Nest predation and the evolution of egg appearance in passerine birds in Europe and North America

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ABSTRACT

Question: Does nest predation influence egg colour appearance among North American and European passerine birds? Analyses of species that lay their eggs directly on the ground provide support for such a contention, but it is less obvious in shrub and canopy nesters. We hypothesized that if predators locate nests by egg colour, nest predation could select for eggs with a less conspicuous background colour and more spots/markings so that they may achieve better camouflage. Thus, intra-clutch variation in egg appearance should be negatively related to rate of predation among passerines. Also, a reduction in intra-clutch variation would induce greater inter-clutch variation.

Data studied: Data on egg appearance and nest predation rate, together with data on variables likely to affect the relationship between these two traits, such as suitability as hosts for brood parasites, level of brood parasitism, nesting habitat and nest location, were gathered for 23 European and 63 North American species of passerines, respectively.

Search method: We controlled for similarity among species due to common descent by adopting the general method of comparative analysis for continuous variables that is based on multiple regression of statistically independent standardized linear contrasts.

Conclusions: Egg appearance within clutches of open nesting passerines was explained by brood parasitic variables but was unrelated to nest predation in Europe. In contrast, neither nest predation nor avian brood parasitism explained variation in egg appearance of North American passerines. Globally, the lack of association between nest predation and egg appearance after accounting for the confounding roles of brood parasitism, nesting habitat and nest location suggested that egg coloration in open nesting passerine birds may be considered a neutral trait with regard to nest predation.

Keywords: avian egg appearance, brood parasitism, inter-clutch variation, intra-clutch variation, nest predation, North America versus Europe.

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INTRODUCTION

Nest predation is a main selective factor shaping the evolution of life-history traits in birds (Martin, 1995). The adaptive value of egg coloration in terms of avoiding predation has been demonstrated for species that lay their eggs directly on the ground, since more cryptic clutches suffer less predation than less cryptic ones (e.g. Tinbergen *et al.*, 1962; Montevecchi, 1976; Solís and de Lope, 1995; Yahner and Mahan, 1996; Lloyd *et al.*, 2000; but see Jobin and Picman, 1997). However, this functional explanation for egg colour is less clear in shrub and canopy nesters (e.g. Götmark, 1992; Weidinger, 2001; Underwood and Sealy, 2002). When faced with this kind of nest, predators may rely on other more obvious cues to denote the presence of a nest than egg appearance, such as parental activity (e.g. Martin *et al.*, 2000) or the nest itself (Møller, 1990; Götmark, 1992). Yet evidence supporting the adaptive role of cryptic coloration of eggs in terms of predation is weak for species where parents build a nest cup (Underwood and Sealy, 2002). Some experimental studies have failed to detect any link between the coloration of artificial eggs in artificial nests and risk of predation, but did find support for a role of nest concealment (Møller, 1990; Götmark, 1992). However, Westmoreland and Best (1986) found differences in level of nest predation to be linked to egg coloration in an experiment using real eggs, nests and sites chosen by birds. Similarly, Weidinger (2001) observed survival rates to differ among varying degrees of egg crypsis in the yellowhammer (*Emberiza citrinella*), consistent with the hypothesis that egg coloration may be adaptive in terms of avoiding predation, but not in the song thrush (*Turdus philomelos*) or the blackcap (*Sylvia atricapilla*). However, despite partial species-specific support for the predation hypothesis (see above), no inter-specific studies have examined whether nest predation may be a major selective force driving the evolution of egg appearance among passerine birds.

The aim of this study was to assess the relative effect of nest predation on the evolution of egg appearance (within and among clutches) in passerine birds, while controlling for similarity among taxa due to common ancestry, the effect of brood parasitism and the potentially confounding effect of nest location and habitat type. We hypothesized that if predators locate nests by egg colour, nest predation could select for eggs with a less conspicuous background colour and more spots/markings so that they may achieve better camouflage against the nest lining (Tinbergen *et al.*, 1962; Montevecchi, 1976). Thus, to produce cryptic eggs a reduction in intra-clutch variation in egg appearance would be adaptive, since nest predators would have difficulty finding a well-camouflaged clutch of eggs. Similarly, a reduction in intra-clutch variation in egg appearance would induce larger inter-clutch variation, which makes it difficult for nest predators to evolve a search image for a particular egg type. We examined these relationships for North American and European passerine birds separately, because the selective forces exerted by brood parasitism and predation would predict different features of egg appearance being adaptive in North America and Europe. In North America, the brown-headed cowbird (*Molothrus ater*) is the most common and most widespread obligate brood parasite and is known to utilize more than 220 passerine species as hosts (Friedmann and Kiff, 1985). The brown-headed cowbird lays eggs of one standard type, which does not generally mimic those of their hosts (Rothstein and Robinson, 1998). In contrast, several gentes or tribes of the common cuckoo in Europe lay eggs that mimic perfectly the eggs of their main hosts (Wyllie, 1981; Álvarez, 1994; Moksnes and Røskaft, 1995). In addition to the cuckoo being a specialist and the cowbird a generalist brood parasite, cowbirds do not reduce host breeding outcome to zero because they are commonly raised alongside the host chicks, while successful cuckoo parasitism often results in the complete

loss of the host clutch (e.g. Davies, 2000). Therefore, differences between North America and Europe in the degree of mimicry between host and parasitic eggs, and in the costs related to successful parasitism, may theoretically result in differences in the adaptive value of host egg phenotype at the within- and among-clutch levels in terms of discrimination of parasitic eggs (see Stokke *et al.*, 2002; Avilés and Møller, 2003). Thus, we expected a higher potential role of brood parasitism as a selective agent shaping egg phenotype at the intra- and inter-clutch levels in Europe.

