

## How is host egg mimicry maintained in the cuckoo (*Cuculus canorus*)?

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To investigate the evolutionary mechanism (host specificity vs. random searching) maintaining mimicry between cuckoo egg appearance and that of different European cuckoo *Cuculus canorus* hosts, we studied the level of mimicry between the appearance of *C. canorus* eggs and that of their hosts' eggs in different habitats in southern Finland by using ultraviolet-visible reflectance spectrophotometry. In the main habitat used by *C. canorus* for reproduction, eggs laid in nests of different host species differed in appearance. Host use by *C. canorus* was not related to the abundance of hosts, and the level of mimicry was not related to host abundance in the habitat. Furthermore, a close match between *C. canorus* egg appearance and that of host eggs within habitats was detected after removing the potentially confounding effect of host abundance. In the only two suitable host species nesting in trees (namely chaffinch *Fringilla coelebs* and brambling *Fringilla montifringilla*) we detected changes in *C. canorus* egg appearance that paralleled those of the two host species. Thus our findings suggest the existence of a correlation between the appearance of *C. canorus* eggs and that of their hosts' eggs within different habitat types, and suggest that mimicry is maintained by strict host preferences by each *C. canorus* female when laying. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, 82, 57–68.

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### INTRODUCTION

The high degree of match between the appearance of cuckoo *Cuculus canorus* eggs and those of some of its favourite hosts has attracted the interest of scientists for a long time (Jourdain, 1925; Chance, 1940; Baker, 1942). *C. canorus* is an obligate brood parasite that receives parental care from unrelated individuals of other species that raise its offspring. Parasitized hosts usually suffer reduced reproductive output (Røskaft, Orians & Beletsky, 1990; Payne, 1997), and parasitism favours the evolution of host defences, which at the same time select for more sophisticated trickeries by the parasite to overcome host defences (Davies & Brooke, 1988; Rothstein, 1990). 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). A generalized host defence against *C. canorus* parasitism is the recognition and rejection of parasite eggs from host nests, which selects for parasite egg mimicry.

The origin of the variability in *C. canorus* egg appearance and the match in phenotype between *C. canorus* and host eggs have been explained as the result of a long coevolutionary relationship between *C. canorus* and different host species (Brooke & Davis, 1988). Thus specialization of *C. canorus* on different host species occurs, and 16 different *C. canorus* gentes or host races have been described in Europe on the basis of subjective assessment of *C. canorus* egg appearance, with females of each gens generally parasitizing one or a few host species (Wyllie, 1981; Álvarez, 1994; Moksnes & Røskaft, 1995).

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Two groups of hypotheses have been proposed to explain the evolution and maintenance of egg mimicry by various *C. canorus* gentes. The host preference hypothesis states that *C. canorus* females of each gens are specialized in laying their eggs in the nest of a single species. Three main mechanisms should be involved in the maintenance of mimicry according to this hypothesis (Brooke & Davies, 1991): (1) rejection of non-mimetic eggs by hosts; (2) inheritance of egg colour in *C. canorus*; (3) inheritance of host preferences by *C. canorus*. Several experimental studies have supported the first mechanism since *C. canorus* hosts are more likely to reject parasite eggs unlike their own, thus selecting for mimicry (Brooke & Davies, 1988; Moksnes *et al.*, 1990; Nakamura, Kubota & Suzuki, 1998; Moskat & Honza, 2002). Although inheritance of egg appearance has not been directly tested for *C. canorus*, while it has for other bird species (Collias, 1993; Gosler *et al.*, 2000), recent genetic analyses provide evidence that a genetic factor controlling the expression of egg appearance is present on the female-specific W chromosome of *C. canorus* (Gibbs *et al.*, 2000). Finally, Brooke & Davies (1991) failed to find evidence of host imprinting in *C. canorus*.

Two alternative hypotheses, the natal philopatry hypothesis (Brooke & Davies, 1991) and the nest site preference hypothesis (Moksnes & Røskaft, 1995), propose that *C. canorus* do not have particular preferences for hosts but prefer specific environmental factors. The first hypothesis states that *C. canorus* generally return each spring to breed in their natal habitat, randomly choosing where to lay, with apparent mimicry resulting from parasitism of the most suitable hosts in terms of abundance and accessibility in a homogeneous area in which only a few hosts are predominant (Brooke & Davies, 1991). The nest site preference hypothesis, however, is based on the random use of hosts by *C. canorus* within a group of species with similar nests and eggs in a given habitat. Although Moksnes & Røskaft (1995) have not proposed the working mechanisms for this hypothesis, Teuschl, Taborsky & Taborsky (1998) have shown that *C. canorus* in captivity spend more time looking at their familiar habitats than at other habitats, suggesting that habitat imprinting might be at work in *C. canorus*. Consequently, if *C. canorus* breed in habitats resembling those where they were imprinted and randomly look for hosts in such habitats, they would have a high probability of parasitizing their foster species.

To distinguish between the two groups of hypotheses we compared the appearance of *C. canorus* eggs laid in different host nests within the same type of habitat. Using this approach we determined the evolutionary mechanism (host specificity vs. random use

of host) explaining the maintenance of mimicry in *C. canorus* (Brooke & Davies, 1991). On the within-habitat scale, with random use, as predicted by the nest site preference hypothesis and the natal philopatry hypothesis, (1) no differences among *C. canorus* eggs laid in the nests of different hosts should be predicted, (2) the frequency of use of each host by *C. canorus* should be positively related to the relative abundance of each host, and (3) a more fine-scale resemblance between *C. canorus* and host eggs should be expected in more abundant hosts. Alternatively, a fine adjustment between *C. canorus* egg appearance and that of hosts independent of host abundance should be expected if *C. canorus* prefer hosts in accordance with the host preference hypothesis.

## MATERIAL AND METHODS

### THE STUDY COLLECTION

We obtained reflectance values from all available host species parasitized by *C. canorus* from the egg collections at the Zoological Museum in Helsinki (Finland). Most clutches in this collection were personally collected by Ernst Wasenius in the first quarter of the 20th century in the surroundings of Helsinki (southern Finland) (Wasenius, 1936).

