

Meadow pipit (*Anthus pratensis*) egg appearance in cuckoo (*Cuculus canorus*) sympatric and allopatric populations

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Host populations tend to show less ability to discriminate against parasites when living in their absence. However, comparison of rejection rates among sympatric and allopatric host populations does not allow determination of whether the greater tolerance in allopatric populations reflects a genetic change or phenotypic plasticity. Here we test the existence of changes in a host's adaptation to brood parasitism in the absence of parasitism by studying intraclutch variation in egg appearance, which is a genetically determined component of host defence favouring discrimination of parasitic eggs. We investigated egg phenotypes of a common host of the European cuckoo, *Cuculus canorus*, in the presence and in the absence of cuckoos. By using objective spectroradiometry techniques of colour assessment we compared intraclutch variation between populations of meadow pipit, *Anthus pratensis*, sympatric (England) and allopatric (Iceland and Faeroe Islands) with *C. canorus*. Allopatric populations of *A. pratensis* showed greater intraclutch variation in egg appearance in the ultraviolet part of the spectrum than did a population sympatric with *C. canorus*. Two possible alternative mechanisms explaining these findings are discussed. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, 79, 543–549.

ADDITIONAL KEYWORDS: adaptation – brood parasitism – cost of defence – cuckoo – genetically determined defence.

INTRODUCTION

Avian brood parasitism constitutes a well-studied example of the coevolutionary process (Rothstein, 1990; Davies, 2000; Soler & Soler, 2000). Brood parasitism is a form of breeding biology in which certain individuals (parasites) receive parental care from unrelated individuals (hosts). Hosts of brood parasitic species usually suffer reduced reproductive output from a successfully parasitized nest (Røskoft, Orians & Beletsky, 1990; Soler, Martínez & Soler, 1996; Payne, 1997). Therefore, parasitism should favour the evolution of host defences, and of more sophisticated techniques by the cuckoo to overcome them (Davies & Brooke, 1988). This coevolutionary 'arms race' leads to intricate adaptations and counter-adaptations by both

sides with each party responding to the selective forces imposed by the other (Dawkins & Krebs, 1979; Soler & Møller, 1990). It is assumed that selection of cuckoo eggs to match those of their host requires the hosts to discriminate cuckoo eggs from their own, thus increasing egg mimicry by the cuckoo and egg discrimination by the host (Davies & Brooke, 1988).

The meadow pipit, *Anthus pratensis*, is a small passerine widely distributed across the north Palaearctic region (Cramp & Perrins, 1988). It constitutes one of the favourite hosts of the European or common cuckoo, *Cuculus canorus*, in moorland and heathland in Europe (Davies, 2000). *C. canorus* is divided into at least 16 host-specific races or gentes (Wyllie, 1981; Álvarez, 1994; Moksnes & Røskoft, 1995), the females of each race laying a distinctive egg type that tends to match the host's eggs (Gibbs, Brooke & Davies, 1996; Gibbs *et al.*, 2000). There is a specific *C. canorus* which specializes in *A. pratensis*, laying a brownish grey

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egg, with grey or brown spots, while *A. pratensis* shows rejection of *C. canorus* eggs (Davies & Brooke, 1989a; Moksnes, Røskaft & Korsnes, 1993), suggesting that in the coevolutionary arms race between *C. canorus* and *A. pratensis* both parties have evolved adaptations and counter-adaptations to enhance their reproductive output.

C. canorus breeds across the Palaearctic region, but it is absent from Iceland and the Faeroe Islands, where it is only a rare vagrant that has never been recorded as a breeder (Cramp & Simmons, 1985). Both Iceland and the Faeroe Islands have, however, breeding populations of *A. pratensis* (Cramp & Perrins, 1988) with evidence of gene flow from Scandinavian and British populations, since neither Iceland nor the Faeroe Islands had breeding populations of *A. pratensis* during glaciations (Einarsson, 1968). In addition, populations of *A. pratensis* on Iceland and the Faeroe Islands have not diverged markedly from European populations since they all belong to the same subspecies (Cramp & Perrins, 1988). There is no indication in the literature suggesting that Iceland has been a suitable breeding site for *C. canorus* since the Viking arrival on the island in 874 AD that led to the devastation of the original forests (Einarsson, 1968). An experimental study by Davies & Brooke (1989a) showed that *A. pratensis* in Iceland had previously been in contact with *C. canorus* parasitism since they rejected non-mimetic eggs when artificially parasitized. However, it remains unclear if the persistence of this rejection behaviour is due to *C. canorus* formerly being a common nester in Iceland or to the existence of gene flow from parasitized *A. pratensis* populations in other parts of Europe (see discussion in Davies & Brooke, 1989a).

