

A comparative analysis of the evolution of variation in appearance of eggs of European passerines in relation to brood parasitism

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Hosts of brood parasites increase the ability of rejecting cuckoo eggs by production of (1) a clutch with little variation among eggs and (2) a clutch that differs the most from the modal phenotype of the population. These hypotheses have been tested by Øien et al. (1995), although they did not control for common phylogenetic ancestry. We analyze the evolution of egg color and marking patterns in European passerines, which are potential hosts of the European cuckoo (*Cuculus canorus*), using Felsenstein's (1985) independent comparative method to control for the effect of common phylogenetic descent. We found a significant positive relationship between interclutch variation in appearance of host eggs and parasitism rate, but this relationship disappeared when hole-nesting species were excluded from the analysis; and we found a highly significant multiple regression between rejection rate and intra- and interclutch variation in egg appearance, even when hole nesters were excluded from the analysis. The partial correlation coefficients were negative for intraclutch variation and positive with interclutch variation in agreement with the hypotheses. Therefore, the use of the independent comparative method strengthens the hypothesis that the evolution of egg patterns in hosts is associated with different stages of coevolution with the brood parasite. *Key words:* brood parasitism, coevolution, *Cuculus canorus*, egg recognition, evolution of pattern and color of host eggs. [*Behav Ecol* 7:89–94 (1996)]

For some time, it has been accepted that species cannot be treated as independent data points in comparative studies because this procedure assumes that the characters investigated have evolved independently in each species. However, species may demonstrate similarity in characters due to effects of common phylogenetic descent (e.g., Harvey and Pagel, 1991). There are many examples where the lack of control for common phylogenetic ancestry among species leads to erroneous conclusions (see examples in Harvey and Pagel, 1991). A recent study of the effects of an obligate brood parasite on the appearance of the eggs of its host, although the conclusions were not erroneous, illustrate these points.

Hosts of brood parasitic cuckoos rear cuckoo offspring, often at a high fitness cost (Rothstein, 1990). Hosts may increase their probability of recognizing and hence rejecting cuckoo eggs by production of a clutch with little variation among eggs and by production of eggs that differ the most from the most common phenotype in the population (Davies and Brooke, 1989a; Møller and Petrie, 1991; Øien et al., 1995).

Variation in egg color and markings in European passerines have been related to (1) the responses of passerine hosts towards the eggs of the European cuckoo (*Cuculus canorus*) (level of egg rejection) and (2) their suitability as cuckoo hosts (Øien et al., 1995). However, the authors did not control for common phylogenetic ancestry, and they stated, "in our present analyses, however, it is probably not correct to treat each species as an independent unit because of phylogenetic constraints" (169). They also argued that the phylogeny of the European passerines is poorly known, but this argument is not completely justifiable because there are many examples

where a traditional phylogeny based on morphology (traditional taxonomy) has been used (e.g., Hartley and Davies, 1994; Owens and Bennett, 1994). Moreover, several recent studies have suggested that phylogenies based on molecular changes may also include inaccuracies (Harvey et al., 1992; Nee et al., 1993). Therefore, it is always preferable to use the available information rather than making no analyses at all, although analyses should be revised when the phylogeny involved becomes better known (Garland et al., 1991).

In this article, we complement the analysis of the evolution of egg color and marking patterns in European passerines using the phylogenetic classification in Howard and Moore (1991).

METHODS

We used the intra- and interclutch variation from Øien et al. (1995). They estimated this variation based on photographs of clutches of different species and scored from 1 to 5 depending on their intra- and interclutch variation (for more information see Øien et al., 1995).

Apparently, using parasitism rate and rejection rate as a good "index" of the duration and the intensity of the co-evolutionary arms race between hosts and parasites species has some problems.

(1) Geographic variation in parasitism rate exists, and the duration of presumed sympatry is not the same for all populations (Soler and Møller, 1990). Therefore, following the hypotheses, parasitism rate and rejection rate could be affected by the locality. However, the parasitism rate and rejection rate data we used in the comparative analyses were mainly from England, while the analyzed clutches mainly came from Denmark. To know whether the use of data from different countries would affect the results of the comparative analysis or whether potential host species are consistent in their frequency of parasitism and rejection rate in different populations, we calculated the repeatability (Becker, 1984) of both vari-

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Received 24 November 1994; first revision 10 February 1995; second revision 10 April 1995; accepted 10 April 1995.