Table 1 shows the 190 *C. canorus* eggs by host and *C. canorus* gentes as classified by Wasenius. Although the match in egg colour appearance between *C. canorus* and host eggs may have resulted in some cases of *C. canorus* egg misidentification we consider this possibility unlikely since *C. canorus* eggs are much larger than those of their Finnish hosts. Moreover, *C. canorus* have been selected for laying eggs of unusually great structural strength relative to host eggs (Honza *et al.*, 2001), which is easily perceptible by touching. Thus sampling biases due to misidentification of the *C. canorus* egg in our sample were presumably negligible. Hosts were also classified in relation to their nesting habitats following Moksnes & Røskaft (1995) as: (t) birds breeding in trees; (l) birds breeding in low vegetation; (l,t) birds breeding in both low vegetation and trees; (g) birds breeding on the ground; (g,l) birds breeding both on the ground and in low vegetation; (h) birds breeding in holes (for more details on this classification, see Moksnes & Røskaft (1995)). Similarly, hosts were classified as suitable or unsuitable *C. canorus* hosts following Moksnes & Røskaft (1995). The unsuitable group comprised seed-eaters which are unsuitable hosts because the *C. canorus* chick needs an invertebrate diet for successful rearing, and species nesting in small holes, inaccessible to the laying female *C. canorus* (Davies, 2000). A recent paper has shown that the redstart *Phoenicurus phoenicurus* may be considered as a limited suitable host since *C. canorus* chicks frequently

grew up with the host's nestlings, reducing *C. canorus* fledgling success (Rutala *et al.*, 2002). However, *P. phoenicurus* showed a very low recognition level against parasitic eggs as compared with other common *C. canorus* hosts (Rutala *et al.*, 2002), and, in spite of its hole-nesting habits, *P. phoenicurus* is currently the favourite *C. canorus* host in Finland. Thus we considered *P. phoenicurus* as a suitable host in our analyses. Moreover, we included the magpie *Pica pica* as an unsuitable *C. canorus* host since we assumed that the large eggs of this species are probably too costly to be evicted by *C. canorus* chicks. Breeding densities of *C. canorus* hosts in Finland in pairs by square kilometre were obtained from Väisänen, Lammi & Koskimies (1998) and used as an estimate of host abundance (Table 1).

#### REFLECTANCE DATA AND ESTIMATION OF DEGREE OF MIMICRY

Previous studies focusing on the evolution of mimicry estimated resemblance between *C. canorus* and host eggs based on human perception (Moksnes & Røskaft, 1995; Edvardson *et al.*, 2001), or measured the difference between the light reflected from *C. canorus* and host eggs using a light-meter that classified eggs in relation to darkness (Brooke & Davies, 1988). The first approach has two main problems: (1) human observers cannot perceive ultraviolet (UV) (300–400 nm) information that birds can detect due to one cone in their retina being sensitive to UV light (Chen, Collins & Gol, 1984; Bowmaker *et al.*, 1997). Because the main selective forces driving evolution of egg colour in *C. canorus* is discrimination of parasite eggs by hosts, which are probably sensitive to UV light, the capacity of humans to assess mimicry might be incomplete (Cuthill *et al.*, 2000); (2) due to anatomical differences between avian and human eyes (Goldsmith, Collins & Licht, 1984; Vorobyev *et al.*, 1998), the assessment of mimicry based on human vision might be insufficiently sensitive to variation in colour components that birds might be able to detect, even within the human visible range (400–700 nm). Moreover, human and spectrophotometric measures were used simultaneously to assess egg mimicry in a recent study (Cherry & Bennett, 2001). The results confirmed the existence of discrepancies between human and spectrophotometric measures of egg mimicry since the eggs of the red-chested cuckoo *Cuculus solitarius* and its African hosts were highly matched for chromatic aspects of eggs invisible to humans (Cherry & Bennett, 2001).

On the other hand, darkness, as measured by Brooke & Davies (1988), does not permit distinction between different components of colour that might be under selection by the host. For example, a greater

darkness in a *C. canorus* egg might be the consequence of a lower reflectance in any part of the avian visual spectra, with apparent mimicry of host eggs being the consequence of reflectance from different spectral regions.

We obtained reflectance spectra in the range 300–700 nm from all clutches using a spectroradiometer (Ocean Optics Europe). We measured colour twice in two randomly selected areas of the surface of the eggs, each *c.* 1 mm<sup>2</sup> in size. 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 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 the dark. We made a reference and dark calibration before measurement of each egg. Taking into account that microspectrophotometric studies of the visual pigments of the hosts of *C. canorus* are lacking and therefore sensitivities of the different hosts at different wavelengths cannot be estimated (see Cuthill *et al.*, 2000), total reflectance was obtained for the UV (300–400 nm), blue (400–500 nm), green (500–600 nm) and red (600–700 nm) intervals. It makes sense to consider these four wavebands, because this is how passerine cone cells divide the spectrum (Cuthill *et al.*, 2000).

The degree of consistency of reflectance data in our study was tested by means of repeatability analyses (Falconer & Mackay, 1996). Firstly, we measured twice in the same randomly selected area of a single egg and found high repeatability ( $F_{853,853} > 165.0$ ,  $r > 0.95$ ,  $P < 0.0001$ ). Secondly, we measured each egg in two randomly selected areas and found significant repeatability ( $F_{853,853} > 11.89$ ,  $r = 0.90$ ,  $P < 0.001$ ). Consequently, all measurements were reliable and, thus, we used mean values for each egg for each established interval.

To estimate degree of mimicry between host and parasite eggs we first calculated the absolute differences of mean reflectance values at the UV, blue, green and red wavebands between all host and *C. canorus* eggs in the same clutch. Mean values of these absolute differences were considered to represent the degree of mimicry of *C. canorus* eggs to those of the hosts.

