Evolution of host egg mimicry in a brood parasite, the great spotted cuckoo

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Brood parasitism in birds is one of the best examples of coevolutionary interactions in vertebrates. Coevolution between hosts and parasites is assumed to occur because the parasite imposes strong selection pressures on its hosts, reducing their fitness and thereby favouring counter-adaptations (e.g. egg rejection) which, in turn, select for parasite resistance (e.g. egg mimicry). Great spotted cuckoos (*Clamator glandarius*) are usually considered a brood parasite with eggs almost perfectly mimicking those of their host, the magpie (*Pica pica*). However, *Cl. glandarius* also exploits South African hosts with very different eggs, both in colour and size, while the *Cl. glandarius* eggs are similar to those laid in nests of European hosts. Here, we used spectrophotometric techniques for the first time to quantify mimicry of parasitic eggs for eight different host species. We found: (1) non-significant differences in appearance of *Cl. glandarius* eggs laid in nests of different host species, although eggs laid in South Africa and Europe differed significantly; (2) contrary to the general assumption that *Cl. glandarius* eggs better mimic those of the main host in Europe (*P. pica*), *Cl. glandarius* eggs more closely resembled those of the azure-winged magpie (*Cyanopica cyana*), a potential host in which there is no evidence of recent parasitism; (3) the appearance of *Cl. glandarius* eggs was not significantly related to the appearance of host eggs. We discuss three possible reasons why *Cl. glandarius* eggs resemble eggs of some of their hosts. We suggest that colouration of *Cl. glandarius* eggs is an apomorphic trait, and that variation between eggs laid in South African and European host nests is due to genetic isolation among these populations and not due to variation in colouration of host eggs.   © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, **79**, 551–563.

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INTRODUCTION

Brood parasitism is a reproductive strategy adopted by approximately 1% of all bird species (Payne, 1977), consisting of laying eggs in the nests of another species, the host, which incubates and takes care of the brood parasitic offspring. Brood parasitism is very costly for parasitized hosts, almost eliminating host reproductive success (Payne, 1977; Rothstein, 1990; Soler, Martínez & Soler, 1996). Thus, brood parasitism induces a strong selection pressure on hosts, favouring host defenses against brood parasites, such as para-

site egg recognition and rejection. Foreign egg recognition by the host provides a strong selection pressure on the brood parasite, favouring the evolution of mimicry of host eggs. This host defense and brood parasite counter-defense could result in an evolutionary 'arms race' between hosts and brood parasites (Dawkins & Krebs, 1979).

Not all host species, however, are able to reject foreign eggs from their nests, this ability being highly variable among species (see data for European cuckoo (*Cuculus canorus*) hosts in Soler & Møller (1996) and for cowbirds (*Molothrus* sp.) in Rothstein (1975)). Variation in egg recognition by hosts has been explained by differences in duration of coevolution between the brood parasite and its hosts (Brooke & Davies, 1988;

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Soler & Møller, 1990). On the other hand, the degree of mimicry of brood parasite eggs varies among parasitizing species: In some, such as *Chrysococcyx lucidus* and *C. malayanus* (Brooker & Brooker, 1989) mimicry is absent, while in others, such as *Clamator jacobinus*, *Cl. coromandus*, *Cuculus varius*, and *Eudynamys scolopacea,* mimicry is almost perfect. These species have eggs showing geographical variation in colour patterns paralleling that of host eggs (see Baker (1923) for a detailed review of host and parasite egg appearance and mimicry). There are, however, other brood parasite species which mimic the eggs of different hosts and lay different eggs in nests of different host species thereby forming host races or gentes (Jourdain, 1925; Chance, 1940; Baker, 1942; Lack, 1968; Wyllie, 1981; Brooke & Davies, 1991). That is the case in species such as *Cuculus poliocephalus*, *Cuculus canorus* and *Hierococcyx sparveroides* (see Baker (1923) for a description of egg morphs of these species).

It is problematic to conclude that egg mimicry has evolved in brood parasite species as an evolutionary response to egg rejection by hosts. For example, the apparent egg mimicry of some cuckoos parasitizing only one or a small group of host species that are very closely related to one another, and that therefore have eggs with similar phenotypes, may not represent mimicry that has arisen due to coevolution. It is possible that egg colour and pattern of the brood parasite were similar to those of the current host species even before the brood parasite started to use these species as hosts. Therefore, the similarity between brood parasite eggs and those of the host may not always imply evolution. To detect a coevolutionary process resulting in mimicry, it is necessary to demonstrate a change in colour and/or pattern of eggs of the brood parasite depending on variation in colour and pattern of eggs of the different hosts used by the brood parasite. This is particularly the case in all brood parasite species with gentes, laying different kinds of eggs in the nests of different kinds of host species. For brood parasites parasitizing only a small number of hosts with eggs very similar to each other, it is necessary to demonstrate small changes in the eggs of the brood parasite depending on the egg pattern and/or colour of the different host species.

The great spotted cuckoo (*Clamator glandarius*) mainly parasitizes corvids, but also starlings and hoopoes. This brood parasite lays only one type of egg (Baker, 1923; Friedman, 1948; Alvarez, Arias de Reyna & Segura, 1976; Soler, 1990), which is elliptical to sub-elliptical with blunt ends, smooth and fairly glossy, pale green-blue in colour and thickly spotted, with light-brown or red-brown colour (Cramp, 1985). *Cl. glandarius* provides an example of the evolution of egg mimicry that has been much discussed. Baker

(1923, 1942) and Jourdain (1925) claimed that *Cl. glandarius* is a perfect example of complete evolution of mimicry. However, they only studied parasitism of magpies (*Pica pica*) and crows (*Corvus corone*) in Europe, which have eggs similar to those of the brood parasite. Friedman (1948) pointed out that in Africa this species parasitizes hosts with eggs different from those of the European corvids, including the pied starling (*Spreo bicolor*), which lays entirely blue eggs, and the black crow (*Corvus capensis*) which, uniquely among crows, lays pink eggs. In these cases, the eggs of *Cl. glandarius* do not mimic those of the South African hosts, and are very similar to those laid in Europe. Moreover, Friedman (1948) investigated possible differences in size between eggs of *Cl. glandarius* in Europe and in Africa, but found none.