1045-2249/96/\$5.00 © 1996 International Society for Behavioral Ecology

Table 1
Parasitism rate and rejection rate of host species used in the comparative analyses for which there was information from different countries

Species	Parasitism rate (%)	Rejection rate (%)
<i>Hirundo rustica</i>		0.0(j) 0.0(k)
<i>Motacilla alba</i>	0.42(a) 0.00(d)	71.0(j) 100.0(k)
<i>Motacilla flava</i>	0.13(c) 0.00(d)	
<i>Anthus pratensis</i>	2.66(a) 6.40(d)	48.3(j) 8.3(k)
<i>Prunella modularis</i>		5.9(j) 0.0(k)
<i>Turdus philomelos</i>	0.01(b) 0.00(d)	58.5(j) 80.0(k)
<i>Turdus iliacus</i>	0.00(c) 0.00(d)	
<i>Oenanthe oenanthe</i>	0.00(a) 0.00(d)	7.7(j) 0.0(k)
<i>Phoenicurus phoenicurus</i>		25.0(j) 12.8(k) 35.0(l) 22.2(m)
<i>Erithacus rubecula</i>	17.24(g) 0.29(a) 0.06(c) 0.00(d)	
<i>Phylloscopus trochilus</i>	50.53(e) 20.59(f)	
<i>Acrocephalus arundinaceus</i>	5.54(a) 23.13(b)	
<i>Acrocephalus scirpaceus</i>	1.90(a) 16.00(h)	
<i>Muscicapa striata</i>		88.9(j) 55.6(k)
<i>Ficedula hypoleuca</i>	0.00(a) 0.00(i)	0.0(j) 0.0(k)
<i>Parus caeruleus</i>		16.7(j) 0.0(k)
<i>Sturnus vulgaris</i>		57.1(j) 7.1(k)
<i>Carduelis chloris</i>		0.0(j) 41.2(k)
<i>Fringilla coelebs</i>		60.0(j) 68.8(k)
<i>Emberiza schoeniclus</i>	0.15(a) 4.50(d)	100.0(j) 90.9(k)

Parasitism rate data were extracted from (a) Davies and Brooke (1989b), (b) Lack (1963), (c) Glue and Murray (1984), (d) Moksnes and Røskaft (1987), (e) Wyllie (1981), (f) Lotem et al. (1992), (g) Blaise (1965), (h) Cramp (1985), and (i) von Haartman (1976). We have used all passerine species in Sharrock (1977), and we assume that the parasitism rate of all species not reported to be parasitized in the previous references to be zero. The rejection rate data are from (j) Davies and Brooke (1989a), (k) Moksnes et al. (1990), (l) Järvinen (1984) and (m) von Haartman (1981).

ables for species in which data were available in the literature for at least two different countries (Table 1). The repeatability of parasitism rate was 0.44 (SE = 0.21) ($F = 2.80$, $df = 12,15$, $p = .03$) and of rejection rate it was 0.73 (SE = 0.13) ($F = 7.12$, $df = 13,16$, $p = .0002$). Therefore, since the repeatability of both variables was significant, we had no apparent reason to assume that the conclusions of the comparative analyses should be invalidated by the use of data from different localities. Obviously, the relationships analyzed should be even stronger if all data used were from the same locality.