Regarding predation, Martin and Clobert (1996) have shown that nest predation among open nesting passerines is more common in North America than in Europe. Regardless of the evolutionary causes that induced variation in predation between continents, differences in nest predation between North America and Europe have resulted in divergent evolution of some basic avian life-history traits (e.g. fecundity, iteroparity and survival) on these continents (Martin and Clobert, 1996). Hence, we expected a relatively greater role of nest predation as a selective agent driving the evolution of variation in egg phenotype among North American passerines. We thus predicted (1) intra-clutch variation in egg appearance to be negatively associated with level of parasitism, and (2) inter-clutch variation in egg appearance to be positively associated with level of parasitism, irrespective of nest predation for the European passerines. However, we predicted (3) intra-clutch variation in egg appearance to be negatively associated with level of predation, and (4) inter-clutch variation to be positively associated with level of predation, irrespective of level of brood parasitism for the North American passerines.

MATERIALS AND METHODS

Data collection

Complete data on egg appearance, nest predation rate, suitability as hosts for brood parasites and level of brood parasitism were gathered for 23 European and 63 North American species of passerines, respectively (see Appendix). Only species that breed in open nests were used in our analyses, since hole nesters might be exposed to different selective forces than open nesters (Lack, 1968; Martin and Li, 1992; Martin, 1995). Data on clutch variation in egg appearance were obtained from Stokke *et al.* (2002), who photographed a random sample of 10 clutches for each species. As in Øien *et al.* (1995), intra-clutch variation in egg appearance was assessed on a scale of 1–5 as follows:

1 = No variation. All the eggs were similar.
2 = At least one egg differed slightly from the others.
3 = At least one egg differed markedly from the others.
4 = At least one egg differed dramatically from the others.
5 = All the eggs were different from one another.

Similarly, inter-clutch variation in egg appearance was assessed on a scale of 1–5 as follows:

1 = No variation. All clutches were similar.
2 = At least one clutch differed slightly from the others.
3 = At least one clutch differed markedly from the others.
4 = At least one clutch differed dramatically from the others.
5 = All the clutches were different from one another.

Four experienced observers scored intra-clutch variation for all ten clutches per species and provided a score for inter-clutch variation based on ten photographs per species. The different assessments were highly consistent [repeatability reported in Stokke *et al.* (2002)], thus justifying the use of the mean values attained for the four observers in all further analyses.

We are aware that the method of estimating variation in egg phenotype based upon human vision does not account for ultraviolet (UV) wavelengths that birds can perceive (e.g. Bennett *et al.*, 1996; Cuthill *et al.*, 2000). However, the results of previous studies focusing on the adaptive value of egg appearance and relying on human vision were in line with expectations based on avian vision (Øien *et al.*, 1995; Soler and Møller, 1996; Jackson, 1998; Stokke *et al.*, 1999, 2002). Indeed, spectrophotometric techniques accounting for UV information and human vision methods provided similar conclusions in a recent comparative study assessing the sexual role of passerine egg coloration (Soler *et al.*, 2005), which would support our assumption that the method used here is satisfactory for assessing variation in egg appearance.

Estimates of nest failure due to predation were obtained from data reported in Martin (1995) for North American passerines and Martin and Clobert (1996) for European passerines and used as an index of selection exerted by predation on egg phenotype. Nest predation was expressed as the simple percentage of nests lost to predation to avoid possible biases in determining causes of partial brood losses, and because predation often results in loss of the entire brood (Lack, 1954; Nice, 1957; Ricklefs, 1969; Nilsson, 1984; Møller, 1989; Martin, 1995; Martin and Clobert, 1996). We used two different indices to assess the intensity of the relationship between each species and brood parasitism: suitability as host and percentage of nests parasitized by a brood parasite. We divided species into three groups based on their suitability as hosts according to data obtained from the *Handbook of the Birds of North America* (Poole *et al.*, 1993–2002) for North American passerines and Moksnes and Røskaft (1995) for European passerines. Species were classified as being unsuitable as brood parasite hosts (score of 3) because: (1) they build their nests in concealed places which makes laying for the parasite difficult; (2) they feed their chicks with food unsuitable for the parasite chick (mainly seed eaters) (Eastzer *et al.*, 1980; Kozlovic *et al.*, 1996); or (3) they have eggs or chicks markedly dissimilar in size to those of the parasite (Ortega, 1998). Some species could be regarded as suitable or unsuitable hosts, since in some part of their range they are available as hosts, whereas in others they are not (see Røskaft *et al.*, 2002). For the present analyses, we included these species in an intermediate group of partially suitable hosts (score of 2). The rest of the species were handled as suitable hosts (score of 1). Note that host suitability based on our 3-point scale can be regarded as a continuous axis, since intermediate states are biologically meaningful.

We used relative frequency of brood parasitism for a particular host species as a measure of brood parasitism, defined as the number of nests parasitized in relation to the total number of nests observed. Data for brood parasitism were retrieved from Appendices B and C in Ortega (1998), and completed using the *Handbook of the Birds of North America* (Poole *et al.*, 1993–2002), for North American species, and from Soler and Møller (1996) and Stokke *et al.* (2002) for European species. We only considered species for which at least one report was available, because it is unclear whether a lack of evidence for brood parasitism in a given species indicates that brood parasitism does not exist, or that it does exist but hasn't been reported. Data for nightingale (*Luscinia megarhynchos*), bullfinch (*Pyrrhula pyrrhula*) and Dartford warbler (*Sylvia undata*) were not reported by Soler and Møller (1996) and Stokke *et al.* (2002). Thus we set the level of parasitism arbitrarily to 0.01 for these three species, since

Moksnes and Røskaft (1995) found cuckoo eggs in the nests of these species, and since a rate of parasitism of 0.01 is typical for rare hosts of the cuckoo (Moksnes and Røskaft, 1995). In addition, in the paper by Soler and Møller (1996) three species (chiffchaff, *Phylloscopus collybita*; magpie, *Pica pica*; blackbird, *Turdus merula*) were reported to have a level of parasitism of 0.0, although Moksnes and Røskaft (1995) found cuckoo eggs in the nests of these species. Therefore, we altered the level of parasitism from 0.0 to 0.01 for these three species. In some species, estimates of brood parasitism were available for more than one population. Based on such information, a one-way analysis of variance revealed consistently greater variance among than within species ($F_{62,286} = 2.09$, $P < 0.0001$). Therefore, we used the mean estimate in the analyses from all studies where more than five host nests had been monitored.

