

The evolution of egg colour and patterning in birds

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ABSTRACT

Avian eggs differ so much in their colour and patterning from species to species that any attempt to account for this diversity might initially seem doomed to failure. Here I present a critical review of the literature which, when combined with the results of some comparative analyses, suggests that just a few selective agents can explain much of the variation in egg appearance. Ancestrally, bird eggs were probably white and immaculate. Ancient diversification in nest location, and hence in the clutch's vulnerability to attack by predators, can explain basic differences between bird families in egg appearance. The ancestral white egg has been retained by species whose nests are safe from attack by predators, while those that have moved to a more vulnerable nest site are now more likely to lay brown eggs, covered in speckles, just as Wallace hypothesized more than a century ago. Even blue eggs might be cryptic in a subset of nests built in vegetation. It is possible that some species have subsequently turned these ancient adaptations to new functions, for example to signal female quality, to protect eggs from damaging solar radiation, or to add structural strength to shells when calcium is in short supply. The threat of predation, together with the use of varying nest sites, appears to have increased the diversity of egg colouring seen among species within families, and among clutches within species. Brood parasites and their hosts have probably secondarily influenced the diversity of egg appearance. Each drives the evolution of the other's egg colour and patterning, as hosts attempt to avoid exploitation by rejecting odd-looking eggs from their nests, and parasites attempt to outwit their hosts by laying eggs that will escape detection. This co-evolutionary arms race has increased variation in egg appearance both within and between species, in parasites and in hosts, sometimes resulting in the evolution of egg colour polymorphisms. It has also reduced variation in egg appearance within host clutches, although the benefit thus gained by hosts is not clear.

Key words: interclutch variation, intraclutch variation, carotenoid, *Cuculus canorus*, pigment, biliverdin, porphyrin.

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I. INTRODUCTION

Bird eggs vary considerably among species in the colour of their shells and the patterns that adorn them. They may be white or chocolate brown, glossy turquoise or brick red, violet or emerald green. They may be immaculate, or covered in dense speckling. Sometimes the speckles are confined to a ring on the blunt end of the egg, sometimes they are fused into blotches and in some species they take the form of a continuous dense squiggle, scrawled over the entire shell. The extent of variation is remarkable, but is spread unevenly across bird taxa. At least 221 hummingbird species lay an immaculate white egg. Yet members of a single species, the Wailing Cisticola (*Cisticola lais*) for example, can produce white eggs or pale blue eggs that are either spotted, streaked or immaculate. In the tinamou family, different species lay either brilliant turquoise, or violet or chocolate brown eggs whereas all kingfishers lay immaculate white eggs.

How can we account for the nature and variety of egg colouring and patterning? In this paper, I take two approaches. I begin by reviewing hypotheses that attempt to explain the evolution of egg appearance. Some ideas consider the functional significance of an egg's particular colour or the extent to which it is speckled. Others dwell more on the variety in egg appearance and try to account for the extent of diversity within and among species. In the second part of the paper, I use multivariate comparative analyses to test the merit of the hypotheses shortlisted from the first part of the paper. The data for these analyses were taken from bird atlases and summarize egg colouring and patterning and its diversity at the family level for 132 bird

families. In general, the aim is to evaluate the relative importance of different selective forces on an egg's appearance, whilst accounting for the influence of phylogenetic history.

II. HOW DO EGGS ACQUIRE THEIR COLOUR AND PATTERNING

We cannot begin to account for the evolution of egg colour and patterning without some brief consideration of the mechanisms responsible for shell manufacture and pigmentation. About 4 h after its release from the ovary the ovum, now fertilized and encapsulated in albumen and a limiting membrane, reaches the shell gland pouch (Board & Sparks, 1991). Here, during the next 20 h or so, eggshell biomineralization takes place. In non-passerines, the bulk of the shell is laid down as densely packed vertical calcite crystals, interlaced with pores (Board & Sparks, 1991), but this structure is absent in small passerines and is replaced with a highly vesiculated squamatic zone (Gosler, Higham & Reynolds, 2005). The outer surface of the shell may be covered with a thin organic cuticle and in some species, such as the Shag (*Phalacrocorax aristotelis*), a further coat of inorganic material may also be added which lends the egg a chalky appearance (Burley & Vadehra, 1989).