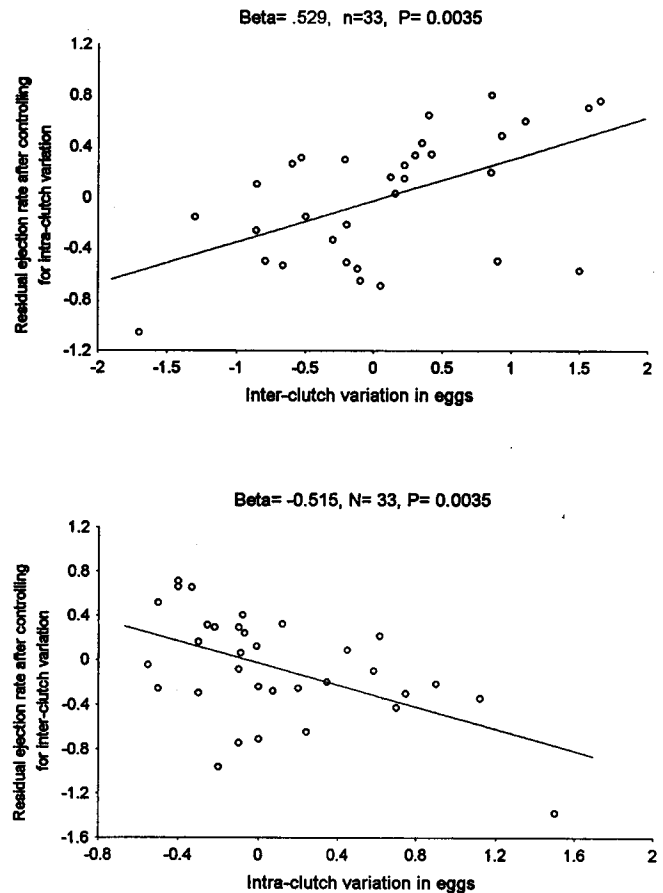


Figure 1

Residual rejection rate after controlling for intraclutch variation in the appearance of eggs in relation to interclutch variation in eggs (upper) and residual rejection rate after controlling for interclutch variation. Values are contrasts. The lines are regression lines, while beta values are standardized regression coefficients and their associated probabilities.

(2) Another possible error is that apparently unparasitized nests may earlier have held a cuckoo egg which has already been rejected by the host. Hence, it may be very difficult to know exactly the true parasitism rate of each species. We attempted to solve this problem by correcting the parasitism rate by the rejection rate for each species. However, the results did not change (Table 2).

(3) Parasitism rate may not be a good index of the level of host and parasite coevolution because the advantage of one party may be large at the beginning of a coevolutionary interaction, while this advantage continuously decreases because of evolution of host defense. The outcome is extinction of the parasite or a parasite advantage due to evolution of a novel parasite adaptation that could result in a higher parasitism rate. Therefore, parasitism rate and host antiparasite behavior will cycle out of phase rather than coevolve linearly (Takasu et al., 1993).

In the analysis, we assume polytomies between different species within the same genus; i.e., we assume that all species from the same genus evolved simultaneously from the common ancestor (multiway speciation events) (see Purvis and Garland, 1993, for problems with polytomies, their implications, and possible solutions). Hence, we have set branch lengths of all species to the same length (=1) (Garland et al., 1993; Purvis and Garland, 1993). To control for the possible effect of common phylogenetic descent, we used Felsenstein's

Table 2

Relationships between contrasts in parasitism and rejection rate (dependent variables) and intra- and interclutch variation (independent variables) (i)

		Multiple R	F	df	Beta (interclutch variation)	Beta (intraclutch variation)
Parasitism rate (all species)	(i) (ii)	0.238	1.678	2, 56	0.278 F(s) = 5.77** F(g) = 2.41	-0.111 F(s) = 1.52 F(g) = 0.02
Parasitism rate (without P.m.)	(i)	0.360*	4.100	2, 55	0.394**	-0.079
Parasitism rate (without hole nesters)	(i) (ii)	0.114	0.288	2, 44	0.126 F(s) = 0.38 F(g) = 0.16	-0.040 F(s) = 4.8* F(g) = 0.4
Parasitism rate (without hole nesters either P.m.)	(i)	0.256	1.506	2, 43	0.250	0.016
Parasitism rate (corrected for rejection and with all species)	(i)	0.339	1.758	2, 27	0.327	0.023
Parasitism rate (corrected for rejection and without hole nesters)	(i)	0.191	0.416	2, 22	0.115	-0.200
Rejection rate (all species)	(i) (ii)	0.550***	6.727	2, 31	0.529*** R(s) = 0.54*** R(g) = 0.60***	-0.515*** R(s) = -0.13 R(g) = -0.08
Rejection rate (without hole nesters)	(i) (ii)	0.556***	5.815	2, 26	0.379* R(s) = 0.43** R(g) = 0.54**	-0.540*** R(s) = -0.29 R(g) = -0.26