We assume that host suitability is more consistent on an evolutionary time scale than parasitism rate, and consequently that it better reflects the long-term intensity of co-evolutionary interactions between hosts and parasites. This is justified by the fact that the three criteria used to establish degree of host suitability (body size, diet and nesting habits) are less variable for species than are parasitism rates. However, the rate of parasitism could be regarded as a short-term index of the intensity of the relationship between host and parasite and thus as a suitable variable for defining current parasite preferences.

A number of potentially confounding factors may affect the association between egg appearance and predation. For instance, the habitat type used may determine the risk of being depredated since predators may have particular habitat preferences leading to habitat-dependence in egg phenotype. To control for such confounding effects, we classified species as inhabiting open (score of 1) or forested habitats (score of 3). Species of open habitats include species nesting in open areas, old fields and riparian habitats. The forest species are mostly strict forest breeders. Some species breed in a variable range of habitats comprising both forested and open habitats. Birds inhabiting both kinds of habitats, or preferring scrubs, clearings or forest edges, were categorized as living in 'mixed' habitats (score of 2). Information on habitat type was taken from Baicich and Harrison (1997) for North American passerines and from Harrison and Castell (1998) for European passerines.

Nest location may also influence egg phenotype variation because conspicuous nests are arguably more detectable by predators than well-concealed nests, and hence the selective pressures exerted by predators may act on nest conspicuousness (Götmark, 1992; Weidinger, 2001). Therefore, differences among species in nest location may cause different exposure to predation and thus different proneness to evolve adaptations against predators. To control for the possible confounding effect of nest location, species were assigned to one of three general nest heights (ground, shrub, subcanopy/canopy). Nests were classified as ground nests (score of 1) if on the ground, shrub nests (score of 2) if off the ground but generally no more than 3 m high, and as subcanopy/canopy nest (score of 3) if higher (see Martin and Badyaev, 1996). Information on nest location was retrieved from Baicich and Harrison (1997) for North American species and from Harrison and Castell (1998) for European species. Habitat type and nest location were treated as continuous variables in the comparative analyses. This procedure makes intuitive sense, since intermediate states of these variables are biologically meaningful. We are aware that the effect of habitat type and nest location on the association between egg variation in phenotype across species and brood parasitism and nest predation may vary between Europe and North America. Common cuckoos and brown-headed cowbirds show different host preferences and predators may also vary in their use of open nesting birds between continents. We thus avoided making evolutionary conclusions for

associations with brood parasite and predator preferences, because it would be well beyond the scope of this paper. However, we did handle the effects of these factors, and we did assess the importance of their confounding effect on the relationships in question.

In addition, a relationship between intra-clutch variation in egg appearance and level of parasitism could be induced by the association between intra-clutch variation in egg appearance and host ability to discriminate and reject parasite eggs. Since species possessing eggs with lower intra-clutch variation in their clutches are more readily discriminators of parasitic eggs (e.g. Øien *et al.*, 1995; Soler and Møller, 1996; Stokke *et al.*, 2002), the percentage of nests parasitized may provide a biased measure of the level of parasitism due to the difficulties in reporting parasitism for those species having low variation in egg appearance. To deal with this potential source of bias, we also entered rejection rate for each species into the models when studying the association between parasitism and egg phenotype (see also Soler and Møller, 1996). Data on level of discrimination against brood parasitism for each species, as expressed by the percentage of parasitized nests rejecting artificial non-mimetic parasitic eggs, were retrieved from the literature [North American species (Rothstein, 1975, 1982, 2001; Friedmann and Kiff, 1985; Briskie and Sealy, 1987; Ortega and Cruz, 1988; Briskie *et al.*, 1992; Bischoff and Murphy, 1993; Dufty, 1994; Sealy, 1995, 1996; Sealy and Bazin, 1995; Ward *et al.*, 1996; Burhans and Freeman, 1997; Haas and Haas, 1998; Sealy and Lorenzana, 1998; Sealy *et al.*, 2000; Ward and Smith, 2000; Banks and Martin, 2001; Lorenzana and Sealy, 2001; Peer *et al.*, 2000, 2002; Strausberger and Burhans, 2001); European species (Davies and Brooke, 1989; Moksnes *et al.*, 1990; Moksnes and Røskaft, 1992; Brooke *et al.*, 1998; Stokke *et al.*, 1999; Lindholm and Thomas, 2000; Grim and Honza, 2001; Soler *et al.*, 2002; Prochazka and Honza, 2003)]. Rejection rates were available for more than one population, and proved to be consistent at the within-species level ($F_{50,59} = 7.01$, $P < 0.00001$). Therefore, we used the mean estimate in the analyses from all studies where the percentage of nests rejecting parasitic eggs was provided.

Information on variation in egg appearance, nest predation, suitability as host, parasitism rate, rejection level, habitat type and nest location for all species is summarized in the Appendix.

