasitism, responses against cuckoo dummies and parasitic eggs in four brambling populations in Fennoscandia

Population	Parasitism rate (# nests)[a]	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	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 1890s–1930s[b,e]	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[c]	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[d], 3 records 40 km northeast of study area 1948–1949[e]	2.21 (0.68)	−2.71 (0.79) [−4.25,−1.16] 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)

Parameter estimates (slopes) with 95% confidence intervals 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

[a] Calculated using nests that were checked at least once close to clutch completion or later

[b] Rosenius (1929), Montell (1917), Wasenius (1936)

[c] Cards available at Gothenburg Natural History Museum

[d] Moksnes and Røskaft (1987), Braa et al. (1992)

[e] 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

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 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 similar across populations (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 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%, $N = 22$).

Since some of the nests were sampled twice, we performed a resampling analysis to evaluate the robustness of the population comparison. For each population, we included all nests where only one trial was conducted. In addition, for nests where two trials were conducted, we included one randomly selected trial. For Tana, all 112 trials were included (since no individual was sampled twice in this population). We then ran a logistic ANCOVA (binary response) with contrast, population and their interaction as explanatory

Table 2 Generalised linear models of the probability of accepting parasitic eggs (0 = reject, 1 = accept) in bramblings

Variable	*N*	df	Deviance	*P*
Model 1				
Contrast	302	1	109.7	<0.0001
Population		3	4.17	0.24
Volume		1	0.63	0.43
Shape		1	0.13	0.72
Volume × population		3	5.47	0.14
Contrast × population		3	3.79	0.29
Shape × population		3	2.39	0.5
Model 2				
ΔT_C	144	1	29.0	<0.0001
ΔT_B		1	9.05	0.003
Population		2	0.41	0.81
ΔT_B × population		2	6.00	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

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. ΔT_C and ΔT_B are chromatic and achromatic contrast, respectively, between the colours of host and parasitic eggs. See "Methods" for further details