Davies & Brooke (1989a) compared the rejection behaviour against non-mimetic eggs introduced into *A. pratensis* nests in Iceland and England to analyze if the duration of sympatry with *C. canorus* determines changes in host defences. A total of 18% of *A. pratensis* rejected non-mimetic eggs in Iceland where *C. canorus* is always absent, while in England, where *C. canorus* often parasitizes *A. pratensis*, and there is a race of *C. canorus* laying eggs mimicking those of *A. pratensis*, non-mimetic eggs were rejected from 48% of the nests (Davies & Brooke, 1989a). The authors concluded that Iceland was colonized by *A. pratensis* that had subsequently partially lost defences to parasitism.

The arms-race hypothesis assumes that, after the fixation of rejection behaviour in hosts, one step in the coevolution between cuckoo and host would be selection for a reduction in intraclutch variation in egg appearance among hosts (Øien, Moksnes & Røskaft, 1995; Soler & Møller, 1996). This reduction in intraclutch variation would favour discrimination of para-

sitic eggs from own eggs when colour mimicry of the cuckoo's egg has been perfected (Victoria, 1972; Davies & Brooke, 1989b). Furthermore, host individuals that lay eggs with more extreme phenotypes will less often be subject to successful parasitism, thereby increasing variation between clutches of different host individuals (Soler & Møller, 1996). Most evidence for a relationship between intraclutch variation and egg recognition in avian brood parasite systems is based on tests of whether passerine species involved in a coevolutionary arms race with the cuckoo show a low degree of intraclutch variation, and, secondly, whether species showing a high frequency of egg rejection have low intraclutch variation compared with species with low rejection rates (Øien *et al.*, 1995; Soler & Møller, 1996; Stokke, Moksnes & Røskaft, 2002). The intraspecific approach also supports the relationship between intraclutch variation and egg recognition, because rejecter individuals within a host population have less intraclutch egg variation in colour than do acceptor individuals (Stokke *et al.*, 1999; Soler, Soler & Møller, 2000), suggesting that differences in intraclutch variation within a species might also be relevant in terms of the arms-race hypothesis.

Maintenance of a low level of intraclutch variation in a host population might be costly to the host when there is a high risk of mistakenly rejecting one's own egg instead of the cuckoo egg. In accordance with this idea, Lotem, Nakamura & Zahavi (1992) found that the acceptance of *C. canorus* eggs by female great reed warblers, *Acrocephalus arundinaceus*, in a Japanese population occurred mainly among young breeders. The naive first-year breeders need time to learn to recognize their own eggs, and thus do not eject a parasitic egg as fast as do older individuals. Thus a high level of intraclutch variation in host egg appearance may cause inexperienced hosts to make recognition errors if they attempt egg rejection.

In this paper we study to what extent the host of an obligate brood parasite such as *C. canorus* retains defences against parasitism when parasitism is no longer occurring. Host populations tend to show less discriminatory abilities against parasitic eggs when they are isolated from brood parasites (Davies & Brooke, 1989a; Cruz & Wiley, 1989; Soler & Møller, 1990; Briskie, Sealy & Hobson, 1992). However, comparison of rejection rates among populations does not permit identification of whether this greater tolerance reflects a genetic change or phenotypic plasticity. The aim of the present study is to test for a decline of one adaptation by studying a genetically determined component of host defences. We specifically focus on retention of intraclutch variation in egg appearance as a defence against *C. canorus* parasitism. By using objective techniques of colour assessment within clutches we compare intraclutch variation in *A. pratensis*

between populations in England (sympatry) and Iceland and the Faeroe Islands, where *C. canorus* is absent (allopatry).

METHODS

Data on 48 *A. pratensis* clutches (Faeroe = 19 clutches, Iceland = 10 clutches and England = 19 clutches) were obtained from the egg collections at the Zoological Museum in Copenhagen (Denmark) and the British Museum of Natural History. The clutches of *A. pratensis* in allopatry with *C. canorus* had been collected during several expeditions to Iceland and the Faeroe Islands between 1880 and 1920, and the clutches of *A. pratensis* from sympatric populations, which were from Surrey in England, had been collected between 1900 and 1914.