Phenotypic differences between *C. canorus* eggs and those of their hosts would depend on the coevolutionary time between the parasite and specific hosts, which are likely to be independent of the phylogenetic relationships among hosts. Therefore, we did not

**Table 1.** Distribution of *Cuculus canorus* gentes in southern Finland according to hosts

Host species	Nest site	Host suitability	Host abundance	Cuckoo gentes							Total	%		
				<i>Sylvia</i>	<i>Anthus</i>	<i>Blue</i>	<i>Motacilla</i>	<i>Fringilla</i>	<i>Emberiza</i>	<i>Muscicapa</i>			Others	
<i>Emberiza citrinella</i>	g	s	2.6	1			1			2			4	2.11
<i>Anthus trivialis</i>	g	s	4.5	1	4		1		1				7	3.68
<i>Anthus pratensis</i>	g	s	6.2		3				1				4	2.11
<i>Motacilla flava</i>	g	s	3.7		1	1	7		1				10	5.26
<i>Motacilla alba</i>	g	s	2.0	1	3		16		3	1			24	12.63
<i>Phylloscopus collybita</i>	g	s	0.8			1	1		2				4	2.11
<i>Phylloscopus trochilus</i>	g	s	27.8			3			1	1			6	3.16
<i>Oenanthe oenanthe</i>	g	u	1.5			3							3	1.58
<i>Saxicola rubetra</i>	g	s	1.4			8							8	4.21
<i>Erithacus rubecula</i>	g	s	2.7			1			1				2	1.05
<i>Lullula arborea</i>	g	s	0.1				2						2	1.05
<i>Emberiza schoeniclus</i>	g,l	s	1.2						1				1	0.53
<i>Jynx torquilla</i>	h	u	0.08			1							1	0.53
<i>Ficedula hypoleuca</i>	h	u	1.6			9							9	4.74
<i>Phoenicurus phoenicurus</i>	h	s	1.7			57							57	30.00
<i>Troglodytes troglodytes</i>	h	s	0.1	1									1	0.53
<i>Carduelis cannabina</i>	l	u	0.04				1						1	0.53
<i>Carpodacus erythrinus</i>	l	u	0.9				1		1				2	1.05
<i>Lanius collurio</i>	l	s	0.3									1	4	2.11
<i>Sylvia borin</i>	l	s	2.3	1		4							5	2.63
<i>Sylvia communis</i>	l	s	0.8	1			1						2	1.05
<i>Sylvia curruca</i>	l	s	0.7			4	1						5	2.63
<i>Sylvia atricapilla</i>	l	s	0.2				1						1	0.53
<i>Prunella modularis</i>	l	s	0.9			1							1	0.53
<i>Carduelis flammea</i>	l,t	u	2.4	1									1	0.53
<i>Chloris chloris</i>	l,t	u	0.2									1	1	0.53
<i>Muscicapa striata</i>	l,t	s	5.0			6			1				10	5.26
<i>Fringilla montifringilla</i>	t	s	7.2						7				7	3.68
<i>Fringilla coelebs</i>	t	s	17.1						6				6	3.16
<i>Pica pica</i>	t	u	0.4									1	1	0.53
Total				9	11	99	34	26	4	1	6	190		
%				4.74	5.79	52.11	17.89	13.68	2.11	0.53	3.16	100		

Hosts are classified in relation to their nesting habitats as: (t) birds breeding in trees; (l) birds breeding in low vegetation; (l,t) birds breeding in both low vegetation and trees; (g) birds breeding on the ground; (g,l) birds breeding both on the ground and in low vegetation, and (h) birds breeding in holes. Likewise hosts are classified as suitable (s) or unsuitable (u) cuckoo hosts. Host abundances are pairs by square kilometre and were obtained from Väisänen *et al.* (1998). The morph category of others included *Cuculus canorus* eggs resembling eggs of redwing *Turdus iliacus* and common crossbill *Loxia curvirostra*.

correct for possible phylogenetic effects explaining levels of mimicry between parasite and host eggs.

#### STATISTICAL ANALYSES

To avoid pseudo-replication we used mean values of colour variables of all eggs of the same species in a nest. Mean values of colour variables of host and parasite eggs in the same nest approximately fitted normal distributions (Kolmogorov–Smirnov test for continuous variables,  $P > 0.20$ ) except for values of UV wavelengths of host and *C. canorus* eggs and red wavelengths of *C. canorus* eggs (Kolmogorov–Smirnov test for continuous variables,  $P < 0.10$ ). However, after logarithmic transformation the frequency distributions did not differ from normality (Kolmogorov–Smirnov test for continuous variables,  $P > 0.20$ ). Thus, we used transformed data and parametric tests for these variables in our statistical analysis, but show mean values for untransformed data in the text and figures. Variables related to differences between parasite and host eggs in the same nest all differed from normal distributions (Kolmogorov–Smirnov test for continuous variables,  $P < 0.20$ ). Therefore, we used non-parametric tests to analyse differences in the level of mimicry. Throughout we always applied sequential Bonferroni correction for the probability of a type-I error. We assumed a  $P$ -value of 0.1 when using two or more tests for checking a common null hypothesis ( $\alpha = 0.1/17$  tests for ground and low vegetation nester analyses and  $\alpha = 0.1/8$  tests for tree nester tests). This assumed error rate is reasonable since 10–15% type I error rates are appropriate levels of control for experiment-wise errors (Chandler, 1995). Values are mean  $\pm$  SD for normally distributed variables and median  $\pm$  range for non-normal ones.

## RESULTS

#### FREQUENCY OF HOSTS

A total of 30 different hosts were parasitized by *C. canorus* in southern Finland with redstart *Phoenicurus phoenicurus* (30.0%), pied wagtail *Motacilla alba* (12.6%), yellow wagtail *Motacilla flava* (5.3%), meadow pipit *Anthus pratensis* (5.3%) and pied flycatcher *Ficedula hypoleuca* (4.7%) being the main *C. canorus* hosts (Table 1). Ground-nesting (38.9%) and hole-nesting (35.8%) birds received most eggs laid by *C. canorus* in the region (Table 1).

#### HOST EGG MIMICRY IN *C. CANORUS* IN RELATION TO HOST NESTING HABITAT

Table 2 shows mean reflectance values in the UV, blue, green, and red regions of the spectrum of different

hosts' eggs and in those of *C. canorus* laid in nests of different hosts with ground-nesting habits in southern Finland.