Comparative and statistical analyses

Comparisons across species are potentially confounded by varying degrees of common phylogenetic ancestry (Harvey and Pagel, 1991). We controlled for similarity among species due to common descent by adopting the general method of comparative analysis for continuous variables that is based on multiple regression of statistically independent standardized linear contrasts (Felsenstein, 1985). Using this approach, evolutionary relationships between different traits can be assessed by regression through the origin, where the expected value of the slope of the regression line equals the true relation between two traits in the absence of phylogenetic effects (Harvey and Pagel, 1991). Statistically independent linear contrasts were calculated for intra-clutch and inter-clutch variation in egg appearance, nest predation, host suitability, parasitism rate, rejection rate, habitat type, nest location and for continent, which was coded as a dummy variable (0 = North America, 1 = Europe) using PDAP 6.0 (Garland *et al.*, 1993, 1999). The phylogenetic hypothesis was based on the tapestry of Sibley and Ahlquist (1990), with lower branches supported by current taxonomic information (Fig. 1) (Avise *et al.*, 1980a, 1980b, 1980c; Zink and Johnson, 1984; Marten and Johnson, 1986; Johnson *et al.*, 1988; Zink and Avise, 1990; Sibley and Ahlquist, 1990; Bermingham *et al.*, 1992; Richman and Price, 1992; Monroe and Sibley, 1993; Tamplin *et al.*, 1993; Watada *et al.*, 1995; Arctander *et al.*, 1996; Blondel *et al.*, 1996; Fehrer, 1996; Helbig *et al.*, 1996; Richman, 1996; Sheldon and Gill, 1996; Zink and Blackwell, 1996; Leisler *et al.*, 1997; Lo Valvo *et al.*, 1997; Price *et al.*, 1997; Arnaiz-Villena *et al.*, 1998;
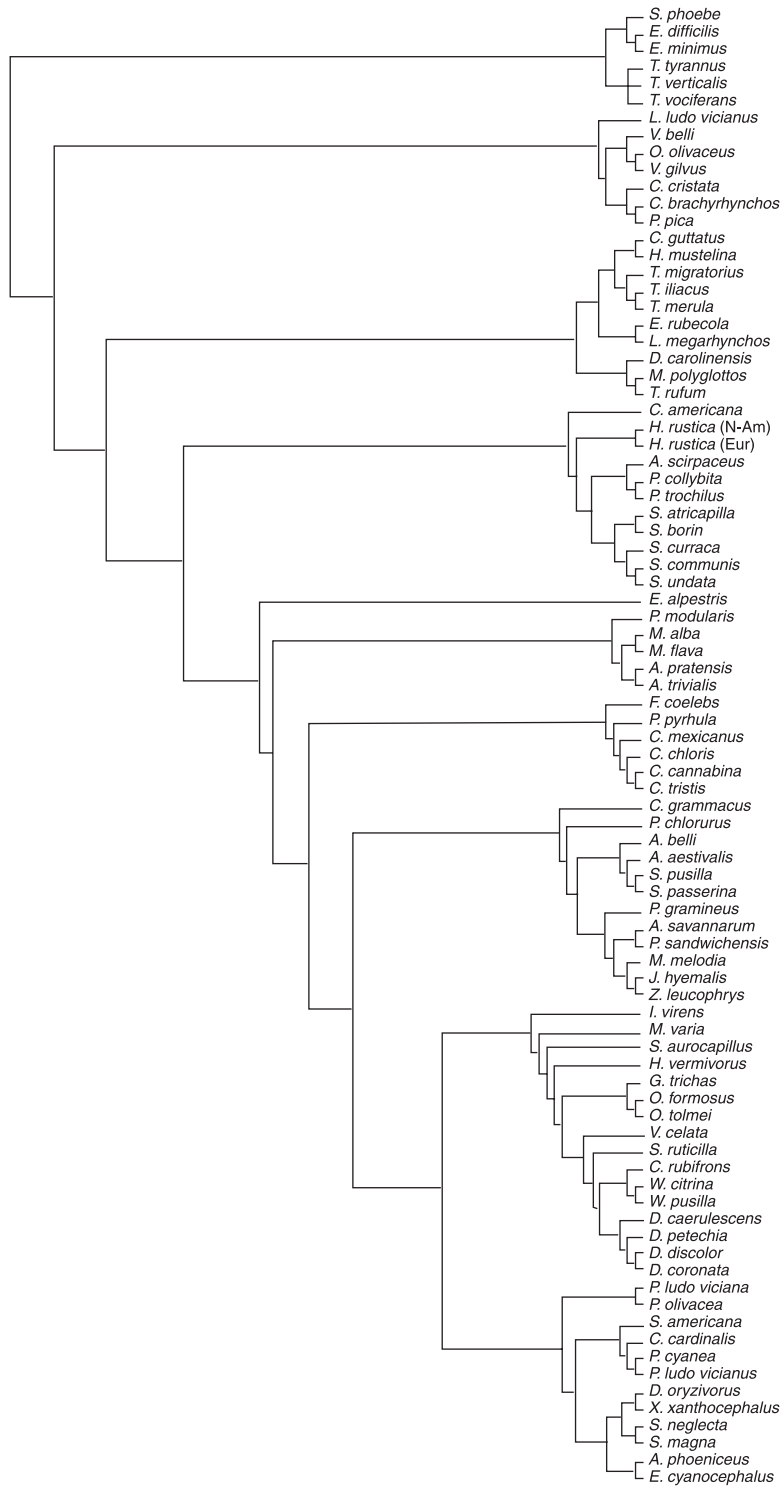
Fig. 1. Phylogenetic relationships among passerine birds used in the analyses.

Zink *et al.*, 1998; Cibois and Pasquet, 1999; Helbig and Seibold, 1999; Johnson and Lanyon, 1999; Lanyon and Omland, 1999; Lovette and Bermingham, 1999; Omland *et al.*, 1999; Voelker, 1999a, 1999b). We did not have consistent estimates of branch lengths because the data originate from studies using different methods. Hence branch lengths were set to be constant (= 1). Linear contrasts were normally distributed and multiple regressions using independent contrasts were forced through the origin (Garland *et al.*, 1992). All tests were two-tailed.

RESULTS

Covariation between egg phenotype traits

A partial correlation analysis revealed that intra-clutch variation in egg appearance was not significantly related to inter-clutch variation for the European passerines ($r_p = 0.18$, d.f. = 21, $P = 0.40$). However, intra-clutch variation was positively and significantly associated with inter-clutch variation across North American species ($r_p = 0.62$, d.f. = 61, $P < 0.00001$; Fig. 2). We found similar results for both continents when the effect of habitat type and nest location was considered in the analyses ($r_p = 0.19$, d.f. = 19, $P = 0.36$ and $r_p = 0.61$, d.f. = 59, $P < 0.00001$ for the European and North American species, respectively). Therefore, we entered intra-clutch and inter-clutch variation, respectively, into the models when analysing the relationship between egg phenotype and nest predation for North American species.