Previous analyses of intraclutch variation in egg appearance in avian brood parasite system studies have been based on human assessment of host egg similarity within a clutch using an arbitrary scale ranging from 1 to 5 (Lotem, Nakamura & Zahavi, 1995; Øien *et al.*, 1995; Soler & Møller, 1996; Stokke *et al.*, 1999; Stokke *et al.*, 2002), or by using photographs and image analysis (Soler *et al.*, 2000). However, avian colour vision differs substantially from that of humans (Cuthill *et al.*, 2000). In fact, most diurnal birds have at least four kinds of photo pigments in the cones of their eyes (Bowmaker *et al.*, 1997), including a spectrally sensitive peak near the ultraviolet (UV) part of the spectrum (Chen, Collins & Goldsmith, 1984; Cuthill *et al.*, 2000). Furthermore, using UV-visible reflectance spectrophotometry, Cherry & Bennett (2001) recently found that the eggs of the red-chested cuckoo, *Cuculus solitarius*, and its African hosts were highly matched for chromatic aspects of eggs invisible to humans. Consequently, reflectance spectra in the range 300–700 nm were obtained from all the eggs of the 48 analyzed clutches using a spectroradiometer (Ocean Optics, Europe). Colour was measured twice in two arbitrarily selected c. 1-mm² areas of the surface of the eggs. The illuminant was a deuterium and halogen light source (DH 2000). The light was transferred to the eggs through a quartz optic fibre (Ocean Optics) and reached the eggs at an angle of 45°. The sampling optic was placed at an angle of 45° to the surface of the sample and was connected to a spectrometer (S2000) by a second quartz fibre-optic cable. Data from the spectroradiometer were converted into digital information by DAQ Card 700 and passed into a computer with appropriate software (Spectrawin 4.1). The measurements were relative and referred to a standard white reference (WS-2) and to darkness. A reference and dark calibration were made prior to the beginning of measurement of each clutch. Total reflectance was obtained over a

100-nm part of the UV region (R_{300–400}), and at 75-nm intervals in the human visible region corresponding to blue (R_{400–475}), green (R_{475–550}), yellow (R_{550–625}) and red (R_{625–700}) wavelengths. Objective reflectance parameters relevant to an avian perceptual colour space were also computed from these total reflectance values. The total intensity of light reaching the avian eye from the egg (brightness, *sensu* Endler, 1990) was the sum of the total reflectance values for all the UV and visible wavelength intervals (R_{300–700}). Reflectance ratios (R_{300–400}/R_{300–700}; R_{400–475}/R_{300–700}; R_{475–550}/R_{300–700}; R_{550–625}/R_{300–700} and R_{625–700}/R_{300–700}, respectively) were used as estimations of ‘UV chroma’, ‘blue chroma’, ‘green chroma’, ‘yellow chroma’ and ‘red chroma’ (see Sheldon *et al.*, 1999). The wavelength of the peak reflectance (λ (R_{max})) over the entire avian visible spectrum (300–700 nm) was used as an estimation of hue (Endler, 1990).

Consistency of colour estimations in our study was tested by means of repeatability analyses (Falconer & Mackay, 1996). First, we measured twice in the same arbitrarily selected area of a single egg and found a high repeatability for all variables except hue (Table 1). Second, we measured each egg in two randomly selected areas and also found a non-significant repeatability for hue with the remaining colour variables being highly repeatable (Table 1). Consequently, we excluded hue from subsequent analyses and calculated from the four measurements of each egg one mean value of brightness, UV chroma, blue chroma, green chroma, yellow chroma and red chroma for each egg.

We calculated the coefficient of variation (CV = standard deviation/mean × 100) from mean values per egg

Table 1. Estimated repeatability for colour measurements of *A. pratensis* eggs (N = 235 eggs from 48 clutches)

Colour characteristic	Same surface	Two different surfaces
Brightness	0.98**	0.92**
Ch _{UV}	0.95**	0.72**
Ch _B	0.98**	0.95**
Ch _G	0.99**	0.94**
Ch _Y	0.97**	0.89**
Ch _R	0.99**	0.94**
Hue	0.00 ^{NS}	0.04 ^{NS}

Two measurements were taken from one randomly selected surface of the egg, and from two randomly selected areas of the same egg.

Ch_{UV}, Ch_B, Ch_G, Ch_Y and Ch_R = estimation of chroma for ultraviolet, blue, green, yellow and red regions, respectively, of the avian visible spectrum. ** = P < 0.001. ^{NS} = P > 0.05.

of all colour variables in each clutch as a measure of intraclutch variation.