Eggs of the 11 host species parasitized by *C. canorus* in ground nests differed in their mean reflectance values in the four regions of the spectrum (Table 2). Interestingly, after sequential Bonferroni correction, *C. canorus* eggs laid in nests of different host species differed for blue and green reflectance (Prediction 1, Table 2). Host use in this habitat type, as estimated by the frequency of *C. canorus* parasitism in Table 1, was not significantly related to the abundance of hosts (Prediction 2,  $r = -0.03$ ,  $P = 0.92$ ,  $n = 11$ ). Furthermore, the level of mimicry estimated by differences in reflectance in the four spectral regions between *C. canorus* and host eggs (Table 3) was not related to host abundance in the habitat (Prediction 3,  $r = 0.21$ ,  $P = 0.52$  for UV,  $r = 0.18$ ,  $P = 0.57$  for blue,  $r = 0.21$ ,  $P = 0.51$  for green, and  $r = 0.33$ ,  $P = 0.31$  for red,  $n = 11$  in each case).

A close match between *C. canorus* egg appearance and that of host eggs at the within-habitat level was detected after removing the possible effect of host abundance when only ground-nesting *C. canorus* hosts were considered. A significant positive correlation in the four regions of the spectrum existed between reflectance values of *C. canorus* and host eggs (Fig. 1), supporting the host preference hypothesis.

Although museum collections have been widely used to investigate the functional role of egg coloration in studies of brood parasitism (Brooke & Davies, 1988; Davies & Brooke, 1989a,b; Moksnes & Røskaft, 1995; Stokke, Moksnes & Røskaft, 2002), they may be a biased source of data for the study of mimicry since they refer to *C. canorus* eggs collected and not to *C. canorus* eggs laid. Thus, if hosts have ejected a proportion of *C. canorus* eggs before collection, and ejection of poorly mimetic eggs is more frequent than that of mimetic ones (Davies & Brooke, 1988, 1989a; Brown *et al.*, 1990; Braa, Moksnes & Røskaft, 1992; Moksnes, 1992), bias may favour a correlation between *C. canorus* and host egg appearance. This may have important consequences for this study since the same correlation is predicted by the host preference hypothesis. Three different sources of evidence can eliminate this possibility. (1) Among ground-nesting host species the meadow pipit *A. pratensis* (26.8%, Davies & Brooke, 1989a; Moksnes *et al.*, 1990) the wheatear *Oenanthe oenanthe* (5.9%, Davies & Brooke, 1989a; Moksnes *et al.*, 1990) and the robin *Erithacus rubecula* (20.0%, Davies & Brooke, 1989a) reject artificial model eggs at very low rates. Since rejection of real *C. canorus* eggs is lower than that of models, it seems unlikely that differences between *C. canorus* eggs in Table 2 could be explained by this possibility. (2) Furthermore, when only those host species with more

**Table 2.** Mean reflectance at ultraviolet, blue, green and red wavelengths of the hosts with ground-nesting habits parasitized by *Cuculus canorus* and of eggs of *C. canorus* laid in the nests of these hosts in southern Finland

	Ultraviolet	Blue	Green	Red
Host eggs				
<i>Anthus pratensis</i> (N = 5)	15.01 (3.23)	15.29 (3.05)	19.02 (3.18)	28.91 (3.87)
<i>Anthus trivialis</i> (N = 6)	16.42 (2.33)	17.87 (3.66)	21.00 (4.28)	33.48 (5.00)
<i>Emberiza citrinella</i> (N = 4)	25.51 (6.35)	31.36 (6.56)	36.12 (6.71)	46.89 (7.16)
<i>Erithacus rubecula</i> (N = 6)	27.82 (6.01)	34.42 (7.39)	44.39 (9.80)	58.72 (13.04)
<i>Lullula arborea</i> (N = 1)	35.79 (0.00)	42.58 (0.00)	48.13 (0.00)	55.65 (0.00)
<i>Motacilla alba</i> (N = 23)	30.49 (6.96)	39.00 (7.23)	45.42 (7.41)	52.93 (7.00)
<i>Motacilla flava</i> (N = 10)	20.16 (3.79)	21.94 (3.80)	28.25 (4.44)	42.25 (6.31)
<i>Oenanthe oenanthe</i> (N = 3)	39.70 (4.80)	55.20 (4.47)	63.81 (4.51)	64.64 (3.52)
<i>Phylloscopus collybita</i> (N = 3)	48.75 (5.29)	60.75 (3.66)	66.65 (3.10)	71.57 (2.16)
<i>Phylloscopus trochilus</i> (N = 6)	46.05 (8.40)	57.18 (8.72)	65.12 (7.61)	75.68 (4.72)
<i>Saxicola rubetra</i> (N = 8)	21.55 (3.54)	33.91 (4.95)	42.58 (5.39)	42.06 (5.03)
MS Effect	648.06	1206.15	1411.10	1167.31
MS Error	32.99	37.64	42.03	46.11
F	19.64	32.04	33.56	25.31
d.f.	10,64	10,64	10,64	10,64
P	0.000001*	0.00001*	0.000001*	0.00001*
Cuckoo eggs				
<i>Anthus pratensis</i> (N = 5)	16.06 (0.37)	19.35 (1.62)	24.85 (2.27)	37.06 (3.54)
<i>Anthus trivialis</i> (N = 6)	15.43 (3.26)	19.12 (2.04)	23.81 (1.92)	36.88 (3.75)
<i>Emberiza citrinella</i> (N = 4)	21.35 (3.15)	28.71 (4.15)	35.70 (4.60)	45.89 (6.05)
<i>Erithacus rubecula</i> (N = 6)	20.85 (2.87)	33.20 (8.54)	41.59 (10.21)	40.67 (6.05)
<i>Lullula arborea</i> (N = 1)	20.25 (0.00)	27.47 (0.00)	36.77 (0.00)	43.92 (0.00)
<i>Motacilla alba</i> (N = 23)	18.57 (4.34)	25.44 (6.70)	32.15 (7.70)	40.75 (6.37)
<i>Motacilla flava</i> (N = 10)	17.64 (6.24)	22.05 (8.85)	28.69 (9.40)	38.81 (7.96)
<i>Oenanthe oenanthe</i> (N = 3)	19.91 (3.72)	34.24 (3.93)	44.77 (3.66)	42.31 (5.01)
<i>Phylloscopus collybita</i> (N = 3)	20.62 (2.58)	29.69 (4.24)	37.57 (5.93)	43.60 (5.05)
<i>Phylloscopus trochilus</i> (N = 6)	26.71 (11.92)	38.85 (12.73)	47.61 (12.86)	50.35 (15.81)
<i>Saxicola rubetra</i> (N = 8)	19.64 (4.84)	33.49 (6.71)	43.36 (7.53)	38.81 (7.20)
MS Effect	54.80	252.38	387.94	92.22
MS Error	28.58	51.83	62.53	56.48
F	1.91	4.86	6.20	1.63
d.f.	10,63	10,63	10,63	10,63
P	0.05	0.00003*	0.00002*	0.117