(ii) Results from Øien et al. (1995). ANOVA in the comparison between suitable and unsuitable hosts and their intra- and interclutch variation; and Spearman correlation coefficient in the relation between rejection rate and intra- and interclutch variation. (s) mean analysis at the species level and (g) at the genus level. * $p < 0.05$, ** $p < .01$, *** $p < .005$. All tests were two-tailed.

(1985) independent comparison method as implemented in a computer program written by Garland et al. (1993). This method finds a set of independent pairwise differences or contrasts, assuming that changes along the branches of the phylogeny can be modelled by a Brownian motion process (successive changes are independent of one another) and that the expected total change summed over many independent changes is zero (Harvey and Pagel, 1991). Therefore, pairwise differences in the phylogenetic tree are independent of each other (Harvey and Pagel, 1991). The advantage of independent comparison approaches is that, by partitioning the variation appropriately, all contrasts can be used to assess a hypothetical comparative relationship (Harvey and Pagel, 1991).

All variables introduced in the analyses were normalized [parasitism rate was transformed to $\log(n + 0.001)$, rejection rate was arcsin transformed, while intra- and interclutch variation were already normally distributed].

Instead of using the classification of suitability of passerine hosts given by Øien et al. (1995), we utilized in the analyses the parasitism rate of the different passerines as reported in the literature (see Table 3).

RESULTS

Relationships between parasitism rate and intra- and interclutch variation

The relationships between contrasts of parasitism rate and intra- and interclutch variation in egg appearance are similar to those of Øien et al. (1995) (Table 2). We found a significant positive relationship between contrasts in interclutch variation

and parasitism rate, and it was even stronger when the duncock (*Prunella modularis*) was excluded from the analysis (this species was an outlier; $p < .025$, Sokal and Rohlf, 1981). However, we did not find any significant relationship when we used contrasts with the hole nesters excluded from the analysis, as did Øien et al. (1995).

Relationships between rejection rate and intra- and interclutch variation

We found a statistically highly significant multiple regression between rejection rate (dependent variable) and intra- and interclutch variation (independent variables) (Table 2, Figure 1). This relationship also held when we excluded hole nesters (Table 2) (the probabilities are small even if we reduce the degrees of freedom because of polytomies, Garland et al., 1993). Also the partial correlation coefficients were highly significant and in the direction predicted by the hypothesis: a negative relationship with intraclutch variation ($r = -.515$, $p = .0043$, Figure 1, Table 2), in agreement with the results of Øien et al. (1995); and, in contrast, a positive correlation with interclutch variation ($r = .529$, $p = .0035$, Figure 1, Table 2). This relationship was less strong, but statistically significant when the hole nesters were excluded from the analysis (Table 2). Therefore, these results support more strongly than in the paper by Øien et al. (1995) the hypothesis that the evolution of egg mimicry by the cuckoo probably is a response to the hosts' rejection behavior, suggesting that a coevolutionary arms race exists between the parasite and its host.

Table 3

Parasitism rate, rejection rate, and inter- and intraclutch variation for 63 potential host species used in the analyses