The pigments responsible for both the colour and patterning of the egg are deposited in the 4 h preceding egg-laying and therefore reside primarily in the outer part of the shell and in its cuticle (Burley & Vadehra, 1989; Soh, Fujihara & Koga, 1993). These are protoporphyrin,

responsible for brownish hues, and biliverdin IX α and its zinc chelate which generate blue and green colours (Kennedy & Vevers, 1976; Burley & Vadehra, 1989). Eggshells also reflect ultra-violet light (e.g. Cherry & Bennett, 2001), but the structures or pigments responsible for reflectance at these wavelengths have not yet been described. The precise amount of pigment deposited by the shell gland appears to be controlled by estradiol and progesterone (Soh & Koga, 1997). The shells of some ducks, parrots, owls, pigeons and swifts which appear immaculate and creamy white externally can, nevertheless, contain some or all of these pigments (Kennedy & Vevers, 1976; Miksik, Holáň & Deyl, 1994), perhaps because they serve a structural function, adding strength and flexibility to the shell (Gosler, Higham & Reynolds, 2005). Indeed, this may be their only function (Gosler *et al.*, 2005). The smaller passerines in particular may depend on these pigments for eggshell strength, because their relatively smaller skeletons can spare only limited amounts of calcium for shell manufacture. Individual Great Tits (*Parus major*), for example, apparently compensate for thinner egg shells by depositing greater amounts of pigment (Gosler *et al.*, 2005). An alternative possibility is that eggshell pigments now serve multiple roles. Perhaps they were integral to the structure of the ancestral avian shell but have been secondarily co-opted to serve signalling or thermoregulatory functions as well. It is the signalling functions of egg colour and patterning that we turn to next.

III. SIGNALLING AND THERMOREGULATORY FUNCTIONS OF EGG COLOUR AND PATTERNING

(1) The evolution of egg colour and patterning

(a) Selection by predators

(i) *Selection for crypsis.* As long ago as 1838, Hewitson noticed that birds nesting in cavities tended to lay white eggs (Newton, 1893). White eggs may be adaptive in dimly lit nests because they are easier to see and so the bird is better able to care for them (Lack, 1958). To Hewitson's list of white-egg-laying species, Wallace (1889) later added birds that construct domed nests (such as Penduline Tits *Remiz pendulinus*), birds that keep their clutch permanently covered during incubation (such as pigeons and doves) and birds that are sufficiently powerful to defend their nests (such as Ostriches *Struthio camelus*). Wallace suggested that the ancestral egg was white and that all other forms of egg colour and patterning were adaptations to the specific microenvironment of each nest, functioning to conceal eggs from predators.

Wallace's hypothesis for egg colouring is intuitively appealing because it can explain why so many bird eggs are white or speckled or some shade of brown in colour, and because it is consistent with observations that more cryptic offspring are less vulnerable to attack by predators (Tinbergen *et al.*, 1962; Solis & de Lope, 1995; Lloyd *et al.*, 2000; Sanchez *et al.*, 2004). Furthermore, Lack (1958) found

that a species' nest site could explain some of the variation in egg patterning and colouring amongst the Turdinae. He found that hole-nesters were more likely to lay white immaculate eggs, whereas about 80% of birds whose nests were placed in exposed sites covered their eggs in red or brown speckling, which he interpreted as an adaptation for concealment.

However, experimental evidence in support of Wallace's hypothesis is rather mixed (comprehensively reviewed by Underwood & Sealy, 2002 and so discussed only briefly here). The typical experimental approach in testing this idea is to paint eggs (often chicken eggs) so that they differ to various degrees from the usual egg appearance of the species in question, and then to compare rates at which eggs in the different experimental treatments are taken by predators (e.g. Tinbergen *et al.*, 1962; Montevecchi, 1976; Götmark, 1992; Weidinger, 2001). The common finding in these experiments is that there is no significant difference in the rate at which predators take the experimental eggs, even when some have been painted white and others painted to mimic the 'cryptic' appearance of the natural egg (e.g. Tinbergen *et al.*, 1962; Montevecchi, 1976; Götmark, 1992; Weidinger, 2001).