Here we use spectrophotometric techniques to objectively quantify mimicry in eggs of *Cl. glandarius* laid in nests of eight different host species by determining egg colour of both *Cl. glandarius and* of the hosts in parasitized nests. We predicted that if egg mimicry has evolved in *Cl. glandarius*, parasitic eggs should differ among host species. Moreover, variation in *Cl. glandarius* egg appearance should be explained by variation in egg phenotype of the different hosts, giving rise to a positive relationship between the colour of the host eggs and the parasite eggs.

MATERIAL AND METHODS

MUSEUM EGG COLLECTIONS

Museum collections are potentially very important for studies on evolutionary ecology (Brooke, 2000). However, similar to other collections, egg collections for studies of brood parasites may be a biased source of data for several reasons (for discussion, see Moksnes & Røskaft, 1995). For example, host nests that contain cuckoo eggs with a low degree of mimicry will be more conspicuous and will therefore most probably be collected at a higher frequency. However, this bias is counteracted by the fact that many host species reject non-mimetic cuckoo eggs, and that the rejection rate increases as the degree of mimicry decreases (Davies & Brooke, 1988, 1989a; Brown *et al.*, 1990; Braa, Moksnes & Røskaft, 1992; Moksnes, 1992). There is also the possibility that some clutches from museum collections have been faked, and that cuckoo eggs may later have been added for exhibition purposes (Baker, 1942). Finally, some host clutches may contain odd eggs, which are host eggs misidentified as cuckoo eggs. However, the egg collection of the British Museum is continuously checked by the curator for such errors (M. Walters, pers. comm.), thereby reducing them. On the other hand, the use of museum egg collections has great advantages such as easy access to material and

no disturbance because of live animals or difficult field conditions (see Brooke, 2000).

We carefully checked for errors in all clutches of two of the host species, the magpie (*Pica pica*) and the carrion crow (*Corvus corone*), species that we have studied intensely in southern Spain for over a decade (see Soler, 1990; Soler & Soler, 2000; Soler *et al.*, 2002). The eggs of *Cl. glandarius* have considerable similarity with the eggs of these two hosts. We only found one supposedly parasitized *P. pica* clutch that may have held only *P. pica* eggs, and we removed this clutch from the analyses to avoid any bias. In all other host species, *Cl. glandarius* eggs are very easy to distinguish from those of the hosts based on egg size or colour patterns. Thus, it can be assumed that there are no errors in the museum data used in this study.

HOST SPECIES

We obtained reflectance values from all available host species parasitized by *Cl. glandarius* from the egg collections at the Zoological Museum in Tring, part of the British Natural History Museum (England), Bonn (Germany) and Helsinki (Finland). We analysed 127 *Cl. glandarius* eggs laid in 67 nests of eight different hosts: the brown-necked raven, *Corvus ruficollis* (4 nests: 14 host and 6 parasitic eggs); the black crow, *Corvus capensis* (4 nests: 9 host and 6 parasitic eggs); the pied crow, *Corvus albus* (7 nests: 22 host and 19 parasitic eggs); the carrion crow, *Corvus corone* (7 nests: 26 host and 11 parasitic eggs); the fan-tailed raven, *Corvus rhipidurus* (1 nest: 1 host and 3 parasitic eggs); the magpie, *Pica pica* (35 nests: 134 host and 72 parasitic eggs); the azure-winged magpie, *Cyanopica cyana* (6 nests: 20 host and 6 parasitic eggs); the pied starling, *Spreo bicolor* (3 nests: 6 host and 4 parasitic eggs).

Among these eight hosts, there are two clearly different categories of egg with respect to their volume: those of *Co. corone*, *Co. capensis*, *Co. albus* and *Co. rhipidurus* are larger than those of *P. pica*, *Cy. cyana* and *S. bicolor*; the eggs of *Co. ruficollis* are of an intermediate size (Fig. 1).

REFLECTANCE DATA AND ESTIMATION OF DEGREE OF MIMICRY

Previous studies focusing on the evolution of mimicry estimated resemblance between cuckoo and host eggs based on human perception (Moksnes & Røskaft, 1995; Edvardsen *et al.*, 2001), or measured the difference between the light reflected from cuckoo 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 observ-