Continental differences in egg appearance

Intra-clutch variation in egg appearance did not differ significantly between North America and Europe when controlling for host suitability, parasitism rate and nest predation (Table 1). However, European passerine species showed significantly larger inter-clutch variation in egg appearance after controlling for the potentially confounding effects of brood parasitism and nest predation (Table 1).
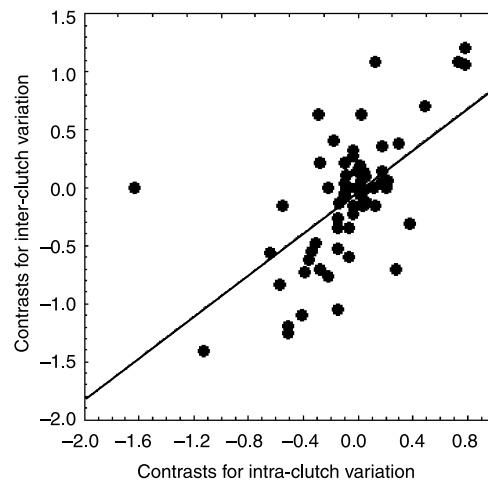

Fig. 2. Relationships between intra-clutch and inter-clutch variation in egg appearance for North American passerines. All values represent standardized phylogenetically independent contrasts ($n = 62$), and the regression line is forced through the origin.

Table 1. Intra-clutch and inter-clutch variation in egg appearance (dependent variables) in relation to continent, nest predation rate, suitability as host and parasitism rate in multiple linear regression models, forced through the origin, based on statistically independent contrasts

Dependent variable	Independent variable	r_p (SE)	t	P
Intra-clutch variation Model: $F_{4,81} = 1.60$, $r^2 = 0.07$, $P = 0.18$				
	Predation	0.05 (0.11)	0.50	0.61
	Continent	0.14 (0.11)	1.25	0.21
	Suitability	0.18 (0.11)	1.70	0.09
	Parasitism	**0.22 (0.11)**	**1.98**	**0.05**
Inter-clutch variation Model: $F_{4,81} = 2.52$, $r^2 = 0.11$, $P = 0.05$				
	Predation	0.09 (0.11)	0.76	0.44
	Continent	**0.35 (0.11)**	**3.15**	**0.002**
	Suitability	0.05 (0.11)	0.50	0.61
	Parasitism	0.07 (0.11)	0.65	0.51

Note: Significant slopes are highlighted in **bold**.

Egg appearance and selection pressures in Europe

We investigated the relationship between intra-clutch variation in egg appearance and nest predation rate, parasitism rate and host suitability as independent variables in a multiple regression. The overall model was significant and only included host suitability and parasitism rate ($F_{3,19} = 9.41$, $r^2 = 0.59$, $P = 0.0005$). When we re-analysed the interspecific association between intra-clutch variation and brood parasitic variables by holding constant the effect of habitat and nest concealment, the patterns remained robust (Table 2). In addition, the results did not change when rejection rate was considered in the model (Table 2). Partial correlations showed that unsuitable cuckoo hosts had high intra-clutch variation in egg appearance ($r_p = 0.65$, d.f. = 19, $P = 0.002$; Fig. 3). In addition, species suffering more frequent parasitism had large intra-clutch variation in egg appearance ($r_p = 0.41$, d.f. = 19, $P = 0.018$; Fig. 3).

A similar analysis using inter-clutch variation as the dependent variable did not reveal any significant effect of nest predation rate, parasitism rate or host suitability ($F_{3,19} = 1.40$, $r^2 = 0.18$, $P = 0.27$). This absence of relationships between inter-clutch variation in egg appearance and brood parasitism and nest predation remained consistent when the effects of habitat and nest location were taken into account (Table 2). Similarly, the inclusion of rejection rate as an independent variable did not affect the absence of association between inter-clutch variation and nest predation and brood parasitic variables (Table 2).

Egg appearance and selection pressures in North America

Neither nest predation nor brood parasitism variables explained intra-clutch variation in egg appearance in North American passerines [$F_{3,59} = 0.43$, $r^2 = 0.02$, $P = 0.72$; r_p (SE) for nest predation = −0.014 (0.13), $P = 0.91$; r_p (SE) for host suitability = 0.035 (0.13), $P = 0.79$; r_p (SE) for parasitism rate = 0.15 (0.14), $P = 0.29$]. Furthermore, inter-clutch variation in

Table 2. Intra-clutch and inter-clutch variation in egg appearance of European passerines (dependent variables) in relation to nest predation rate, suitability as host, parasitism rate, habitat type and nest concealment in multiple linear regression models, forced through the origin, based on statistically independent contrasts

Dependent variable	Independent variable	r_p (SE)	t	P
Intra-clutch variation Model: $F_{5,17} = 5.32$, $r^2 = 0.61$, $P = 0.004$				
	Predation	0.17 (0.17)	1.01	0.32
	Suitability	**0.64 (0.17)**	**3.86**	**0.001**
	Parasitism	**0.37 (0.17)**	**2.18**	**0.043**
	Habitat type	−0.08 (0.17)	−0.53	0.60
	Nest location	−0.08 (0.16)	−0.50	0.62
Inter-clutch variation Model: $F_{5,17} = 0.77$, $r^2 = 0.18$, $P = 0.58$				
	Predation	0.35 (0.25)	1.41	0.17
	Suitability	0.007 (0.24)	0.03	0.97
	Parasitism	−0.44 (0.25)	−1.78	0.09
	Habitat type	−0.07 (0.24)	−0.30	0.76
	Nest location	0.002 (0.23)	0.009	0.99
Including rejection rate in the model Intra-clutch variation Model: $F_{6,12} = 4.55$, $r^2 = 0.69$, $P = 0.01$				
	Predation	0.21 (0.18)	1.14	0.27
	Suitability	**0.73 (0.22)**	**3.32**	**0.006**
	Parasitism	**0.64 (0.22)**	**2.80**	**0.02**
	Habitat type	−0.27 (0.17)	−1.56	0.14
	Nest location	−0.35 (0.17)	−1.97	0.07
	Rejection rate	0.34 (0.22)	1.54	0.14
Inter-clutch variation Model: $F_{6,12} = 0.89$, $r^2 = 0.31$, $P = 0.53$				
	Predation	0.25 (0.28)	0.91	0.37
	Suitability	0.01 (0.33)	0.05	0.95
	Parasitism	−0.18 (0.34)	−0.54	0.59
	Habitat type	−0.31 (0.26)	−1.17	0.26
	Nest location	−0.19 (0.26)	−0.71	0.48
	Rejection rate	0.44 (0.33)	1.31	0.21

Note: Significant slopes are highlighted in **bold**.