Species	Parasitism rate (%)	Rejection rate (%)	Interclutch variation	Intraclutch variation
Alaudidae				
<i>A. arvensis</i>	0.04(c)		3.4	1.8
Hirundinidae				
<i>R. riparia</i>	0.00(c)		1.3	1.2
<i>H. rustica</i>	0.01(d)	0.0	2.8	1.8
<i>D. urbica</i>	0.00(c)		1.3	1.2
Motacillidae				
<i>A. spinoletta</i>	1.75(c)		2.4	2.1
<i>A. trivialis</i>	0.74(c)		3.4	2.0
<i>A. pratensis</i>	2.66(a)	26.8	4.2	1.5
<i>M. flava</i>	0.13(c)	80.0	2.9	1.5
<i>M. cinerea</i>	0.03(c)		3.0	1.8
<i>M. alba</i>	0.42(a)	73.2	2.5	1.9
Laniidae				
<i>L. collurio</i>	0.01(b)		4.2	2.2
Troglodytidae				
<i>T. troglodytes</i>	0.04(a)	0.0	2.1	1.8
Prunellidae				
<i>P. modularis</i>	1.93(a)	3.1	1.1	1.2
Turdidae				
<i>E. rubecula</i>	0.29(a)	20.0	2.6	2.2
<i>P. ochruros</i>	0.00(c)		1.5	1.1
<i>P. phoenicurus</i>	0.03(a)	31.5	2.3	1.3
<i>S. rubetra</i>	0.01(b)		2.2	1.6
<i>O. oenanthe</i>	0.00(a)	5.9	2.1	1.3
<i>T. torquatus</i>	0.11(c)		3.6	2.5
<i>T. merula</i>	0.01(a)	63.9	3.3	2.3
<i>T. pilaris</i>	0.00(c)	9.1	3.4	2.4
<i>T. philomelos</i>	0.01(b)	62.7	2.3	1.6
<i>T. iliacus</i>	0.00(c)	34.9	3.0	2.3
<i>T. viscivorus</i>	0.00(c)		3.2	2.4
Sylviidae				
<i>A. schoenobaenus</i>	0.33(a)	20.0	2.4	1.8
<i>A. palustris</i>	1.88(c)	86.8	3.7	2.3
<i>A. scirpaceus</i>	5.54(a)	61.8	2.9	1.9
<i>A. arundinaceus</i>		85.7	3.1	2.2
<i>H. icterina</i>		66.7	2.8	1.3
<i>P. sibilatrix</i>	0.09(c)		3.0	1.7
<i>P. collybita</i>	0.00(c)	100.0	2.9	1.6
<i>P. trochilus</i>	0.06(c)	90.0	3.8	1.5
<i>S. curruca</i>	0.01(b)		3.0	1.9
<i>S. communis</i>	0.07(c)		3.6	1.8
<i>S. borin</i>	0.32(c)	66.7	3.7	1.8
<i>S. atricapilla</i>	0.17(c)	76.9	3.9	1.9
<i>R. regulus</i>	0.01(b)		2.8	1.8
<i>R. ignicapillus</i>	0.00(c)		2.4	1.6
Muscicapidae				
<i>M. striata</i>	0.12(c)	72.2	3.2	1.8
<i>F. hypoleuca</i>	0.00(a)	0.0	1.5	1.3
Paridae				
<i>P. cristatus</i>	0.00(c)		2.4	1.9
<i>P. ater</i>	0.00(c)		2.8	2.2
<i>P. caeruleus</i>	0.00(a)	0.0	2.6	2.2
<i>P. palustris</i>	0.00(c)	0.0	2.1	1.9
Sittidae				
<i>S. europaea</i>	0.00(c)		2.9	2.4
Certhiidae				
<i>C. familiaris</i>	0.00(c)		2.8	1.8

Table 3
Continued

Species	Parasitism rate (%)	Rejection rate (%)	Interclutch variation	Intraclutch variation
Ploceidae				
<i>P. domesticus</i>	0.00(c)		3.6	2.9
<i>P. montanus</i>	0.00(c)		3.6	3.6
Emberizidae				
<i>E. citrinella</i>	0.01(b)	100.0	3.6	1.6
<i>E. schoenichus</i>	0.15(a)	95.0	3.4	1.8
<i>E. calandra</i>	0.01(b)		3.4	2.1
<i>C. lapponicus</i>		0.0	3.4	3.2
<i>P. nivalis</i>	0.00(c)		3.6	2.6
Fringillidae				
<i>F. coelebs</i>	0.01(b)	61.3	4.2	2.3
<i>F. montifringilla</i>		90.3	3.6	1.9
<i>C. chloris</i>	0.05(a)	24.1	2.8	2.2
<i>C. carduelis</i>	0.01(b)		2.8	2.3
<i>A. cannabina</i>	0.11(a)	0.0	2.5	2.4
<i>L. curvirostra</i>	0.00(c)		2.5	2.2
<i>C. coccothraustes</i>	0.01(b)		3.3	2.0
Sturnidae				
<i>S. vulgaris</i>	0.00(a)	23.8	1.5	1.1
Corvidae				
<i>G. glandarius</i>	0.00(c)		3.3	1.6
<i>P. pica</i>	0.00(c)		3.6	2.5