ers cannot perceive ultraviolet (UV) light (300–400 nm), information that birds can detect due to the sensitivity of one cone in their retina (Bowmaker *et al.*, 1997). Because the main selective forces driving evolution of egg colour in cuckoos 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 (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 range visible to humans (400–700 nm). Moreover, human and spectrophotometric measures have simultaneously been used to assess egg mimicry in a recent study (Cherry & Bennett, 2001), and 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 cuckoo egg might be the consequence of a lower reflectance in any of the UV (300–400 nm), blue (400–475 nm), green (475–550), yellow (550–625 nm) or red (625–700 nm) regions of the avian visual spectra, with apparent mimicry of the host egg 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 arbitrarily selected areas of the surface of the eggs, each *c*. 1 mm². 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 egg. Total reflectance was obtained over intervals in the UV (300–400 nm), blue (400–475 nm), green (475–550 nm), yellow (550–625 nm) and red (625–700 nm) regions of the spectrum. Estimation of the mean reflectance in these light intervals was obtained by
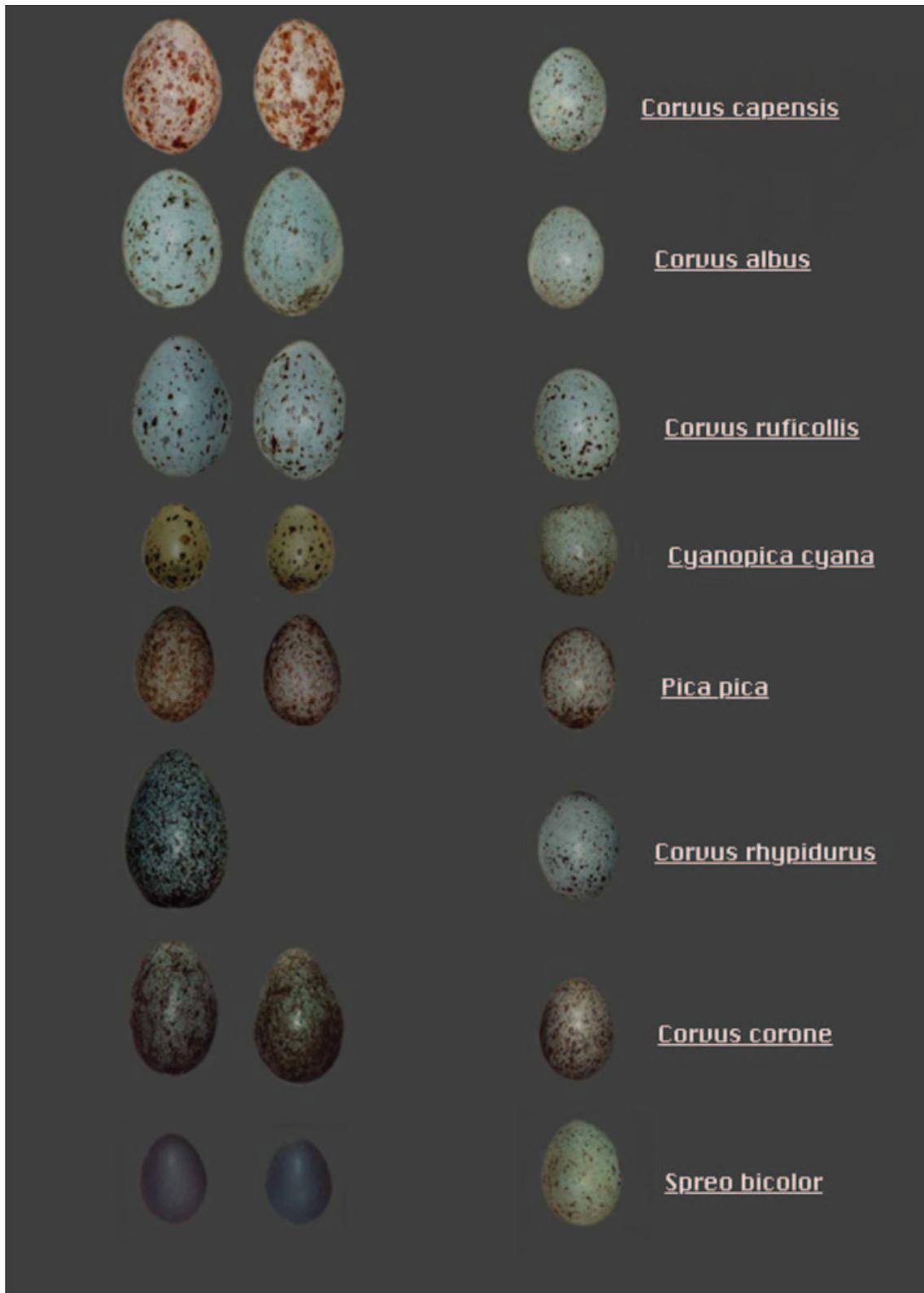
Figure 1. *Clamator glandarius* eggs in the nests of the eight hosts used in this study. The two left-hand columns show eggs of the species parasitized by *Clamator glandarius*. The right-hand column shows *Clamator glandarius* eggs laid in the nests of the corresponding host.

dividing the total reflectance over each interval by its amplitude in nm.

Consistency of reflectance data 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 ($r > 0.95$; $P < 0.0001$). Then we measured each egg in two arbitrarily selected areas and found a significant repeatability ($r = 0.90$; $P < 0.001$). Consequently, all our measurements were reliable and, thus, we used mean values for each egg for each established light interval.

To estimate the degree of mimicry between host and parasite eggs we first calculated the absolute differences of mean reflectance values in the UV, blue, green, yellow, and red wavelengths between all host and *Cl. glandarius* eggs in the same clutch. Mean values of these absolute differences were considered to represent the degree of mimicry by *Cl. glandarius* eggs of those of the hosts. Looking at differences in reflectance over these five intervals is the only objective way for assuring mimicry between the *Cl. glandarius* eggs and those of the host because microspectrophotometric studies of the visual pigments of the hosts of *Cl. glandarius* are lacking and therefore sensitivities of the different hosts at different wavelengths cannot be estimated. Moreover, information from microsprectophotometry only exists for seven passerines (Cuthill *et al.*, 2000). Among these species the most closely related to the *Cl. glandarius* hosts is the rook (*Corvus frugilevus*) in which only the situation of the spectral cones at medium and large wavelengths has been determined.

When evolution of mimicry occurs, differences between cuckoo eggs and those of their hosts will depend on the duration of coevolutionary interaction between the parasite and a specific host which may be independent of the phylogenetic relationships among hosts. Thus, we did not correct for possible phylogenetic effects when analyzing the level of mimicry between parasitic 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. We performed a principal component analysis (PCA) resulting in a single axis explaining 93.6% of the total variance in colour variables, scores from this axis being highly and positively related to all colour variables ($r > 0.95$). Thus, we used the scores from the PCA analysis as an additional variable in our analyses due to the possibility of *Cl. glandarius* egg mimicry mainly occurring for only one colour.

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 blue wavelengths of host eggs (Kolmogorov–Smirnov test for continuous variables, $P < 0.10$). However, after logarithmic transformation, the frequency distribution did not differ from normality (Kolmogorov–Smirnov test for continuous variables, $P > 0.20$). Thus, we used transformed data for this variable in our statistical analysis but show mean values for untransformed data in the text and figures. Variables related to differences among parasitic and non-parasitic eggs in the same nest did not differ from normal distributions (Kolmogorov–Smirnov test for continuous variables, $P > 0.20$), so we used parametric tests. Throughout we applied sequential Bonferroni correction for the probability of a type-I error when using two or more tests for checking a common null hypothesis (Rice, 1989). Unless otherwise stated, values in text, figures and tables are means ± SE.