Values are mean (SD). \* $P < 0.1$  after sequential Bonferroni correction.

than five collected clutches were considered, we failed to find a significant correlation for any colour region between colour of *C. canorus* and host eggs for each species, as would be expected if hosts were discriminating very accurately (meadow pipit *A. pratensis*:  $0.21 < P < 0.95$ ,  $-0.38 < r < 0.67$ ,  $n = 5$ ; tree pipit *A. trivialis*:  $0.17 < P < 0.72$ ,  $-0.72 < r < -0.18$ ,  $n = 6$ ; yellow wagtail *M. flava*:  $0.28 < P < 0.45$ ,  $-0.37 < r < 0.31$ ,  $n = 10$ ; whinchat *Saxicola rubetra*:  $0.23 < P < 0.39$ ,  $-0.47 < r < 0.45$ ,  $n = 8$ ; white wagtail *Motacilla alba*:  $0.20 < r < 0.62$ ,  $-0.27 < r < 0.10$ ,  $n = 23$  and willow warbler *Phylloscopus trochilus*:  $0.63 < P < 0.86$ ,  $-0.25 < r < -0.09$ ,  $n = 6$ ). (3) Finally, several detailed radio telemetry studies have shown that radio-tagged *C. canorus* show strict host special-

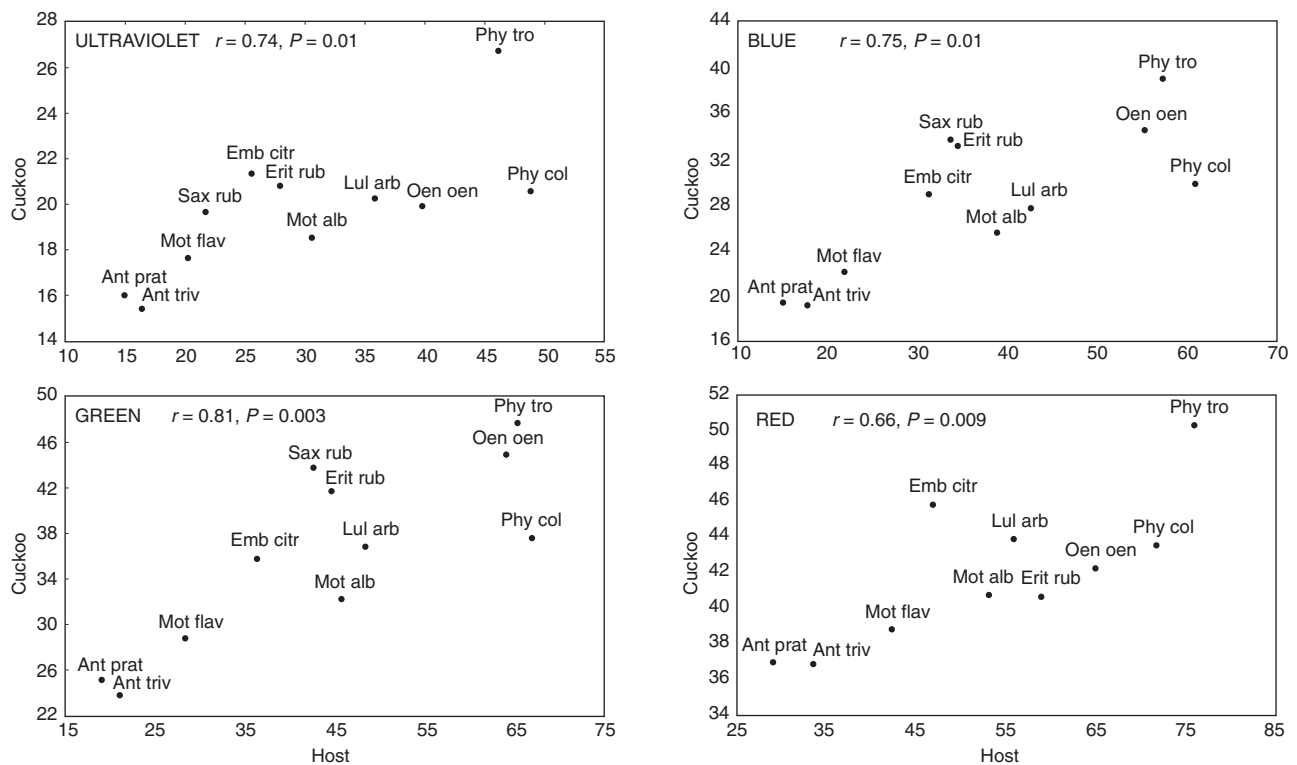
ization when laying (Wyllie, 1981; Dröscher, 1988; Nakamura & Miyazawa, 1997; Nakamura *et al.*, 1998). Therefore, the evidence suggests that the observed correlations between host and *C. canorus* eggs in ground habitats were not due to egg discrimination by hosts. Thus, they are a consequence of a strict host preference by *C. canorus* females.