STATISTICAL ANALYSES

We tested whether intraclutch variation of the colour variables of *A. pratensis* eggs were normally distributed. Transformation of variables was not required because all intraclutch colour variables fitted normality assumptions (Kolmogorov–Smirnov tests for continuous variables, $P > 0.20$ in all six cases). Because colour variables are typically interrelated (Endler, 1990), we used multivariate analysis of variance (MANOVA) as an a priori test (Scheiner, 2001) to analyze differences in egg appearance between populations of *A. pratensis* sympatric and allopatric with *C. canorus*. *A. pratensis* intraclutch variation in egg appearance did not significantly vary between the two allopatric populations in Iceland and the Faeroe Islands (Wilks' lambda = 0.78, d.f.₁ = 6, d.f.₂ = 22, $P = 0.43$), and consequently we pooled the Iceland and Faeroe Island clutches. Two tailed *t*-tests were used for post hoc testing. To avoid type-I errors we applied Bonferroni correction for multiple comparisons with the adjusted level of significance at 10% being 0.02 (Chandler, 1995). In all analyses equality of variances was checked using Levene's test.

RESULTS

Intraclutch variation in egg appearance differed between sympatric and allopatric populations of *A. pratensis* (Wilks' lambda = 0.68, d.f.₁ = 6, d.f.₂ = 41, $P = 0.012$). In accordance with the hypothetical relaxation of host defences to parasitism, intraclutch variation in UV chroma was significantly higher in Iceland and the Faeroe Islands than in England where *C. canorus* still parasitizes *A. pratensis* (Table 2, Fig. 1). Variation within clutches for the remaining colour components (blue chroma, green chroma, yellow chroma, red chroma and brightness) did not vary significantly between sympatric and allopatric populations of *A. pratensis* (Table 2, Fig. 1).

DISCUSSION

Previous results showing a decline in rejection rates in the absence of parasitism in avian brood parasite studies do not allow identification of whether this greater tolerance reflects a genetic change or phenotypic flexibility (Rothstein, 2001). As far as we know our study constitutes the first test of the loss of a host defence in the absence of parasitism in an avian brood parasite for a genetically determined component of host defence (Victoria, 1972; Collias, 1984, 1993). Our results provide direct evidence supporting a lower

Table 2. Analyses of effects of sympatry vs. allopatry with *C. canorus* on egg colour appearance within clutches of *A. pratensis*

Colour characteristic	<i>t</i>	d.f.	<i>P</i>
Brightness	1.39	46	0.16
Ch _{UV}	2.41	46	0.02*
Ch _B	0.02	46	0.98
Ch _G	0.42	46	0.67
Ch _Y	0.50	46	0.61
Ch _R	0.06	46	0.94

*Significantly different with sequential Bonferroni adjustment. Ch_{UV}, Ch_B, Ch_G, Ch_Y and Ch_R = estimation of chroma for ultraviolet, blue, green, yellow and red regions, respectively, of the avian visible spectrum.

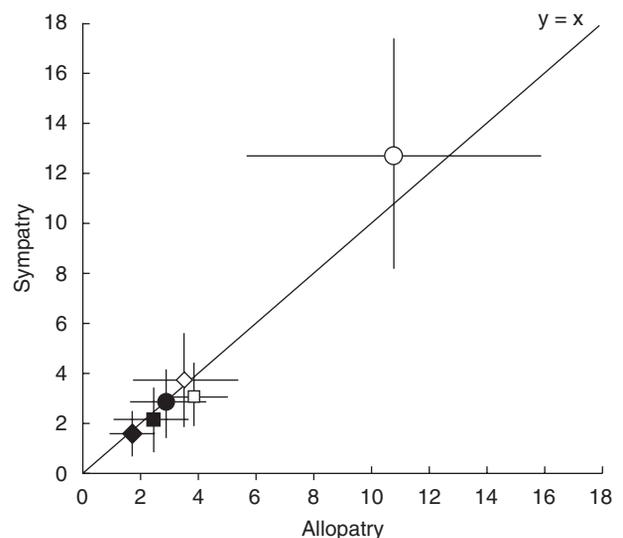


Figure 1. Mean (\pm standard deviation) variation in ultraviolet chroma (\square), blue chroma (\diamond), green chroma (\blacksquare), yellow chroma (\blacklozenge), red chroma (\bullet) and brightness (\circ) within clutches in *A. pratensis* populations sympatric and allopatric with *C. canorus*.

level of host defences in *A. pratensis* in the absence of *C. canorus* parasitism. We measured, using spectroradiometry techniques considering the complete avian range of vision (300–700 nm), the appearance of host eggs within clutches of *A. pratensis* in allopatry and in sympatry with *C. canorus*. We detected larger intraclutch variation in colour appearance in the UV part of the spectrum in populations of *A. pratensis* allopatric to *C. canorus* populations compared with that of a sympatric population ($r^2 = 11.21\%$, intermediate effect size according to Cohen (1988)).