RESULTS

Figure 2 shows mean reflectance values in the UV, blue, green, yellow and red regions of the spectrum, as well as mean values of scores from the PCA, of different host eggs and those of *Cl. glandarius* laid in the nests of different hosts.

Eggs of the eight host species differed in their mean reflectance values in the five regions of the spectrum, and in their mean scores from the PCA (Table 1, Fig. 2). However, after sequential Bonferroni correc-

Table 1. Comparisons of egg appearance of host and great spotted cuckoo eggs among different host species and great spotted cuckoo eggs laid in nests of different host species

Spectrum	F	MS	d.f.	P
Host eggs				
Ultraviolet	3.83	111.51	7, 58	0.0017*
Blue	4.58	245.87	7, 58	0.0006*
Green	4.88	317.14	7, 58	0.0002*
Yellow	5.59	309.36	7, 58	0.0005*
Red	9.32	274.45	7, 58	0.0000*
PCA	4.42	2.80	7, 58	0.0005*
Clamator glandarius eggs				
Ultraviolet	2.72	26.32	7, 58	0.017
Blue	0.68	10.34	7, 58	0.69
Green	0.67	11.31	7, 58	0.70
Yellow	2.67	35.93	7, 58	0.018
Red	3.48	26.69	7, 58	0.0034*
PCA	1.47	0.23	7, 58	0.20

*$P < 0.05$ after sequential Bonferroni correction. PCA = principal component analysis.
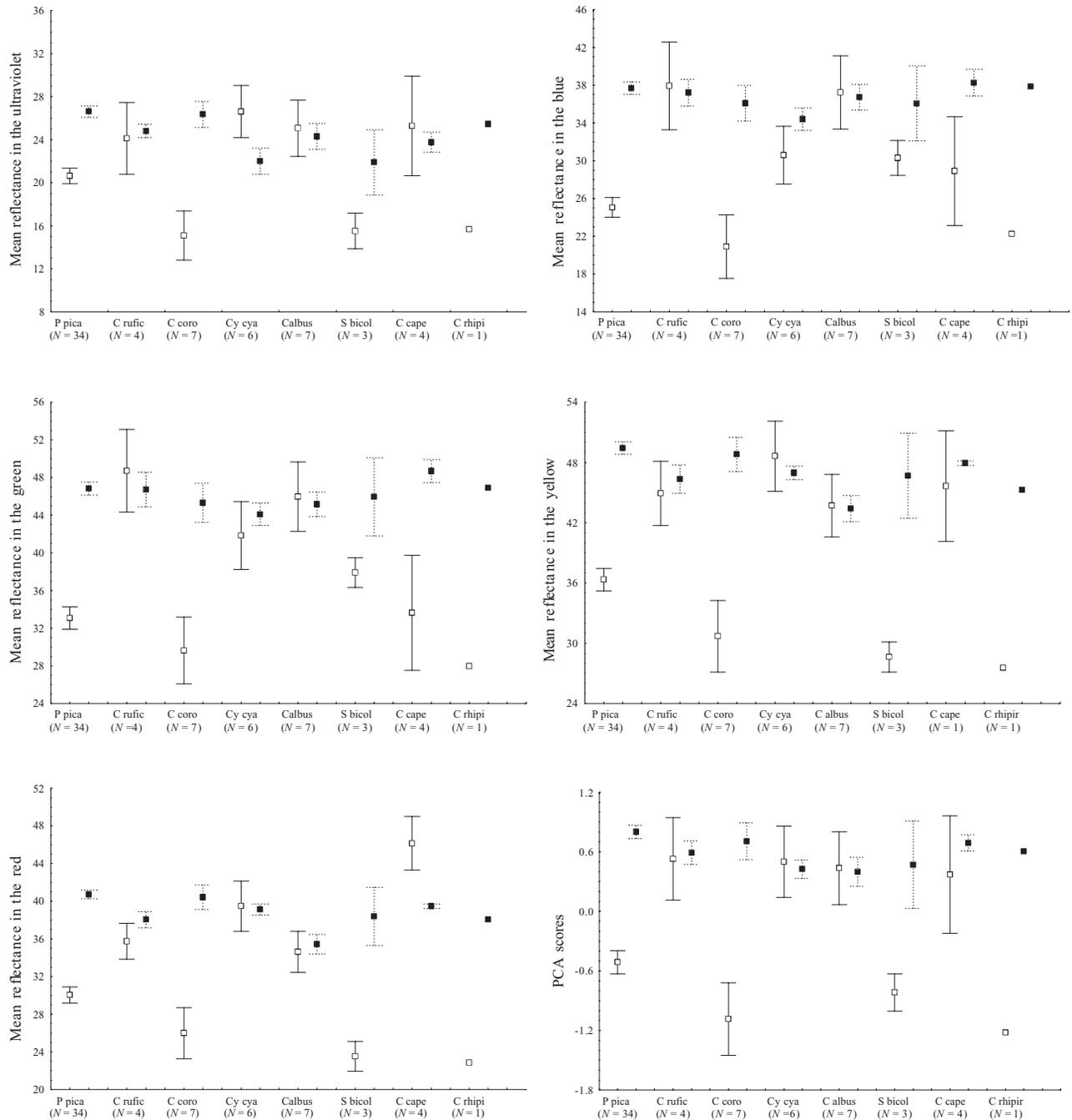
Figure 2. Mean reflectance in the ultraviolet, blue, green, yellow and red regions of the spectrum of *Clamator glandarius* eggs (■) laid in the nests of eight different host species. Reflectance values of host eggs (□) are also shown. Values are means (SE). P pica = *Pica pica*, C rufic = *Corvus ruficollis*, C coro = *Corvus corone*, C cya = *Cyanopica cyana*, C albus = *Corvus albus*, S bicol = *Spreo bicolor*, C cape = *Corvus capensis*, C rhipi = *Corvus rhipidurus*.

tion, *Cl. glandarius* eggs laid in nests of different host species only differed for red reflectance (Table 1).