One interpretation is that Wallace's hypothesis simply does not withstand experimental testing, because egg colour and patterning do not enhance crypsis. But an alternative possibility is that the methodology used is flawed. Perhaps, for example, mammalian predators are quickly drawn to a manipulated nest site reeking of interesting new odours. In addition, eggs that are painted to appear cryptic to us may nevertheless look extremely obvious to avian predators (see Bennett, Cuthill & Norris, 1994). Painted eggs were more likely to be taken than were naturally laid eggs (e.g. Tinbergen *et al.*, 1962; Montevecchi, 1976), which suggests that we can never match natural levels of crypsis, no matter how skilled our painting. However, it may be possible to increase the degree to which a naturally conspicuous egg is concealed by using paints. Pigeons and doves lay bright white eggs in cup nests, but conceal their eggs from predators through constant incubation. Westmoreland & Best (1976) disrupted the incubation schedule of Mourning Doves (*Zenaidura macroura*) by flushing them from the nest, and reduced the conspicuousness of the eggs by painting them with brown tempera paint. They report that flushing increased the vulnerability of the eggs to predators, but that the effect was less pronounced when the eggs were painted brown. Similarly, Bertram & Burger (1981) were able to reduce the incidence of attack on ostrich eggs by painting the naturally white shell a shade of brown.

A further complication in interpreting experimental tests of Wallace's (1889) hypothesis is that painted eggs are sometimes presented in artificial nests, which typically are far less cryptic than nests constructed by the birds themselves and so may attract greater levels of interest from would-be predators than is usual (Underwood & Sealy, 2002). In 19 studies testing Wallace's hypothesis, 10 used artificial nests while nine presented eggs without nests at all. Only one of the studies involving artificial nests found that egg colour enhanced crypsis, which was less than the

improvement in crypsis detected in the five studies in which no nest was used (studies summarized in Underwood & Sealy, 2002; Fisher Exact $P=0.0573$). Taken together, the results suggest that egg colouration can enhance crypsis, but that it is of secondary importance to nest crypsis in concealing eggs from predators (Underwood & Sealy, 2002). According to this view, the most cryptic eggs should be laid by birds that do not build nests, an idea for which there is some support (see Götmark, 1992, 1993; Underwood & Sealy, 2002).

(ii) *Selection for aposematism.* With so much work suggesting that cryptic eggs have evolved in response to the actions of nest predators, it initially seems paradoxical to think that predators could also have caused the evolution of conspicuous eggs. This possibility was first raised in the thoughtful writings of Swynnerton (1916), an entomologist with a keen interest in the evolution of warning colouration and a sceptical view of Wallace's (1889) hypothesis. Working as a game warden in Tanzania, Swynnerton was struck by the bright colour and patterning of bird eggs, especially those whose colouring contrasted sharply with the nest background. These colours, he suggested, were aposematic, advertising the egg's unpalatability to any potential predator. He tested his ideas experimentally by offering eggs of many species to a rat, a lemur and an Indian Mongoose and noting the enthusiasm of their response. In addition, he collated personal reports of egg palatability from his house guests and correspondents. The results were mixed. Mrs A. Sclater's brothers and Mr H. M. Wallis found the blue eggs of thrushes (*Turdus* spp.), Nightingales (*Luscinia megarhynchos*) and Blackbirds (*Turdus merula*) 'beastly' but enormously enjoyed the white eggs laid by the Little Bittern (*Ixobrychus minutus*) and Barn Owl (*Tyto alba*). The Indian Mongoose preferred chicken eggs, and the blue eggs laid by the Blackbird and Dunnock (*Prunella modularis*), but refused the white eggs produced by the Wren (*Troglodytes troglodytes*) and Great Tit. Swynnerton (1916) concluded that eggs certainly varied among species in their palatability, but not in a way that was obviously correlated with their shell colour.