Data of rejection rate, interclutch variation and intraclutch variation are from Øien et al. (1995), and the parasitism rate data were extracted from (a) Davies and Brooke (1989b), (b) Lack (1963), (c) Glue and Murray (1984), and (d) Wyllie (1981). We have used all passerine species in Sharrock (1977), and we assume that the parasitism rate of all species not reported to be parasitized in the previous references to be zero. Phylogenetic information are from Howard and Moore (1991).

DISCUSSION

The hypotheses listed by Øien et al. (1995) were that (1) selection favors a high degree of interclutch variation in color and marking patterns of the eggs laid by different individuals in European host species of the cuckoo (Davies and Brooke, 1989a), and (2) a low intraclutch variation should spread in host populations because of the continuous arms race between host and parasite (Øien et al., 1995) because low variation will allow the host a better ability to recognize foreign eggs (Freeman, 1988; Victoria, 1972). Thus, the predictions were that species that have been involved in a coevolutionary arms race with the cuckoo should show a high degree of interclutch variation and a low degree of intraclutch variation.

Øien et al. (1995) only support the first prediction, and they conclude that selection for low intraclutch variation will be weaker than selection for high interclutch variation. However, because group selection is unlikely (Williams, 1992), it is very difficult to imagine a scenario in which increasing interclutch variation could be selectively advantageous. If intraclutch variation is high, disruptive selection on interclutch variation will initially have no or only weak effects on the ability of hosts to discriminate between parasite eggs and own eggs. The selective advantage for the host will always be maximized by laying eggs as different as possible from those of other hosts because the parasite would exploit the most common host in the population (Haldane, 1949). This will particularly be the case if intraclutch variation is low.

We believe that parasitism first would select for a reduction in intraclutch variation among hosts because it would be easier for hosts both to learn the appearance of their own eggs and recognize foreign eggs. The second step would be an in-

crease in interclutch variation as a consequence of the reduction in intraclutch variation.

The contrast analysis for parasitism rate gave results similar to those of Øien et al. (1995), although the relationships are not strong (even weaker if we correct for polytomies, Garland et al., 1993). One explanation could be that parasitism rate is not a good index of the duration and the intensity of the coevolutionary arms race between hosts and parasites (see Methods).

Since the increase in egg recognition level by the host (measured by rejection rate of non-mimetic eggs, Davies and Brooke, 1989a) is the defense of the host against the perfection level in mimicry by the parasite, we can assume that the host-parasite interaction is a continuous arms race (Davies and Brooke, 1989a). If that is the case, different degrees of host rejection reflect different stages in that arms race. Therefore, we should find a negative relationship between rejection rate and intraclutch variation and a positive relationship with interclutch variation in the appearance of host eggs. That is the case in the analysis of independent contrasts. These relationships are predicted from rejection being proportional to the degree of difference between the eggs of hosts and parasites (Freeman, 1988; Victoria, 1972).

In summary, we conclude that the use of the independent comparative method allows us to understand a more logical evolutionary process where individual variation and associated selection processes easily can explain the evolution of intra- and interclutch variation because of the significant relationship between intraclutch variation and the rejection rate. Furthermore, the analysis strengthens the hypothesis that the evolution of egg patterns in both parasite and host is associated with different stages of a continuous arms race.

We are most grateful to Arne Moksnes, Manuel Soler, Risto A. Väisänen, and one anonymous referee for valuable comments on the manuscript. Funds were provided by the Commission of the European Communities (SCI*-CT92-0772) to A.P.M. and European Communities postdoctoral grant (ERBCHBCT930307) to J.J.S.

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