Cl. glandarius eggs laid in nests of *Cy. cyana* and *Co. ruficollis* closely matched the host eggs in appearance (Table 2; Fig. 2). Moreover, the largest differ-

ences between *Cl. glandarius* and host eggs appeared in some of their main current hosts in Europe: *P. pica* (parasitism rate in Spain = 28.0% (Soler *et al.*, 1999)) and *Co. corone* (parasitism rate in Spain = 7.4% (Soler *et al.*, 2002)). The eggs of the remaining European

Table 2. Mean absolute differences between colour variables of *Clamator glandarius* eggs and those of the hosts

Species	Ultraviolet	Blue	Green	Yellow	Red	PCA
Pica pica	6.67 (0.53)	13.05 (0.96)	14.22 (1.05)	13.48 (0.97)	10.82 (0.77)	1.36 (0.09)
Corvus ruficollis	4.32 (1.94)	5.051 (1.79)	4.79(1.63)	4.40 (0.99)	3.27 (1.37)	0.51 (0.16)
Corvus corone	11.27 (2.35)	15.18 (3.38)	15.68 (3.49)	18.10 (3.63)	14.43 (2.79)	1.79 (0.36)
Cyanopica cyana	5.33 (1.46)	4.68 (2.12)	5.22 (1.92)	5.99 (1.26)	4.20 (1.30)	0.59 (0.10)
Corvus albus	4.95 (1.92)	7.68 (2.66)	7.21 (2.68)	6.94 (2.37)	5.45 (1.52)	0.77 (0.26)
Spreo bicolor	6.38 (2.72)	5.77 (3.17)	8.05 (3.35)	18.06 (4.86)	14.88 (3.95)	1.29 (0.43)
Corvus capensis	6.51 (3.00)	11.74 (3.05)	15.05 (5.38)	9.07 (2.17)	6.67 (2.97)	0.96 (0.22)
Corvus rhipidulus	9.80 (–)	15.60 (–)	18.95 (–)	17.70 (–)	15.20 (–)	1.83 (–)
All species	6.74 (0.52)	11.09 (0.83)	12.08 (0.92)	12.05 (0.87)	9.58 (0.71)	1.20 (0.08)

Values are mean (SE).
PCA = principal component analysis.

Table 3. Comparisons of appearance of *Clamator glandarius* eggs and of the absolute differences between host and *Cl. glandarius* eggs between Europe and South Africa

	Europe (N = 47)	South Africa (N = 19)	$F_{(1,64)}$	MS	P
Absolute differences between *Clamator glandarius* and host eggs					
Ultraviolet	7.18 (0.59)	5.62 (1.06)	1.82	32.73	0.18
Blue	12.30 (0.98)	3.09 (1.40)	5.56	239.22	0.021
Green	13.28 (1.03)	9.09 (1.78)	4.44	237.50	0.038
Yellow	13.21 (0.99)	9.17 (1.60)	4.65	220.44	0.034
Red	10.51 (0.80)	7.24 (1.57)	4.50	144.31	0.037
PCA	1.32 (0.10)	0.89 (0.14)	5.78	2.59	0.019
Clamator glandarius eggs laid in nests of two categories of hosts					
Ultraviolet	25.99 (0.49)	23.97 (0.66)	5.12	55.28	0.027
Blue	37.01 (0.58)	37.10 (0.82)	0.07	0.10	0.03
Green	46.25 (0.60)	46.65 (0.88)	0.02	0.49	0.86
Yellow	49.03 (0.53)	45.59 (0.88)	11.68	159.45	0.001
Red	40.47 (0.40)	37.44 (0.68)	15.70	124.37	0.0001
PCA	0.73 (0.05)	0.52 (0.08)	4.05	0.64	0.04

Values are mean (SE).
PCA = principal component analysis.

host, *Cy. cyana*, for which there is no evidence of parasitism in current populations (Arias de Reyna, 1998), closely match those of *Cl. glandarius*. Although this pattern does not occur in Africa (*Co. albus* parasitism rate in South-Africa and Zimbabwe = 13% (Fry, Keith & Urban, 1988) and in Nigeria = 21.7% (N = 23, Mundy & Cook, 1977); *Co. capensis* parasitism rate in South Africa and Zimbabwe = 10% (Fry *et al.*, 1988)) (Table 2), differences between parasitic and host eggs in nests of *S. bicolor* (another common host in South Africa and Zimbabwe, parasitism rate = 5% (Fry *et al.*, 1988)), are large, and *Cl. glandarius* eggs laid in nests of the three common host species in South Africa are very similar (Table 2).

Cl. glandarius may lay eggs of different appearance in South Africa and Europe, or a single morph of *Cl. glandarius* egg may be more similar to eggs of South African hosts than to eggs of European hosts. The first suggestion has some support because *Cl. glandarius* eggs laid in South Africa reflected less in the yellow and red wavelengths than did those laid in Europe (Table 3). However, South African hosts laid more red eggs (Europe mean (SD) = 30.64 (6.56); Africa = 34.91 (8.82); $F_{1,64} = 4.66, P = 0.034$) and yellow eggs (Europe mean (SD) = 37.07 (8.60); Africa = 41.14 (9.84); $F_{1,64} = 2.77, P = 0.1$). Thus, differences between *Cl. glandarius* eggs laid in different continents are not related to differences in colour of host eggs. With

respect to the second possible explanation, after Bon-ferroni correction, South African *Cl. glandarius* eggs did not match those of their respective hosts better than did European *Cl. glandarius* eggs (Table 3). However, all mean values are in the predicted direction with differences between *Cl. glandarius and* host eggs laid in the same nest being smaller in South Africa than in Europe.