Thirty years later, Cott (1948, 1952) resurrected Swynnerton's hypothesis. The privations of food rationing in Britain during the Second World War led to the establishment of testing panels, trained in the art of objectively grading food for taste. Cott took advantage of one panel's skills to score the edibility of a range of wild bird eggs. The eggs of 81 species were lightly scrambled over steam and presented blind to the panel who then ranked them on a scale from 2.0 (inedible) to 10.0 (excellent flavour). The tastes of the panel and Swynnerton's Indian Mongoose were in accord. Chicken eggs were rated most edible, while Great Tit eggs were far down the list at 77th most palatable, just above Wren eggs which were judged least palatable. Cott (1948) reported that the palatability of the egg was linearly related to its size, with the smallest eggs tasting most horrible. He also claimed that the more palatable eggs were cryptic, while the least palatable were the most conspicuous, thereby supporting Swynnerton's (1916) contention that bright egg colouring serves an aposematic function.

One problem with Cott's interpretation of his data lies in his subjective assessment of egg crypsis (Lack, 1958). For example, he classified all passerine eggs as cryptic, even the blue eggs laid by Blackbirds. Since passerine eggs are generally smaller than those laid by other birds, and smaller eggs have a more revolting taste, Lack (1958) argued that the correlation between crypsis and egg palatability was simply a by-product of the relationship between egg size and palatability. His reanalysis of the relationship between egg palatability and colour within the passerines does not demonstrate an aposematic function for egg colour. The most distasteful eggs in his analysis were white and speckled and laid by cavity-nesting species. Their 'quiet speckling' hardly compares with the vibrant reds and yellows more typically seen in other warning displays (Lack, 1958).

There is therefore little evidence to suggest that conspicuous eggshells have evolved to warn predators of the egg's distastefulness, and the substantial variation in egg palatability remains largely unexplained. Perhaps an egg's taste will turn out to be explained by its internal colouring instead, if the carotenoids packed in the yolk to protect the offspring from free radicals (Blount, Houston & Møller, 2000) happen to enhance the flavour of the yolk as well (C. M. Spottiswoode, *personal communication*).

(b) *Selection by mates*

What can account for the evolution of blue eggs? Lack (1958) speculated that the sky-blue eggs laid by chats and thrushes might be cryptic in the filtered light environment of their nest sites, such as a dark hedge or forest understorey, and recent observations are consistent with that possibility. The ambient light at Blackbird nests is predominantly yellow (S. Hunt, N. E. Langmore, A. T. D. Bennett and R. M. Kilner, unpublished data) which means that blue Blackbird eggs might appear essentially black when viewed in their nest. But blue eggs cannot have evolved only through selection for crypsis in nests that are tucked into vegetation. Starlings (*Sturnus vulgaris*), for example, lay blue eggs in cavity nests, while Blackcaps (*Sylvia atricapillus*) lay creamy white speckled eggs even though their nests are hidden in bushes.

Moreno & Osorno (2003) have recently suggested that blue egg colouring may have been selected by male birds, keen to assess the quality of parental investment offered by their partner that they might adjust their contribution of offspring care accordingly. Biliverdin, the pigment primarily responsible for the blue-green tinge to egg shells, is also known to have strong antioxidant properties. Thus, the argument goes, females must balance the use of biliverdin in pigmenting their eggs with the use of biliverdin in protecting themselves from attack by free radicals. Any female that manages to lay richly blue eggs is therefore advertising her high quality to her partner, who may then choose to allocate more effort to looking after the resulting superior offspring.

The theory underlying this idea is perhaps not as straightforward as its proponents suggest. The hypothesis depends on a key assumption: that males will increase their contribution to care if they perceive their female to be of

high genetic or phenotypic quality. But if high-quality females are capable of rearing offspring more or less single-handedly then it is equally possible that a male will respond by reducing his involvement in parental care. Females should then go to great lengths to conceal their quality to be sure of extracting as much care as possible from their partner.

Despite these theoretical difficulties, a comparative study has produced evidence that is intriguingly consistent with this idea (Soler *et al.*, 2005). Passerine species that spend longer raising their chicks, and so have a greater interest in assessing the parental qualities of their mates, are more likely to lay blue eggs (Soler *et al.*, 2005). In addition, polygynous passerine species, in which females must compete for paternal care, lay bluer eggs than their monogamous counterparts (Soler *et al.*, 2005). However, each relationship is relatively weak (unfortunately R is not reported in either case) and the greatest contrasts in egg blueness correspond with near-zero contrasts in both the duration of parental care and type of mating system.