egg appearance was not significantly associated with nest predation, host suitability or parasitism rate by brown-headed cowbirds in North America [$F_{3,59} = 0.34$, $r^2 = 0.01$, $P = 0.79$; r_p (SE) for nest predation = 0.09 (0.13), $P = 0.52$; r_p (SE) for host suitability = −0.03 (0.14), $P = 0.82$; r_p (SE) for parasitism rate = 0.12 (0.14), $P = 0.35$]. These results were qualitatively supported when we controlled for the effect of habitat, nest location and the relationship between intra- and inter-clutch variation and rejection rate (analyses not shown).
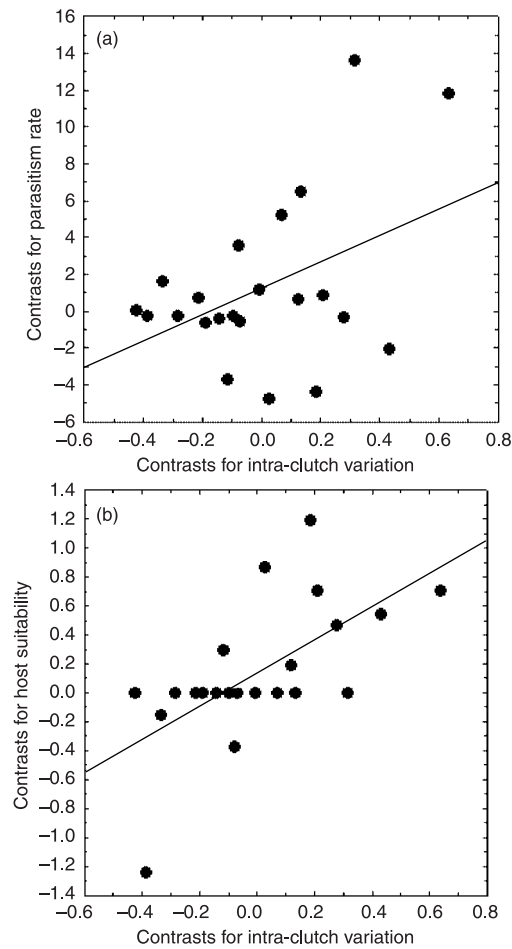
Fig. 3. Relationships between intra-clutch variation in egg appearance in European passerine birds and (a) rate of nest predation and (b) suitability as cuckoo host. All values represent standardized phylogenetically independent contrasts ($n = 22$), and the regression line is forced through the origin. Partial correlation coefficients are shown in Table 2.

DISCUSSION

Egg appearance and nest predation

The role of nest predation in the evolution of egg appearance of birds has been experimentally demonstrated for ground-nesting species (e.g. Tinbergen *et al.*, 1962; Montevecchi, 1976; Solís and de Lope, 1995; Yahner and Mahan, 1996; Lloyd *et al.*, 2000). However, no clear pattern of association between egg coloration and nest predation has so far been shown for shrub or canopy nesters that build conspicuous nest cups (reviewed in Underwood and Sealy, 2002). Moreover, no comparative study has examined the pattern of covariation between nest predation and egg phenotype for a large set of species differing in nest location and habitat used for reproduction while controlling for common descent. Here we failed to find such a relationship

between nest predation and egg phenotype (i.e. intra- and inter-clutch variation in egg appearance) for European and North American passerines. Moreover, we repeated our analyses while controlling for nest location, and the fact that species were classified as ground, shrub or subcanopy/canopy nesters did not alter the results. In addition, the results were unaffected by the fact that species were using open, forested or mixed habitats. Finally, the results remained unchanged when the intensity of brood parasitism was controlled in the analyses. Therefore, we found no support for the hypothesis that current variation in egg phenotype across open nesting passerines may be explained by nest predation.

These findings are consistent with previous experimental studies in which predation was not associated with egg colour but with nest conspicuousness (Götmark, 1992; Weidinger, 2001), and egg coloration in open nesting passerine birds was suggested to be a neutral trait with regard to nest predation. The comparative approach we used here relies on documenting interspecific associations between different traits and thus it does not account for intra-specific variation in the studied traits (Bennett and Owens, 2002). Therefore, our conclusion of an absence of effect of nest predation on egg phenotype for open nesting passerines should not be weakened by the fact that particular experimental studies showed an association between variation in egg colour and nest predation for some ground-nesting species (see above). In other words, we cannot preclude that predation may potentially explain egg appearance for particular ground-nesting birds, but we can reasonably conclude that nest predation is unlikely to be a major selective force influencing variation in egg appearance among open-nesting passerine species in Europe and North America.

Why is nest predation not linked to variation in egg phenotype across open-nesting passerines? The hypothesis that nest predation influences egg appearance in open-nesting passerines rests on the assumption that visually oriented predators locate nests by using egg colour as a basic cue. However, evidence of a nest-searching mechanism by predators relying exclusively on egg coloration is absent for shrub and canopy nesters that build a nest cup (see above). Instead, several sources of evidence suggest that predators may locate nests based on parental activity (e.g. Martin *et al.*, 2000) or female brightness during the incubation (Martin and Badyaev, 1996). Alternatively, predators may search directly for conspicuous nests (e.g. Møller, 1990). Thus adults and/or nests and not eggs would be detected first by a predator, which would reduce the adaptive value of cryptic eggs in terms of predation.

The absence of an association between egg appearance and nest predation and/or brood parasitism in North America is puzzling. The higher nest predation rates reported for North American than European passerines (Martin and Clobert, 1996), and the relatively low contribution of brood parasitism as an explanation for global egg appearance on that continent (Stokke *et al.*, 2002; present study), would suggest that egg appearance should be relatively more predation-dependent in North America than in Europe. Our finding is even more surprising if we consider that intra-clutch variation in egg appearance for North American species does not differ from that reported for European species (see also Stokke *et al.*, 2002). Several possible explanations may account for this result.

First, recent modification of the environment by humans in North America may have induced changes in rates of predation so that the rates used in this study may not correspond with the rates at which current egg appearance evolved. A number of studies have shown that recent human settlement contributed to an increase in nest predation in North America (Wilcove, 1985; Small and Hunter, 1988). However, it is impossible to infer how these changes in predation rates occurred for each of the species used in the present study.