Cl. glandarius eggs laid in nests of *Cy. cyana*, *Co. ruficollis*, and *Co. albus* closely match those of their hosts (Table 2; Fig. 2). Since *Co. ruficollis* and *Co. albus* are currently the most common hosts in South Africa (see above), we further explored the possibility of *Cl. glandarius* eggs in this area, but not in Europe, mimicking eggs of its main hosts. We classified hosts in Europe and South Africa as primary or secondary hosts based on the literature (% of parasitism, see above), and compared degree of mimicry (i.e. absolute differences between *Cl. glandarius and* host eggs in the same nest) and colour variables for these two categories of species (Tables 4, 5). While we did not find statistically significant differences for any of the analyzed variables using clutches from South Africa, we found for Europe that *Cl. glandarius* eggs matched those of the secondary hosts significantly better than those of the primary hosts.

A further prediction of the hypothesis of *Cl. glandarius* mimicking host eggs is that colour variables of host eggs should explain a significant proportion of the variance in the colour of *Cl. glandarius* eggs laid in nests of different host species (see Introduction). However, we did not find support for this prediction since host egg colour variables did not explain a significant amount of variance in those of *Cl. glandarius* (Fig. 3). Although similarity between eggs of two of the main hosts in South Africa is large, our data suggest that *Cl. glandarius* eggs do not mimic those of its current main hosts. First, parasitic eggs do not vary according to egg colour of *Cl. glandarius* hosts in Africa and Europe. Second, at least in Europe, *Cl. glandarius* egg colour better resembles eggs of hosts not currently parasitized.

DISCUSSION

Brood parasitism in birds is one of the best examples of coevolutionary interactions in vertebrates (Davies & Brooke, 1988, 1989a,b; Moksnes *et al.*, 1990; Rothstein, 1990; Davies, Brooke & Kacelnik, 1996). Coevolution between hosts and parasites is assumed to occur because the parasites impose strong selection pressures on the hosts, reducing their fitness, thereby favouring counter-adaptations (e.g. egg rejection), which in turn select for parasite resistance (e.g. egg mimicry) (see Brooker & Brooker (1990) and Brooker, Brooker & Brooker, (1990) for an alternative explanation of cuckoo egg mimicry).

There are clear examples demonstrating that the appearance of eggs of certain brood parasite species is related to the appearance of eggs of their main hosts

Table 4. Comparisons of appearance of *Clamator glandarius* eggs and of absolute differences between host and *Cl. glandarius* eggs in relation to host suitability in Europe

	Primary hosts *Pica pica* *Corvus corone* (N = 41)	Secondary host *Cyanopica cyana* (N = 6)	$F_{(1,45)}$	MS	P
Absolute differences between *Clamator glandarius* and host eggs					
Ultraviolet	7.45 (0.64)	5.32 (1.46)	1.44	23.68	0.24
Blue	13.41 (0.96)	4.67 (2.12)	10.70	399.49	0.002
Green	14.47 (1.03)	5.22 (1.92)	10.70	447.65	0.002
Yellow	14.26 (1.03)	5.98 (1.26)	9.01	358.74	0.004
Red	11.43 (0.81)	4.20 (1.30)	10.89	274.22	0.001
PCA	1.43 (0.10)	0.59 (0.10)	9.40	3.74	0.003
Clamator glandarius eggs laid in nests of the two groups of host species					
Ultraviolet	26.58 (0.48)	22.00 (1.23)	11.49	109.72	0.001
Blue	37.40 (0.62)	34.39 (1.18)	3.11	47.21	0.08
Green	46.57 (0.66)	44.09 (1.18)	1.90	32.24	0.17
Yellow	49.33 (0.58)	46.96 (0.66)	2.27	29.23	0.13
Red	40.67 (0.44)	39.11 (0.58)	1.70	12.62	0.19
PCA	0.78 (0.06)	0.42 (0.09)	4.41	0.67	0.04

Values are mean (SE).
PCA = principal component analysis.

Table 5. Comparisons of appearance of *Clamator glandarius* eggs and of absolute differences between host and *Cl. glandarius* eggs in relation to host suitability in South Africa

	Primary hosts *Corvus albus* *Corvus ruficollsis* *Spreo bicolor* (N = 14)	Secondary hosts *Corvus capensis* *Corvus rhipidurlus* (N = 5)	$F_{(1,17)}$	MS	P
Absolute differences between Clamator glandarius and host eggs					
Ultraviolet	5.70 (1.31)	5.41 (1.86)	0.01	0.30	0.90
Blue	8.42 (1.72)	7.16 (2.52)	0.15	5.92	0.70
Green	9.62 (2.20)	7.62 (3.10)	0.23	14.81	0.63
Yellow	9.93 (1.95)	7.05 (2.77)	0.60	30.42	0.44
Red	7.81 (1.64)	5.65 (2.61)	0.46	17.19	0.50
PCA	0.93 (0.16)	0.77 (0.29)	0.24	0.10	0.62
Clamator glandarius eggs laid in nests of the two groups of host species					
Ultraviolet	23.63 (0.87)	24.94 (0.49)	0.74	6.33	0.40
Blue	37.02 (1.06)	37.33 (1.11)	0.26	0.35	0.87
Green	46.33 (1.11)	46.76 (1.42)	0.04	0.68	0.83
Yellow	45.40 (1.14)	46.12 (1.12)	0.12	1.86	0.73
Red	37.22 (0.90)	38.05 (0.66)	0.27	2.54	0.60
PCA	0.49 (0.11)	0.59 (0.09)	0.23	0.03	0.63

Values are mean (SE).
PCA = principal component analysis.

(see review in Rothstein, 1990). Host rejection of eggs unlike their own has selected for the evolution of host egg mimicry by the European cuckoo (Davies & Brooke, 1988), resulting in sympatric host-specific subgroups (gentes) of cuckoos that lay eggs matching those of their particular host species (Brooke & Davies, 1988; Moksnes & Røskaft, 1995; Gibbs, Brooke & Davies, 1996).