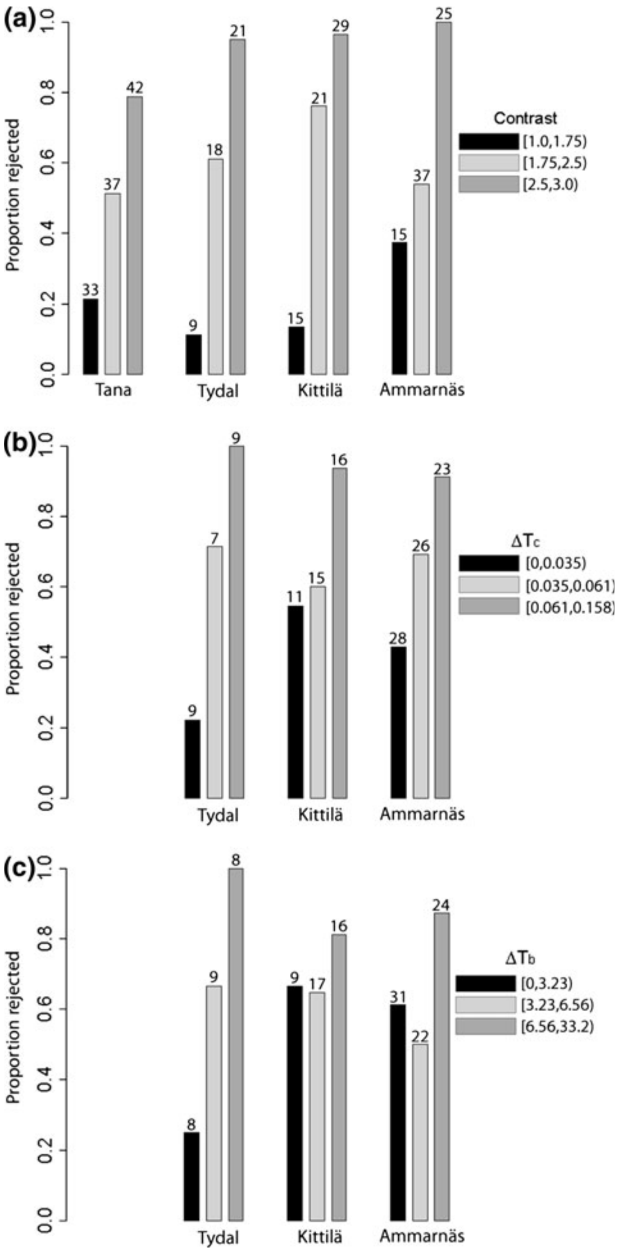

Fig. 3 Rates of rejection of parasitic eggs in four brambling populations for different extents of similarity between host and parasitic egg as measured by **a** Contrast, **b** ΔT_C **c** ΔT_B (see "Methods"). Sample sizes above the bars. ΔT_C and ΔT_B are chromatic and achromatic contrast, respectively, between the colours of host and parasitic eggs. Categories were defined by the 33.3 and 66.7% percentiles of the respective distributions. Note that categories were created only for illustrative purposes

variables. The *P*-values for "Population" and "Contrast × Population" were extracted in each repeat. The Population term had a *P*-value <0.05 in one of the 1,000 runs, whereas the interaction term had a *P*-value >0.05 in all the runs. The mean *P*-values for the population and interaction terms were 0.33 and 0.44, respectively. This shows that conclusions based on the full dataset are robust (i.e. there are no notable population differences in the intercept or slopes).

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 ($\chi^2 = 11.6$, df = 1, $P < 0.0001$).

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% (1/119) 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, Tana and Kittilä in the proportion of host pairs that behaved aggressively against the cuckoo dummy (Tydal: 19/23; Tana: 77/93; Kittilä: 8/10; $\chi^2 = 0.05$, df = 2, $P = 0.98$).

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 (Martín-Gálvez 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. Although the sample size for the parasitised population was low, this suggests that 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, Moskát 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 it shows 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). In addition, when populations are not independent evolutionary units, intense egg rejection can be maintained in non-parasitised populations even if rejection behaviour incurs fitness costs (Rothstein 2001; Stokke et al. 2002; Soler et al. 1999). 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 very low. 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 (Swynnerton 1918; Brooke and Davies 1988; 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, BG Stokke, H Jensen, D Fainová, E Bellinvia, F Fossøy, JR Vikan, J Bryja, M Soler submitted ms), 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).

Although data on the occurrence of natural parasitism is scant, it is worth discussing why bramblings are not parasitised in the three alpine birch forests (i.e. Ammarnäs, Tana, Tydal) and if there exist factors that can predict a general geographical pattern of parasitism. Host density and temporal variations in density are likely to influence the establishment of cuckoo host races (Soler et al. 2009; Stokke et al. 2007a). In the birch forests of the Scandinavian mountain chain, the brambling shows a numerical response to larval abundance of the defoliating geometrid moth *Epirrita autumnata*, which results in marked fluctuations in brambling abundance with 10–11 years intervals between peaks (Enemar et al. 2004; Hogstad 2000, 2005; Lindström 1987). By contrast, in an old growth spruce forest in Finnish Lapland, the brambling ranks among the most stable host species (Virkkala 1989). However, average density tends to be higher in mountain birch forests (Hogstad and Väisänen 1997), and this could potentially compensate for the large fluctuations in abundance. It is also likely that variation in brambling productivity is higher in mountain birch forests. In Ammarnäs, for example, the yearly variation in brambling per capita productivity (number of juveniles per adult trapped) was explained to 30–40% by the abundance of *E. autumnata* larvae (Lindström et al. 2005, see also Hogstad 2005). Moreover, bramblings have also been observed to desert their nests *en masse* (including nests with chicks) during inclement weather if *E. autumnata* abundance is low (Hogstad 2000). Thus, it can be hypothesized that fluctuations in brambling density and/or productivity makes it more difficult for the brambling host race to maintain viable populations in mountain birch forests (i.e. Ammarnäs, Tana, Tydal) than in boreal coniferous forests (i.e. Kittilä). Differences in vegetation structure could also affect whether cuckoos are able to parasitise bramblings profitably. For example, spruces are likely to provide better cover for cuckoo females than birches, especially in early season before leafing. Tall stands of spruce might also be superior vantage points that enable more efficient nest search and monitoring. Finally, parasitism could be more prevalent in Finnish Lapland simply because this area is closer to the centre of distribution for bramblings (Cramp and Perrins 1994; Hogstad and Väisänen 1997), implying that the rate of colonisation of this area might be higher than for areas towards the periphery of the distribution.

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 possible 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 other than host defences.

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