The second possibility is that our results were affected by the current avifauna of North America having been modified due to immigration from other continents where nest predation and/or brood parasitism have played a different role as selective agents on egg phenotype. Rothstein (2001) reported that currently unparasitized populations of the grey catbird (*Dumetella carolinensis*) on Bermuda have particularly strong anti-parasite defence against the cowbirds, which apparently obtains from North American conspecifics that were cowbird hosts (see also Bolen *et al.*, 2000). In the same vein, some North American species may have immigrated from other areas where brood parasitism was the main factor selecting for a specific egg phenotype, while nest predation may have been relatively unimportant. The arrival of new breeders therefore may hamper the detection of possible relationships between nest predation and egg appearance among the original inhabitants of a continent.

A third possibility is that egg appearance in North America could currently have adaptive value in a context other than interspecific brood parasitism and nest predation. Intraspecific brood parasitism is a common breeding strategy among colonially breeding birds (Brown and Brown, 1988, 1989; Yom-Tov, 2001) and species with precocial young (Andersson, 1984; Yom-Tov, 2001). Victoria (1972) predicted that just as in species that are affected by interspecific brood parasitism, a reduction in intra-clutch variability and an increase in inter-clutch variability might increase the probability of discrimination of conspecific eggs when the probability of intraspecific brood parasitism is high. Only 12 (19.0%) of the 63 North American passerines in this study have been reported to suffer from intraspecific brood parasitism, whereas 2 (8.7%) of 23 European species suffered from this kind of parasitism (Yom-Tov, 2001) – a proportion that does not differ significantly between continents (Fisher exact test, $P = 0.33$). This suggests that it is unlikely that intraspecific brood parasitism was the main selective force shaping egg appearance in North American passerines.

Differences in egg appearance between continents

In a previous study, Stokke *et al.* (2002) found that passerine species considered to be suitable hosts for brood parasites showed greater inter-clutch variation in egg appearance in Europe than North America. Because they did not report differences in inter-clutch variation among European and North American passerines, they concluded that brood parasitism by the common cuckoo could be regarded as the main selective agent responsible for current continental differences in egg phenotype. Here, we examined whether inter-clutch variation in egg appearance differs between continents, after controlling for host suitability, parasitism rate and nest predation. We found that larger inter-clutch variation in egg phenotype among European species exists irrespective of these possible confounding factors (Table 1). Moreover, we failed to find any significant association between inter-clutch variation in egg appearance and host suitability and rate of parasitism, respectively, both in Europe and North America, after controlling for nest predation. In conclusion, we found no support for the hypothesis that brood parasitism is the main selective agent responsible for differences in inter-clutch variation in egg appearance between North America and Europe. More importantly, neither current levels of predation nor the intensity of the co-evolutionary interaction of each potential host species with brood parasitism explained the reported differences in egg phenotype between continents. It has to be noted, however, that because of the lack of information on nest predation for many species, the data set used in the present study is considerably smaller than that used by Stokke *et al.* (2002) [221 species in

Stokke *et al.* (2002) vs. 86 in the present study]. Hence, we cannot definitively conclude that differences in the role of brood parasitism between studies were the result of differences in the sets of species used in the analyses.

In conclusion, we found no support for the hypothesis that nest predation affects egg phenotype variation among open-nesting passerines. We failed to explain the adaptive value of egg appearance among North American passerines in terms of recognition of parasitic eggs and avoidance of nest predation by increasing camouflage. Finally, differences in inter-clutch variation between North American and European species were not explained by brood parasitism or nest predation.

ACKNOWLEDGEMENTS

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APPENDIX

Egg appearance (ITA = intra-clutch variation in egg appearance; ITE = inter-clutch variation in egg appearance) of North American and European passerines [CON = continent (1 = North America, 2 = Europe)], nest predation (PRE; % of nests lost to predators), brood parasitism (PAR; frequency of nests parasitized, %), suitability host (SUI), rejection level (REJ; % of experimentally parasitized nests rejecting non-mimetic eggs), nesting habitat (HAB) and nest location (NES)]. See main text for sources of data.

Species	CON	ITA	ITE	PRE	PAR	SUI	REJ	HAB	NES
Agelaius phoeniceus	1	2.1	2.8	44.4	16.2	1	4.1	2	2
Aimophila aestivalis	1	1.0	1.0	45.8	0.2	1		2	1
Ammodramus savannarum	1	1.8	3.5	58.9	22.6	1	0.0	1	1
Amphispiza belli	1	2.5	3.5	43.2	50.0	1		2	2
Cardellina rubrifrons	1	1.8	2.2	48.0	0.0	1		3	1
Cardinalis cardinalis	1	2.1	4.0	54.0	35.5	1	14.3	2	2
Carduelis tristis	1	1.1	1.3	46.8	4.9	3	16.7	3	2
Carpodacus mexicanus	1	1.8	2.3	45.8	19.4	3	0.0	2	2
Catharus guttatus	1	1.2	1.3	94.0	8.9	1		3	1
Certhia americana	1	1.9	2.8	35.3	0.2	3		3	3
Chondestes grammacus	1	1.8	3.3	38.7	33.3	1	0.0	2	1
Corvus brachyrhynchos	1	3.6	3.0	49.1	0.2	3		3	3
Cyanocitta cristata	1	1.3	3.0	38.4	0.2	3	100.0	3	3
Dendroica caerulescens	1	2.1	3.5	42.8	17.5	1		3	2
Dendroica coronata	1	2.2	3.0	53.0	23.2	1		3	3
Dendroica discolor	1	1.9	3.0	61.8	18.4	1	0.0	3	2
Dendroica petechia	1	2.1	4.0	34.2	27.1	1	3.1	3	2