Some scientists have considered the *Cl. glandarius* to be an example of a brood parasite that mimics the size and colour of host eggs (Lack, 1968; Alvarez & Arias de Reyna, 1974). However, eggs of *Cl. glandarius* are very similar independent of host species (Friedman, 1948). In accordance with this statement, we showed that the phenotypes of eggs of *Cl. glandarius* laid in the nests of different host species were similar for several colour variables (Table 1). Moreover, eggs of the main European hosts differed the most from those of *Cl. glandarius* (Table 2). Finally, variation in colour of *Cl. glandarius* eggs did not depend on the appearance of those of the host (Fig. 3). Therefore, it seems likely that mimicry has not evolved in this brood parasite, at least in Europe.

Surprisingly, *Cl. glandarius* eggs mimicked the eggs of *Cy. cyana* (Table 2; Fig. 2), which is a species currently not being parasitized (Arias de Reyna, 1998). However, seven clutches of *Cy. cyana* parasitized by *Cl. glandarius* were collected from Spain and Portugal at the end of the 19th century and kept in the British Museum of Natural History. The higher degree of similarity between parasitic and host eggs in nests of *Cy. cyana* relative to that in nests of other hosts is mainly due to variation in egg colour of different host species, but not to parasite eggs laid in *Cy. cyana* nests differing from those laid in nests of primary host species (Table 2). There are three different explanations for the apparent mimicry of eggs of *Cy. cyana*. First, it is possible that *Cl. glandarius* once exploited mainly *Cy. cyana* as hosts, but when recognition ability spread in the host population, *Cl. glandarius* switched to *P. pica* and *Co. corone* as hosts. Second, *Cl. glandarius* eggs probably mimic eggs of African hosts because this parasite evolved in Africa (Voous, 1960; but see Friedman, 1964). The larger similarity of eggs of *Cy. cyana* to those of *Cl. glandarius* may simply be due to eggs of *Cy. cyana* being more similar to the eggs of African hosts. Finally, appearance of *Cl. glandarius* eggs may not have evolved and similarity between host and parasite eggs may simply be due to chance.

In accordance with the first explanation, *Cy. cyana* ejects non-mimetic eggs from nests at a similar rate to that of *P. pica* (*P. pica*: 50%, N = 138 (Soler *et al.*, 1999); *Cy. cyana*: 62.5%, N = 23 (Arias de Reyna & Hidalgo, 1982; Arias de Reyna, 1998)). Because brood parasitism is the most likely explanation for the evolution of ability to recognize foreign eggs (Davies & Brooke, 1989b), *Cy. cyana* may previously have been heavily exploited by brood parasites (Arias de Reyna,
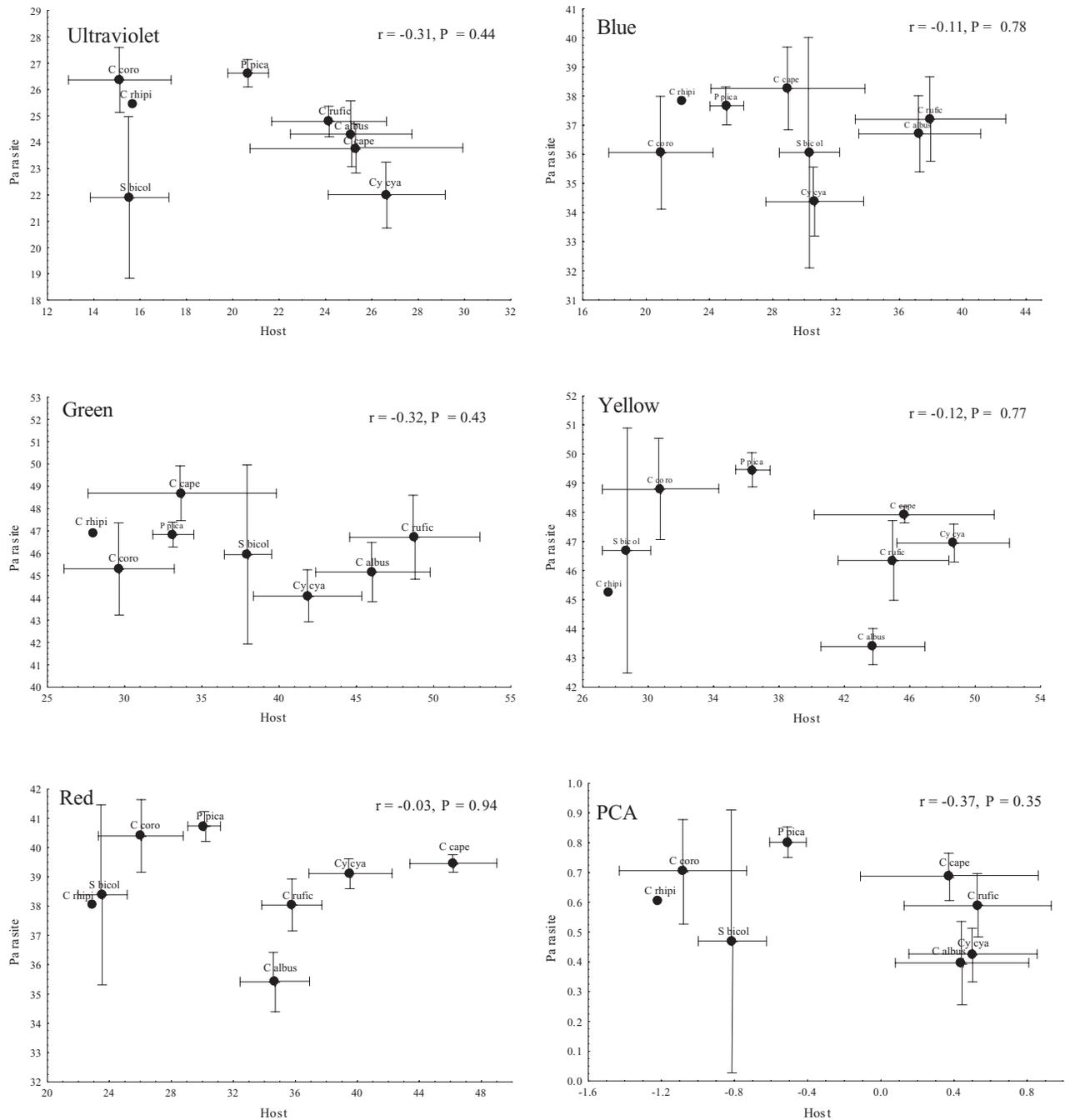
Figure 3. Relationship between mean values of ultraviolet, blue, green, yellow, and red regions of the spectrum and PCA values of *Clamator glandarius* eggs and those of their hosts. Although correlation coefficients were estimated using mean values per species, horizontal and vertical bars show SE for host and parasite eggs, respectively. Abbreviations as in Fig. 1.