Further comparative evidence poses greater problems for this hypothesis. The avian radiation exhibiting perhaps the widest diversity in patterns of parental care is the shorebirds (order Charadriiformes), and we should expect to see a corresponding range in egg colouring, with blue eggs prevailing in species with biparental or male only care (Moreno & Osorno, 2003). I searched for data in *The Handbook of the Birds of the World* Vol. 3 (del Hoyo, Elliott & Sargatal, 1996), supplementing that source of information with data from *The Birds of the Western Palearctic* Vol. 3 (Cramp, 1983); *The Birds of Africa* Vol. 2 (Urban, Fry & Keith, 1986); *The Handbook of Australian, New Zealand and Antarctic Birds* Vol. 2 (Marchant & Higgins, 1993) and the *Guide to the Nests, Eggs and Nestlings of North American birds* (Baicich & Harrison, 1997). I found descriptions of both egg colour and mating systems for 112 species (Table 1). Ninety-two species laid brown spotted eggs and of these, 64 had a monogamous mating system, five were polygynous, eight were polyandrous and 15 had a variable mating system. Fourteen species produced blue spotted eggs, and 12 of these were monogamous while the remaining two species had a variable mating system. Birds that lay blue eggs might therefore be more likely to be monogamous but there is no indication that monogamous birds are more likely to lay blue eggs. In short, the comparative data do not suggest that blue eggs evolved specifically to signal female quality, although it is possible that blue eggs may have been co-opted for this purpose subsequently, an interpretation that is also consistent with evidence from Pied Flycatchers (*Ficedula hypoleuca*). Young, healthy female flycatchers lay eggs that are more intensely blue (Moreno *et al.*, 2005) and females with more intensely blue eggs are more likely to be assisted in chick rearing by hard-working males (Moreno *et al.*, 2004). Nevertheless, a direct causal link between male effort and egg colour has yet to be shown.

(c) Thermoregulation

Egg pigmentation might bring the benefit of crypsis but it also carries an associated risk that the egg will overheat

when in direct sunlight. Montevecchi (1976) painted chicken and gull eggs with a khaki paint and compared the temperatures of the yolks with those in control white eggs after all four egg types had been left in direct sunlight for an afternoon. He found that yolk temperatures in the khaki eggs were roughly 33 °C, about 3 °C warmer than those in the white eggs (Montevecchi, 1976). Bertram & Burger (1981) used a similar technique to investigate the adaptive significance of Ostrich egg colouring. They used crayons to change the naturally creamy white Ostrich shell brown, and measured the effect on egg temperature with thermistors inserted within. In the middle of the Kenyan day, natural egg temperatures soared to 39.8 °C, but the temperatures of the brown eggs crept higher still, peaking at 43.4 °C, above the lethal upper limit for embryonic development (42.2 °C; Bertram & Burger, 1981).

Birds that lay their eggs in exposed nests on the ground must therefore trade-off the risk of depredation that follows if their eggshells bear too little pigmentation, with the danger of embryonic overheating if they are too pigmented. Bertram & Burger (1981) argue that, despite their conspicuousness, white eggs represent the optimal trade-off for Ostriches. In this species, overheating poses the greater threat to the developing young because parents are effective guards against the principal egg predator, the Egyptian Vulture (*Neophron percnopterus*). Perhaps this explains why Ostrich eggs gleam so whitely and brightly from their ground nest that they can be seen by aeroplane passengers flying overhead (Bertram & Burger, 1981).

In other species, the trade-off may be minimized by the nature of the pigments that are incorporated in the egg shell (Bakken *et al.*, 1978). More than half the sunlight that falls on an eggshell is in the near-infrared portion of the spectrum. Bakken *et al.* (1978) found that the pigments responsible for both brown (protoporphyrin) and blue (biliverdin) eggs reflect more than 90 % of light in the near-infrared, thereby minimizing heating of the egg by the sun. By contrast, the melanic pigments responsible for dark brown colouring in feathers absorb a far greater fraction of light at these wavelengths. Bakken *et al.* (1978) calculate that eggs pigmented with protoporphyrin or biliverdin could be left unattended in direct sunlight for 36 min without risk of injury to the embryo, whereas eggs pigmented with melanin would last just 20 min in the same conditions. It would be interesting to pursue this line of research further, with comparisons of closely related species whose eggs experience substantially different levels of solar radiation. Are eggs laid in exposed nests specially pigmented to reflect near-infrared light, or is this just a common feature of all egg pigmentation?