Analyses of mimicry among hosts breeding in low vegetation showed that eggs of host species parasitized differed in their mean reflectance values in the four regions of the spectrum (Table 4). However, *C. canorus* eggs laid in nests of different host species did not differ for any colour variable (Prediction 1, Table 4). Host use in this habitat type was not significantly related to abundance of hosts (Prediction 2,

**Table 3.** Mean absolute differences between colour variables of *Cuculus canorus* eggs and those of their hosts with ground-nesting habits in southern Finland

Species	Ultraviolet	Blue	Green	Red
<i>Anthus pratensis</i> (N = 5)	2.61 (1.39)	4.30 (3.65)	5.83 (4.54)	8.14 (5.17)
<i>Anthus trivialis</i> (N = 6)	2.98 (1.89)	4.18 (2.20)	4.98 (3.76)	6.06 (3.97)
<i>Emberiza citrinella</i> (N = 4)	4.16 (3.62)	2.65 (2.85)	2.84 (1.36)	2.12 (1.32)
<i>Erithacus rubecula</i> (N = 6)	12.47 (6.98)	10.78 (1.58)	14.64 (11.84)	27.63 (17.31)
<i>Lullula arborea</i> (N = 1)	15.54 (0.00)	15.11 (0.00)	11.35 (0.00)	11.72 (0.00)
<i>Motacilla alba</i> (N = 23)	12.41 (7.02)	14.49 (8.23)	14.30 (8.69)	13.21 (7.25)
<i>Motacilla flava</i> (N = 10)	5.63 (3.14)	6.79 (5.90)	6.82 (6.86)	6.71 (5.91)
<i>Oenanthe oenanthe</i> (N = 3)	19.79 (2.28)	20.95 (1.07)	19.03 (1.30)	22.33 (2.09)
<i>Phylloscopus collybita</i> (N = 3)	28.12 (5.64)	31.05 (7.70)	29.08 (8.38)	27.97 (2.90)
<i>Phylloscopus trochilus</i> (N = 6)	21.25 (11.37)	21.39 (11.28)	20.59 (10.34)	27.26 (13.06)
<i>Saxicola rubetra</i> (N = 8)	4.20 (1.74)	4.17 (3.51)	5.05 (3.63)	6.11 (3.67)

Values are mean (SD).



**Figure 1.** Relationship between mean values of reflectance at ultraviolet, blue, green and red wavelengths of ground-nesting host eggs from southern Finland and those of *Cuculus canorus* parasitizing each host. Tests are partial correlations with host nest density as a covariate. Lul arb = *Lullula arborea*, Ant prat = *Anthus pratensis*, Ant triv = *Anthus trivialis*, Mot flav = *Motacilla flava*, Mot alb = *Motacilla alba*, Erit rub = *Erithacus rubecula*, Sax rub = *Saxicola rubetra*, Oen oen = *Oenanthe oenanthe*, Emb citr = *Emberiza citrinella*, Phy tro = *Phylloscopus trochilus* and Phy col = *Phylloscopus collybita*.

$r = 0.53$ ,  $P = 0.20$ ,  $n = 8$ ). Furthermore, the level of mimicry between *C. canorus* and host eggs (Table 5) was not related to host abundance (Prediction 3,  $r = -0.31$ ,  $P = 0.48$  for UV,  $r = -0.19$ ,  $P = 0.68$  for blue,

$r = -0.26$ ,  $P = -0.30$  for green, and  $r = -0.30$ ,  $P = 0.51$  for red,  $n = 7$  in the four cases). Finally, we did not detect a significant correlation in any of the four regions of the spectrum between colour of *C. canorus*

**Table 4.** Mean reflectance at ultraviolet, blue, green, and red wavelengths of the hosts nesting in low vegetation parasitized by *Cuculus canorus* and of eggs of *C. canorus* laid in the nests of these hosts in southern Finland

	Ultraviolet	Blue	Green	Red
Host eggs				
<i>Carduelis cannabina</i> (N = 1)	29.68 (0.00)	42.87 (0.00)	51.30 (0.00)	58.46 (0.00)
<i>Carpodacus erythrinus</i> (N = 2)	23.81 (3.51)	38.57 (4.43)	47.03 (4.79)	43.78 (3.36)
<i>Lanius collurio</i> (N = 6)	32.84 (4.88)	41.43 (6.39)	52.78 (7.32)	63.74 (6.24)
<i>Sylvia atricapilla</i> (N = 1)	36.47 (0.00)	37.76 (0.00)	48.05 (0.00)	59.70 (0.00)
<i>Sylvia borin</i> (N = 6)	26.87 (5.37)	30.48 (8.17)	40.59 (8.10)	52.60 (5.78)
<i>Sylvia communis</i> (N = 4)	22.25 (5.59)	24.70 (7.59)	34.96 (8.42)	47.17 (7.75)
<i>Sylvia curruca</i> (N = 5)	34.67 (4.78)	41.75 (7.40)	51.95 (6.97)	61.14 (5.75)
MS Effect	94.18	183.18	191.68	198.53
MS Error	25.65	52.80	57.06	38.12
F	3.67	3.46	3.35	5.20
d.f.	6,18	6,18	6,18	6,18
P	0.014*	0.018*	0.02*	0.002*
Cuckoo eggs				
<i>Carduelis cannabina</i> (N = 1)	19.62 (0.00)	24.07 (0.00)	29.84 (0.00)	38.53 (0.00)
<i>Carpodacus erythrinus</i> (N = 2)	20.60 (2.72)	27.84 (0.91)	35.62 (0.24)	43.51 (2.35)
<i>Lanius collurio</i> (N = 6)	30.00 (3.92)	38.16 (6.64)	47.13 (8.33)	57.03 (7.25)
<i>Sylvia atricapilla</i> (N = 1)	28.55 (0.00)	33.98 (0.00)	43.46 (0.00)	51.43 (0.00)
<i>Sylvia borin</i> (N = 6)	22.16 (4.53)	34.48 (4.58)	45.02 (5.08)	43.64 (9.20)
<i>Sylvia communis</i> (N = 4)	23.41 (7.54)	29.13 (9.00)	37.41 (9.91)	47.13 (9.12)
<i>Sylvia curruca</i> (N = 5)	19.95 (4.13)	31.53 (8.40)	39.97 (10.49)	40.59 (3.77)
MS Effect	63.70	62.84	91.42	165.30
MS Error	23.69	47.36	67.83	55.52
F	2.68	1.32	1.35	2.97
d.f.	6,18	6,18	6,18	6,18
P	0.048	0.29	0.28	0.03

Values are mean (SD). \* $P < 0.1$  after sequential Bonferroni correction.