Appendix—*continued*

Species	CON	ITA	ITE	PRE	PAR	SUI	REJ	HAB	NES
Dolichonyx oryzivorus	1	2.1	2.8	29.8	12.4	1		1	1
Dumetella carolinensis	1	1.1	1.0	31.2	5.9	1	96.7	3	2
Empidonax minimus	1	1.0	1.3	53.3	8.0	1	0.0	3	3
Empidonax difficilis	1	2.1	3.0	58.9	41.7	1		3	3
Eremophila alpestris	1	2.0	2.5	24.9	21.8	1		1	1
Euphagus cyanocephalus	1	2.3	4.3	45.5	16.2	1		3	3
Geothlypis trichas	1	2.1	3.3	14.5	25.5	1		2	2
Helmitheros vermivorus	1	2.1	3.5	25.6	31.7	1		3	1
Hirundo rustica	1	1.9	2.8	0.1	0.0	3	7.7	1	2
Hylocichla mustelina	1	1.1	1.5	52.5	31.8	1	0.0	3	2
Icteria virens	1	2.2	3.5	66.9	32.5	1	31.8	2	2
Junco hyemalis	1	2.4	3.0	31.7	15.1	1		3	1
Lanius ludovicianus	1	2.1	3.0	19.4	0.0	1	92.5	3	2
Melospiza melodia	1	2.8	3.0	28.1	34.9	1	11.11	2	2
Mimus polyglottos	1	2.3	3.5	47.1	0.0	1	46.51	3	2
Mniotilta varia	1	1.9	3.3	26.3	22.7	1		3	1
Oporornis formosus	1	1.8	3.3	30.0	40.0	1		3	1
Oporornis tolmiei	1	2.0	3.8	49.3	20.0	1		3	2
Passerculus sandwichensis	1	2.7	4.3	43.4	8.8	1		1	1
Passerina cyanea	1	1.1	1.3	54.0	38.9	1		3	2
Pheucticus ludovicianus	1	2.7	3.3	50.0	4.6	1	0.0	3	3
Pipilo chlorurus	1	1.4	3.0	78.0	0.2	1		2	1
Piranga ludoviciana	1	1.3	2.3	46.2	0.2	1		3	3
Piranga olivacea	1	2.1	3.5	32.6	69.6	1		3	3
Pooecetes gramineus	1	2.7	3.8	52.9	13.9	1	0.0	2	1
Sayornis phoebe	1	1.7	2.3	15.9	17.3	2	6.0	2	2
Seiurus aurocapillus	1	1.9	3.8	24.5	35.9	1		3	1
Setophaga ruticila	1	1.9	3.5	37.8	23.4	1		3	2
Spiza americana	1	1.2	1.3	48.8	46.6	1	11.1	2	2
Spizella passerina	1	1.8	2.8	41.2	20.4	1	15.8	3	3
Spizella pusilla	1	1.8	3.0	60.4	20.4	1	26.8	2	2
Sturnella magna	1	2.6	4.0	48.6	26.6	1	35.4	2	1
Sturnella neglecta	1	2.2	3.0	46.9	12.7	1	85.2	2	1
Toxostoma rufum	1	1.2	2.0	29.0	8.4	1	77.0	2	2
Turdus migratorius	1	1.1	1.5	40.2	0.5	3	91.1	3	3
Tyrannus tyrannus	1	1.9	2.5	32.7	2.5	1	91.9	3	3
Tyrannus verticalis	1	1.6	2.5	37.6	0.0	1	94.4	3	3
Tyrannus vociferans	1	1.6	2.5	42.6	0.2	1		3	3
Vermivora celata	1	2.0	3.3	50.0	0.2	1		2	2
Vireo bellii	1	2.0	1.5	11.4	43.2	1		3	2
Vireo gilvus	1	1.6	2.5	45.0	28.9	1	31.7	3	3
Vireo olivaceus	1	1.5	2.5	24.9	40.7	1	33.3	3	2
Wilsonia citrina	1	1.7	3.3	47.0	0.2	1		3	2
Wilsonia pusilla	1	2.1	3.0	34.9	27.3	1		2	1
Xanthocephalus xanthocephalus	1	2.2	3.3	34.4	0.7	1	13.6	2	2
Zonotrichia leucophrys	1	2.0	4.0	51.1	11.6	1		2	1

Species	CON	ITA	ITE	PRE	PAR	SUI	REJ	HAB	NES
Acrocephalus scirpaceus	2	2.0	2.5	49.5	14.34	1	31.3	2	2
Anthus pratensis	2	1.8	3.5	30.0	4.53	1	28.3	2	1
Anthus trivialis	2	1.7	4.8	39.3	0.74	1		3	1
Carduelis cannabina	2	2.1	2.5	41.3	0.11	3	0.0	2	2
Carduelis chloris	2	1.9	2.3	31.7	0.05	3	13.7	3	2
Erithacus rubecula	2	2.3	3.0	22.0	8.77	2	10.0	3	1
Fringilla coelebs	2	1.2	4.0	51.5	0.01	1	83.4	3	3
Hirundo rustica	2	2.0	3.5	8.5	0.01	3	0.0	1	2
Luscinia megarhynchos	2	1.4	3.0	7.5	0.01	1		3	1
Motacilla alba	2	1.7	2.8	23.6	0.21	2	90.4	2	2
Motacilla flava	2	1.4	2.8	29.2	0.07	1	80.0	2	1
Phylloscopus collybita	2	1.3	3.3	10.7	0.01	1	100.0	3	1
Phylloscopus trochilus	2	1.7	3.3	30.0	0.03	1	86.7	3	1
Pica pica	2	2.5	4.3	14.6	0.01	3		3	3
Prunella modularis	2	1.1	1.3	15.9	1.93	1	3.0	3	2
Pyrrhula pyrrhula	2	1.7	3.0	45.0	0.01	3	0.0	3	2
Sylvia atricapilla	2	1.5	3.3	21.9	0.17	1	95.4	3	2
Sylvia borin	2	1.6	4.0	21.6	0.32	1	66.7	3	2
Sylvia communis	2	1.5	4.8	21.3	0.07	1	100.0	2	2
Sylvia curruca	2	1.5	3.0	26.8	0.01	1		3	2
Sylvia undata	2	1.8	3.3	20.8	0.01	1	100.0	2	2
Turdus iliacus	2	1.6	2.5	32.0	0.01	3	34.9	3	2
Turdus merula	2	2.2	3.8	35.7	0.01	3	82.1	3	2