Brief reports

Conspicuous nests may select for non-cryptic eggs: a comparative study of avian families

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Introduction

The colour and markings on bird eggs are probably primarily cryptic, i.e. they serve to reduce the risk of nest predation (e.g., Tinbergen et al. 1962, Montevecchi 1976, Harrison 1985, O'Connor 1985). However, the great variation in egg coloration remains to be explained. Closely related species may have pure white, brown, or blue-green eggs, or spotted eggs with various backgrounds (Harrison 1985). The blue eggs of many passerines have especially puzzled ornithologists. Lack (1958, 1968) tentatively suggested that blue eggs are "adapted for concealment from predators in extremely well screened or dark nests". Recently, Oniki (1985) studied egg coloration in Amazonian birds and suggested that blue pigmentation is "a protective coloration in situations of contrasting light on green foliage".

I evaluated Lack's and Oniki's hypothesis by studying nest predation in the Song Thrush *Turdus philomelos*, which lays blue eggs in open, cup-shaped nests (Götmark 1992). I used artificial nests with eggs, painted white, blue, or beige with spots (the latter cryptic to the human eye). There was no difference in predation on nests containing eggs of different coloration. Predators apparently detected the nests first, and not the eggs. I also placed groups of eggs without nests in trees to study the effect of colour *per se*. Predation of spotted egg groups was significantly lower than that of white and blue egg groups. Thus, blue eggs in the song thrush do not seem to be cryptic, but may be selectively neutral, or even maladaptive, with regard to nest predation (Götmark 1992; see also Janzen 1978 and Slagsvold 1980).

Egg coloration did not influence egg survival when eggs were placed in nests, apparently because these were relatively easy to detect for nest predators (mostly Jays, *Garrulus glandarius*). Natural nests are also usually easy to locate, and are often preyed upon by predators (Götmark 1992). These results have implications for the evolution of egg coloration in birds. It is likely that production of egg pigments entails some cost to the female, even though it may be low. For instance, body pigmentation has disappeared in many animals that live isolated in dark caves. I assumed that pigmentation has some cost and predicted that birds with conspicuous nests should have immaculate, non-cryptic eggs, whereas birds that lack nests and lay their eggs on the ground should have variously spotted, cryptic eggs (in the absence of a conspicuous nest, selection should favour crypsis in eggs; Tinbergen et al. 1962, Montevecchi 1976, Lank et al. 1991, Götmark 1992). This should apply to species in which both the nest and the eggs can be seen by predators. In many passerines, nests are often hidden in vegetation, and the degree to which the eggs are visible has rarely been quantified. I therefore tested the prediction on non-passerine birds, for which classification of eggs and nests is relatively easy.

Material and methods

I included 27 families distinguished by Sibley et al. (1988), for which data were available in Harrison (1985). Within 25 families, all species considered could be allocated to the same category of nest (nest conspicuous, i. e. easily seen in trees or as large cup/platform on ground; or nest absent/inconspicuous, i. e. no or little material added by parents to site used). In the Falconidae and Pelecanidae, both nest categories were recorded (see below); these families were counted twice.

I distinguished four categories of eggs: (1) white or light (without spots; e.g., grebes and ducks), (2) sparsely spotted (e.g., Water Rail, *Rallus aquaticus*), (3) intermediately spotted (e.g., Oystercatcher, *Haematopus ostralegus*), and (4) heavily spotted (e.g., many plovers and gulls). Categories 2–4 were later pooled in the analysis because they seemed to represent crypsis in different habitats, whereas white or light eggs, as judged by the human eye, do not seem to be cryptic; they are called 'conspicuous' below. In one family (Accipitridae) both categories 1 and 2–4 were represented (see below); this family was counted twice. Burrow- or hole-nesting families and species, and a few other species with hidden nests, were not included.

Results and discussion

Among 15 families with species using conspicuous ground or tree nests, 12 had conspicuous eggs and 4 spotted eggs. In contrast, among 14 families with species using no nest or an inconspicuous ground nest, only 2 had conspicuous eggs, and 12 had spotted eggs (Table 1; $P < 0.005$, χ-test, one-tailed). The result is similar if I use the families distinguished by Harrison (instead of Sibley et al. 1988). Thus, selection for cryptic (spotted) eggs may disappear or may be reduced in the case of conspicuous nests. This trend might be more apparent among non-passerine birds than among passerines, because passerines generally have smaller nests and eggs, which may be more difficult for predators to detect.

Table 1. Categorization of nests and extent of markings on eggs (from 1 = conspicuous, or white or light egg, to 4 = heavily spotted) in 27 European non-passerine families (Harrison 1985). The classification is that proposed by Sibley et al. (1988)[a]. Species or families in which eggs or nests are completely hidden were excluded.