**Table 5.** Mean absolute differences between colour variables of *Cuculus canorus* eggs and those of their hosts nesting in low vegetation habitats in southern Finland

Species	Ultraviolet	Blue	Green	Red
<i>Carduelis cannabina</i> (N = 1)	10.06 (0.00)	18.79 (0.00)	21.45 (0.00)	19.92 (0.00)
<i>Carpodacus erythrinus</i> (N = 2)	3.21 (0.78)	10.72 (3.52)	11.41 (4.54)	0.71 (0.38)
<i>Lanius collurio</i> (N = 6)	4.94 (3.93)	9.23 (6.87)	11.84 (8.67)	10.34 (7.98)
<i>Sylvia atricapilla</i> (N = 1)	7.91 (0.00)	3.78 (0.00)	4.58 (0.00)	8.27 (0.00)
<i>Sylvia borin</i> (N = 6)	4.93 (4.27)	9.03 (4.42)	9.79 (4.52)	8.96 (5.32)
<i>Sylvia communis</i> (N = 4)	3.38 (1.91)	6.64 (1.92)	7.64 (2.55)	4.85 (3.89)
<i>Sylvia curruca</i> (N = 5)	14.72 (5.11)	10.21 (8.65)	11.97 (10.27)	20.54 (6.62)

Values are mean (SD).

and host eggs when the seven bird species breeding in low vegetation in southern Finland were considered ( $r = 0.42$ ,  $P = 0.34$  for UV,  $r = -0.04$ ,  $P = 0.92$  for blue,  $r = -0.002$ ,  $P = 0.99$  for green,  $r = 0.27$ , and  $r = 0.30$ ,  $P = 0.51$  for the red) (listed in Table 1 are eight *C. canorus* hosts typically nesting in low vegetation, but we could not obtain reflectance values from the

only dunnock *Prunella modularis* clutch because the *C. canorus* egg was broken). However, this result is not surprising since linnet *Carduelis cannabina* and scarlet rosefinch *Carpodacus erythrinus* are unsuitable hosts of *C. canorus* because they mainly feed their chicks with seeds (Stjernberg, 1979; Cramp & Perrins, 1992) that are an unsuitable food source for *C. canorus*



chicks. Although *P. modularis* is among the five favourite *C. canorus* hosts in Great Britain (Davies, 2000), where rejection of *C. canorus* eggs has evolved (rejection rate: 5.9%, Davies & Brooke, 1989a), it is very rarely parasitized by *C. canorus* in Finland (one clutch in Finland (Wasenius, 1936)). Moreover, rejection of *C. canorus* eggs has not evolved in Norway (Moksnes *et al.*, 1990), which would suggest that *P. modularis* is an unsuitable *C. canorus* host in Scandinavia, and that its exclusion from the analyses did not affect our results.

We could not test whether matches between *C. canorus* and host eggs occurred in the other two main habitats used by *C. canorus* in the region since only four and three species were parasitized in holes and trees (Table 1). Moreover, among the hole-nesting hosts the pied flycatcher *F. hypoleuca* and the wryneck *Jynx torquilla* were unsuitable hosts and just a single clutch parasitizing the wren *Troglodytes troglodytes* was available in the study collection, precluding comparative analyses. However, the colour of the eggs of the chaffinch *Fringilla coelebs* and the brambling *F. montifringilla*, the only two suitable host species nesting in trees in southern Finland, differed in the blue and red regions of the spectrum after Bonferroni correction, with *F. coelebs* eggs being more brightly coloured (Table 6). Curiously all these clutches were parasitized by a single morph according to the human eye (Wasenius, 1936; Table 1). *C. canorus* eggs laid in the nests of *F. coelebs* were also more strongly coloured in the blue region after Bonferroni correction (Table 6). Alternatively, it could be argued that

*C. canorus* females may randomly lay a single morph for parasitizing the nests of the genus *Fringilla* and thus that differences would arise from the rejection of poorly mimetic *C. canorus* eggs by the two species. However, this possibility is clearly unlikely because spectrophotometric values of *C. canorus* eggs laid in nests of the two *Fringilla* species did not overlap (Table 6).

## DISCUSSION

The spectrophotometric analyses of host mimicry by *C. canorus* in southern Finland at the level of different habitats supported the host preference hypothesis, with individual *C. canorus* being strict host specialists. Firstly, within the main habitat used by *C. canorus* for reproduction in southern Finland, we detected a close match between *C. canorus* egg appearance and that of each host (Fig. 1) when controlling for host abundance. Furthermore (1) *C. canorus* eggs laid in the nests of different hosts differed in appearance, (2) the frequency of use of each host by *C. canorus* was not associated with the relative abundance of each host, and (3) more abundant hosts were not parasitized with relatively more mimetic *C. canorus* eggs, contrary to expectations from a random mechanism of searching for hosts by *C. canorus*. Finally, in the only two suitable host species nesting in trees, we detected changes in *C. canorus* egg appearance that paralleled those of the eggs of the two host species.

Our results are in agreement with genetic studies that have supported observational studies reporting

**Table 6.** Mean reflectance at ultraviolet, blue, green, yellow and red wavelengths of the main hosts nesting in trees parasitized by *Cuculus canorus* and of eggs of *Cuculus canorus* laid in the nests of these hosts in southern Finland

	Ultraviolet	Blue	Green	Red
Host eggs				
<i>Fringilla coelebs</i> (N = 6)	25.37 (1.65)	33.35 (2.80)	39.65 (3.10)	48.15 (1.77)
<i>Fringilla montifringilla</i> (N = 7)	17.74 (1.43)	23.56 (1.50)	30.21 (1.47)	38.15 (1.65)
MS Effect	4.76	309.44	288.11	322.97
MS Error	3.41	30.15	34.68	19.10
F	1.39	10.26	8.30	16.90
d.f.	1,11	1,11	1,11	1,11
P	0.004*	0.008*	0.01*	0.001*
Cuckoo eggs				
<i>Fringilla coelebs</i> (N = 6)	19.53 (0.99)	27.49 (1.47)	34.50 (2.03)	41.39 (2.12)
<i>Fringilla montifringilla</i> (N = 7)	15.79 (1.21)	22.25 (1.39)	29.06 (1.77)	36.65 (1.38)
MS Effect	45.18	88.75	95.60	72.66
MS Error	8.33	13.35	23.35	19.65
F	5.42	6.64	4.09	3.69
d.f.	1,11	1,11	1,11	1,11
P	0.04	0.02*	0.06	0.08