Previous studies compared the rejection behaviour against non-mimetic eggs in *A. pratensis* nests in Iceland and England to analyze if time of sympatry with *C. canorus* affected the level of host defences (Davies & Brooke, 1989a). However, the comparison of rejection rates from the two populations may not be the best way to detect a change of host defences since variation in host response to different levels of cuckoo parasitism may exist (Brooke, Davies & Noble, 1998). The experiments in Iceland were made in the absence of *C. canorus*, while in England *A. pratensis* had encountered *C. canorus* during the breeding season. Moreover, Moksnes *et al.* (1993) found that rejection rates of *A. pratensis* in Norway of both mimetic and non-mimetic eggs increased to more than 32.0% with a *C. canorus* dummy mounted beside the nest. Consequently, the detected decrease of host defences to *C. canorus* parasitism in Iceland by Davies & Brooke (1989a) might be explained by phenotypic plasticity.

The higher intraclutch variation in egg appearance in *A. pratensis* populations allopatric with *C. canorus* might be the consequence of the loss of defence in the absence of *C. canorus* parasitism. Theoretical studies have proposed that in the absence of parasitism the costs of recognition errors are the only ones that may counteract the benefits of rejection and this may explain the loss of a defence (Lotem *et al.*, 1992, 1995). However, Rothstein (2001) stated that no clear evidence exists of recognition errors at unparasitized nests in avian brood parasite studies, suggesting that available data from the literature are consistent with the maintenance of host defences. Moksnes *et al.* (1993) studied the rejection behaviour of unparasitized *A. pratensis* nests in Norway in the presence and absence of a *C. canorus* dummy and failed to find differences in the rejection rate. This would suggest that recognition errors, if they exist, should be negligible in unparasitized *A. pratensis* nests. However, we can not preclude this possibility since differences among populations in the level of recognition errors may exist and no information on the occurrence of such costs exists for the British *A. pratensis* population.

An alternative explanation is that patterning of *A. pratensis* eggs in allopatry with *C. canorus* populations has not changed from the ancestral state, and that higher intraclutch variation in the islands is a result of genetic drift in the absence of *C. canorus* parasitism maintaining this trait favoured by a very low level of gene flow between populations. Information about the level of mimicry between *C. canorus* eggs and those of the ancestors of current *A. pratensis* populations in Iceland and the Faeroes is lacking. Thus, according to this idea, a reduction in intraclutch variation has never been selected for in island *A. pratensis* populations because there was a bad match between the appearance of the *C. canorus* eggs and the appear-

ance of the eggs of the ancestors of the current *A. pratensis* on the islands. In accordance with this, Davies & Brooke (1989a) did not find evidence of gene flow between Iceland and continental populations of *A. pratensis* after analyzing the Iceland ringing recoveries for the species. Moreover, measurements of Icelandic and British *A. pratensis* in museums also showed significant differences in size, which may indicate genetic differences (Davies & Brooke, 1989a).

Nonetheless, *A. pratensis* still rejects in areas of allopatry with *C. canorus* even when no recent history of co-occurrence is known (Davies & Brooke, 1989a). Interestingly, they rejected five of the ten redstart type models introduced into their nests by Davies & Brooke (1989a) in Iceland. Theoretical models have shown that a rejection rate of about 50% is sufficiently strong to result in the evolution of mimicry (Kelly, 1987). Thus, it is likely that *C. canorus* mimicry of the eggs of the ancestors of current *A. pratensis* populations had already evolved, and therefore that a reduction of intraclutch variation in the appearance of *A. pratensis* eggs was advantageous for discriminating against *C. canorus* eggs.

We found differences within the part of the spectrum not visible to the human eye in intraclutch variation in egg appearance between populations of *A. pratensis* sympatric and allopatric with *C. canorus*. When in allopatry with *C. canorus*, *A. pratensis* had a higher intraclutch variation in UV chroma than it had when in sympatry. Therefore, our results suggest that methods of assessment of egg appearance within clutches based on human vision might not be sufficiently sensitive to assess variation in certain colour components that could be crucial for host discrimination of parasite eggs.

In summary, our study is the first documenting intraspecific evolutionary changes in a genetically determined component of host defence to brood parasitism. Further work reporting the real occurrence of recognition errors in *A. pratensis* populations in allopatry and sympatry with *C. canorus* is needed, because these data are crucial for explaining the evolution of host defences in the absence of *C. canorus* parasitism.

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