Family	Extent of markings on eggs Nest conspicuous	 Nest absent or inconspicuous
Gaviidae	–	3
Podicipedidae	1	–
Procellaridae (= *Fulmarus glacialis*)[b]	–	1
Sulidae (= *Sula bassana*)[b]	1	–
Phalacrocoracidae	1	–
Anhingidae (= *Anhinga melanogaster*)[b]	1	–
Pelecanidae	1	1
Ardeidae	1	–
Ciconiidae	1	–
Threskiornithidae	1	–
Phoenicopteridae (= *Phoenicopterus ruber*)[b]	1	–
Anatidae	1	–
Accipitridae	1–4	–
Falconidae	3–4	3–4
Phasianidae	–	2–4
Rallidae (= *Fulica atra*)[b]	2	–
Gruidae	3	–
Otididae	–	3
Rostratulidae	–	4
Burhinidae	–	3–4
Glareolidae	–	3–4
Charadriidae	–	2–4
Scolopacidae	–	2–4
Laridae	–	3–4
Pteroclidae	–	3
Columbidae	1	–
Caprimulgidae	–	3–4
Mean rank ± SD[c]	1.5 ± 0.8	2.9 ± 0.9
No. of families	15	14

[a] This means that the Pandionidae, Tetraonidae, Haematopidae, Recurvirostridae, Dromadidae and Alcidae (Harrison 1985) were not distinguished.
[b] Only one species available in Harrison (1985).
[c] Based on the median value for each family.

However, some of the families may be closely related and could therefore share traits due to common ancestry. In other words, families may not be independent units, which may violate the assumption of independence in the statistical test (Harvey & Pagel 1991). I performed two phylogenetic analyses that check for this problem (see Ridley 1983, Oakes 1992), but the sample sizes were too small to allow definite conclusions. Further analysis will be possible when a handbook of the birds of the world is available (similar to Harrison 1985). However, I improved the statistical analysis by pooling families in Table 1 that are closely related and share nest and egg characteristics. I used the phylogeny of Sibley et al. (1988) and combined families that were on the same branch or next to this branch ($T_{50}H$ values $\leq$ 12.1; see Sibley et al. 1988). Thus, I combined the Sulidae, Phalacrocoracidae and Anhingidae; Pelecanidae, Ciconiidae, Threskiornithidae and Phoenicopteridae; Burhinidae and Charadriidae; and Glareolidae and Laridae. This reduced the sample size in Table 1 from 29 to 22, but the difference in egg coloration between families (or units) with conspicuous and inconspicuous nests remains significant in this analysis as well ($P = 0.05$, Fisher's exact probability test, one-tailed).

Thus, nest visibility may have influenced the evolution of egg coloration, but other factors may also have been important. For instance, large species may be relatively immune from predation on adults and nests, in which case there may be no selection for cryptic eggs. Among species with conspicuous nests (Table 1), there are indeed many large species. A detailed analysis requires comparative data on predation risk in all families, but such data are difficult to obtain.

In the Falconidae and Pelecanidae, both conspicuous and inconspicuous nests were recorded (Table 1). Falcons nest in trees (in relatively large nests of twigs), on rock ledges, or on the ground, a variation that occurs within the species as well. The eggs are usually chestnut-red and spotted, rarely light (Harrison 1985). Falcon nests on rocks or on the ground are inconspicuous and the eggs are cryptic as predicted. However, such eggs are also laid in conspicuous tree nests. This may be due to flexible intraspecific nest site choice, a strong advantage of cryptic eggs in ground and rock nests, and a comparatively low cost of producing pigments (or gene flow between populations). Of two pelican species, White Pelicans *Pelecanus onocrotalus* build inconspicuous nests, whereas Dalmatian Pelicans *P. crispus* build conspicuous ones, but both species lay conspicuous eggs (Harrison 1985). This may be due to size and immunity from predation: the pelicans are among the largest flying birds in the world.

In the Accipitridae, the eggs vary markedly in coloration among and within the species, which all have conspicuous nests (Harrison 1985). White or relatively light eggs (sometimes faintly spotted) predominate, but markedly spotted ones also occur. Several larger species that build large conspicuous tree nests (e.g., White-tailed Eagle *Haliaëtus albicilla* and Goshawk *Accipiter gentilis*) lay white eggs and lack intraspecific variation in egg coloration. However, the large variation in egg-shell pigmentation in this family remains to be explained, and needs to be studied in the field (egg collections cannot be used, since collectors often have preferences for odd and rare egg types).

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Sammanfattning: **Selektion för okamouflerade ägg**

Kamouflerade, fläckiga fågelägg kan minska risken för bopredation, men många arter har ljusa, enfärgade ägg. En studie av taltrasten, som lägger ljusa, blågröna ägg, visade att dessa inte minskar risken för bopredation — predatorerna tycks upptäcka det relativt iögonfallande boet före äggen (Götmark 1992). Utifrån mina resultat testar jag en förutsägelse om att arter (familjer) med iögonfallande bon bör ha icke-kryptiska ägg (ljusa utan fläckar), förutsatt att det finns en kostnad av att producera pigment, medan arter (familjer) som saknar eller har rudimentära bon bör ha kryptiska ägg (mer eller mindre fläckiga).

En jämförande analys av 27 fågelfamiljer (icke-tättingar) stöder förutsägelsen, även om variationen inom ett par familjer är oförklarad. Boets utseende kan således ha påverkat evolutionen av färger och mönster på fågelägg.

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