Values are mean (SE). \* $P < 0.1$  after sequential Bonferroni correction.

the laying history of a *C. canorus* female showing remarkable host specificity (Chance, 1940; Baker, 1942). Genetic analyses have revealed that genes are restricted to female lineages that specialize on specific host species (Marchetti, Nakamura & Gibbs, 1998), with cross-mating by males maintaining *C. canorus* as a single species (Gibbs *et al.*, 2000). Further evidence of host preference by *C. canorus* comes from radio telemetry studies showing that radio-tagged *C. canorus* females in general show strict host specialization when laying [Rudolfson, 1999 (cited in Edvardson *et al.*, 2001); Wyllie, 1981; Dröscher, 1988; Nakamura & Miyazawa, 1997; Nakamura *et al.*, 1998 (cited in Edvardson *et al.*, 2001); Honza *et al.*, 2002]. Thus current evidence supports that mimicry is maintained by strict *C. canorus* host preferences when laying.

Interestingly, this is the first study in which strict host preference by *C. canorus* females has been demonstrated from analyses of mimicry between *C. canorus* and host eggs. Brooke & Davies (1991) used a similar approach and found no differences between *C. canorus* egg appearance laid in the nests of three pairs of species living in similar habitats, which might suggest random searching. Further evidence supporting the nest site preference hypothesis and the natal philopatry hypothesis came from analyses of 11 870 *C. canorus* eggs kept in egg collections analysed by Moksnes & Røskaft (1995). They showed that 76.5% of all *C. canorus* eggs were laid either in nests of host species with high resemblance of *C. canorus* eggs, or in nests of species with similar nesting habits as the main host. More recently Edvardson *et al.* (2001) also found support for random use of hosts by *C. canorus* females in an area of the Czech Republic in which four different *Acrocephalus* species occurred sympatrically with *C. canorus*. Edvardson *et al.* (2001) failed to find differences in appearance among *C. canorus* eggs laid in the nests of these four hosts.

Why does the analysis of mimicry between *C. canorus* and host eggs provide such different results? Our approach and those previously testing the host preference hypothesis diverged in the method of assessment of mimicry and/or the spatial scale. These differences might greatly affect the main prediction of random use of hosts by *C. canorus*. Firstly, previous studies estimated mimicry based on photographs and human perception of matching (Moksnes & Røskaft, 1995; Edvardson *et al.*, 2001; but see Brooke & Davies, 1991). Human and bird vision differs in several ways, some of which greatly affect assessment of mimicry (Cherry & Bennett, 2001). Here we detected previously unreported differences in egg appearance between *C. canorus* eggs belonging to a single *C. canorus* race that confirm discrepancies between human and spectrophotometric estimates of mimicry. Therefore, studies in which humans assess

mimicry should be carefully considered, since the main selective force driving *C. canorus* egg appearance is rejection of poorly matching *C. canorus* eggs as assessed by hosts.

Secondly, geographical differences in preferences of female *C. canorus* by a host may also partially explain the low level of matching found by Moksnes & Røskaft (1995) in their analyses of *C. canorus* clutches in museums. In their study clutches parasitizing primary hosts in one geographical area were pooled with clutches of the same host from different areas where the host is only accidentally used by *C. canorus*. Since mimicry is expected to evolve as a consequence of rejection behaviour by the main hosts (Brooke & Davies, 1988), a generally poor match between *C. canorus* and host eggs is expected if clutches are pooled from different regions. This bias may be partially counteracted by the fact that unsuitable hosts are under-represented in egg collections in museums, since poor matching often induces higher rejection rates by hosts, reducing the probability of finding such nests in the field (Davies & Brooke, 1989a). However, nests with poor mimicry by *C. canorus* are probably more easily detected and thus more easily found by scientists searching for nests (Moksnes & Røskaft, 1995). In consequence, since the direction and the effect of these biases cannot be evaluated, analyses of the local relationship between *C. canorus* and their hosts are preferable (see Brooke & Davies, 1988; this study). Such analyses greatly reduce geographical biases and provide us with a more reliable scenario for testing hypotheses concerning the evolution of mimicry.

Interestingly, the degree of matching as estimated from the spectroradiometer was not perfect (Fig. 1). However, a perfect correlation in coloration between host and *C. canorus* eggs would never be expected in the system studied. Egg matching should be considered as perceived by the host but not as indicated by spectrophotometric measurements. The host decides to reject or accept the *C. canorus* egg on the basis of its perception of unmatching and thus it is the main force driving the evolution of mimicry. A perfect correlation in spectroradiometric measures of *C. canorus* and host eggs would only be expected if all the hosts had showed (1) similar spectral sensitivities, (2) similar perception of the risk of parasitism and (3) similar history with the parasite. Current evidence suggests that (1) among passerines there exists at least some small variation in spectral sensitivity (Cuthill *et al.*, 2000), (2) hosts may vary in their proneness to reject *C. canorus* eggs on the basis of their perception of the risk of being parasitized (Davies, Brooke & Kacelnik, 1996) and (3) time of sympatry between host and parasites may vary greatly (Davies & Brooke, 1989a). Thus, taking into account these sources of variation,

we can tentatively consider the level of matching shown in Figure 1 as good. However, future studies could usefully focus on these aspects.

In conclusion, we found support for the host preference hypothesis since a close match was detected between the appearance of *C. canorus* eggs and that of the eggs of suitable hosts within habitats in a single geographical area. Furthermore, the use of spectrophotometric techniques of colour assessment revealed the existence of previously undetected differences between *C. canorus* eggs and those of the hosts. Thus objective techniques of colour assessment are necessary in future studies of brood parasitism focusing on the evolution of mimicry.

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