1998). There are fossil records from the Pleistocene (Cooper, 2000) of *Cy. cyana*, *Cl. glandarius* and of *P. pica* from Europe (Tyrberg, 1998), and the opportunity for coevolution between *Cl. glandarius* and *Cy. cyana* is at least possible. Moreover, *Cl. glandarius* nestlings grew at a similar rate when raised by *P.*

pica and by *Cy. cyana*, demonstrating that it is a suitable host for *Cl. glandarius* (Arias de Reyna, 1998). However *Cl. glandarius* eggs laid in *P. pica* and *Co. corone* nests are similar to those laid in *Cy. cyana* nests, contrary to this first explanation (Fig. 1; Table 4). *P. pica* has been the main European host of

Cl. glandarius for a long time, with some populations ejecting 100% of non-mimetic *Cl. glandarius* eggs (Soler *et al.*, 1999). If *Cl. glandarius* were able to mimic eggs of their main hosts, current *Cl. glandarius* eggs should increasingly reflect at green and blue wavelengths and decreasingly in red and yellow regions (Fig. 2). However, this is far from the case because *Cl. glandarius* eggs in Europe are more red and yellow than are those in Africa (see below), where hosts lay almost completely red eggs. Although this possibility cannot be excluded, it seem unlikely that the similarity between eggs of *Cl. glandarius* and *Cy. cyana* is due to evolution of mimetic eggs during previous coevolutionary interactions.

In accordance with the second explanation, eggs of *Cy. cyana* better matched those of the African than the European hosts (Fig. 2). However, eggs of the African hosts are more red and yellow than those of the European hosts, while *Cl. glandarius* eggs show the opposite pattern when comparing eggs laid in Africa and Europe (Table 3). Under this hypothesis, *Cl. glandarius* eggs in Africa should not change when an African population starts to exploit European hosts. However, we found significant differences between *Cl. glandarius* eggs laid in Africa and Europe. This continental variation of *Cl. glandarius* eggs may be explained as an effect of random genetic drift due to a very low level of gene flow between these populations. In accordance with this hypothetical genetic isolation two different races of *Cl. glandarius* have been described, one in South Africa and the other in Europe (Payne, 1997). Although this second explanation cannot be rejected because *Cy. cyana* lays eggs similar in colour to those laid by the South African host, we consider it to be unlikely. First, parasitic eggs in Africa and Europe differ significantly in appearance. Second, *Cl. glandarius* parasitizing European hosts should start to produce eggs that more closely resemble host eggs, which is not the case.

Finally, *Cl. glandarius* eggs may mimic neither South African nor European host eggs, and colour of *Cl. glandarius* eggs may just be an apomorphic trait closely related to ancestral egg colouration of the genus *Clamator*. This explanation can be tested by determining whether *Cl. glandarius* eggs, on average, mimic those of their South African hosts. However, these hosts lay very different eggs, from completely blue with no spots to white with red spots, while *Cl. glandarius* eggs vary little among different host species. In addition, *Cl. glandarius* eggs laid in nests of primary and secondary hosts in South Africa did not differ, and *Cl. glandarius* eggs equally matched eggs of primary and secondary hosts. Finally, the host eggs that best match *Cl. glandarius* eggs are those of a European host, *Cy. cyana*. Thus, it is very difficult to explain mimicry as a result of coevolution between *Cl. glandarius* and *Cy. cyana* because the most likely

origin of *Cy. cyana* is Asia (Voous, 1960) where *Cl. glandarius* is absent. However, Friedman (1964) suggested the ancestral great spotted cuckoo to have arisen in Asia, although he did not support this claim. If true, this would imply an early coevolutionary process between *Clamator* and *Cyanopica* resulting in parasitic species mimicking eggs of the host species.

Although we cannot entirely reject any of the three possible explanations, we believe that the third one is the most likely. Thus we consider that egg mimicry has not evolved in *Cl. glandarius*, and that different levels of similarity between parasitic eggs and eggs of different host species is just a random event.

The evolution of mimicry is assumed to occur due to selection pressure arising from host egg recognition and ejection of brood parasite eggs. Information on the ability of hosts of *Cl. glandarius* to recognize *Cl. glandarius* eggs only exists for *P. pica* (50%, see above), *Co. corone* (0%, Soler, 1990), and *Cy. cyana* (62.5%, see above). Thus we cannot test this relationship at the moment.

Alternative hypotheses to the arms-race hypothesis may provide an explanation for host specialization in cuckoos and egg colour variation in hosts (Brooker & Brooker, 1990). Egg colour variation in birds is likely to occur as a response to selection pressures imposed by predators in different environments like the material used for nest building resulting in different colours of nest cups or different types of nests (open, semiopen or hole nests) (Collias & Collias, 1984). Since different host species differ under different environmental conditions, it is possible that lack of covariation in brood parasitic eggs and those of the hosts may have appeared because of similar environmental conditions for all host species. However, host eggs, which should primarily be under selection pressure due to environmental conditions, should differ in colour with no covariation with colour of *Cl. glandarius* eggs laid in different host nests (Fig. 3). This hypothesis on the evolution of colour egg morphs in birds is not supported by our results, since it predicts similar results to the arms-race hypothesis.

In summary, we found support for the hypothesis that *Cl. glandarius* eggs do not mimic those of their current main hosts because there is a lack of variation among *Cl. glandarius* eggs laid in nests of different host species. Different degrees of similarity between *Cl. glandarius* and host eggs in different species is likely to be due to different host eggs being more or less similar to the original single apomorphic *Cl. glandarius* egg morph.

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