(d) Selection by brood parasites and their hosts

Brood parasites lay their eggs in nests belonging to other birds, so transferring the costs of parental care to their victims. Parasites may facultatively cheat on members of their own species (Yom-Tov, 2001), or they may never rear their own young, and lay their eggs in nests belonging to a different species. The latter type of parasitism is especially costly for hosts, who typically lose reproductive success as well as incurring the extra cost of rearing unrelated

Table 1. The mating system and ground colouring of eggs laid by 112 species of the Charadriiformes. Descriptions of egg colouring were cast into three categories: brown, blue and white using the criteria described in Section IV (1a)

Species	Mating system	Egg shell ground colour
<i>Hydrophasianus chirugus</i>	polyandry	brown
<i>Jacana spinosa</i>	polyandry	brown
<i>Jacana jacana</i>	polyandry	brown
<i>Actophilornis africanus</i>	variable	brown
<i>Actophilornis albinucha</i>	polyandry	brown
<i>Metopidius indicus</i>	polyandry	brown
<i>Microparra capensis</i>	monogamy	brown
<i>Irediparra gallinacea</i>	polyandry	brown
<i>Rostratula benghalensis</i>	variable	brown
<i>Rostratula semicollaris</i>	monogamy	brown
<i>Thinocorus rumicivorus</i>	monogamy	brown
<i>Attagis gayi</i>	monogamy	brown
<i>Pedionomus torquatus</i>	polyandry	brown
<i>Bartramia longicauda</i>	monogamy	brown
<i>Numenius phaopus</i>	monogamy	brown
<i>Numenius arquata</i>	monogamy	brown
<i>Limosa limosa</i>	monogamy	brown
<i>Limosa lapponica</i>	monogamy	brown
<i>Coenocorypha aucklandia</i>	variable	brown
<i>Coenocorypha pusilla</i>	polygyny	brown
<i>Lymnocyptes minimus</i>	monogamy	brown
<i>Scotopax rusticola</i>	polygyny	brown
<i>Gallinago stenura</i>	monogamy	brown
<i>Gallinago media</i>	polygyny	brown
<i>Gallinago gallinago</i>	variable	brown
<i>Calidris pusilla</i>	monogamy	brown
<i>Calidris minuta</i>	variable	blue
<i>Calidris minutilla</i>	monogamy	brown
<i>Calidris fuscicollis</i>	polygyny	brown
<i>Calidris bairdii</i>	monogamy	brown
<i>Calidris alpina</i>	monogamy	blue
<i>Calidris melanotos</i>	variable	brown
<i>Calidris alba</i>	monogamy	blue
<i>Calidris mauri</i>	monogamy	brown
<i>Calidris maritima</i>	monogamy	blue
<i>Calidris ptilocnemis</i>	monogamy	blue
<i>Calidris temminckii</i>	variable	brown
<i>Tryngites subruficollis</i>	polygyny	brown
<i>Limicola falcinellus</i>	monogamy	brown
<i>Calidris canutus</i>	monogamy	blue
<i>Aphriza virgata</i>	monogamy	brown
<i>Micropalama himantopus</i>	monogamy	brown
<i>Arenaria interpres</i>	monogamy	brown
<i>Tringa erythropus</i>	variable	blue
<i>Tringa stagnatilis</i>	monogamy	brown
<i>Tringa totanus</i>	monogamy	brown
<i>Tringa nebularia</i>	monogamy	blue
<i>Tringa glareola</i>	monogamy	blue
<i>Tringa ochropus</i>	monogamy	brown
<i>Catotrophorus semipalmatus</i>	monogamy	brown
<i>Phalaropus lobatus</i>	variable	brown
<i>Phalaropus fulicaria</i>	variable	brown
<i>Steganopus tricolor</i>	variable	brown
<i>Actitis hypoleucos</i>	monogamy	brown

Table 1 (cont.)

Species	Mating system	Egg shell ground colour
<i>Actitis macularia</i>	polyandry	brown
<i>Chionis alba</i>	monogamy	white
<i>Chionis minor</i>	monogamy	white
<i>Pluvianus aegyptius</i>	monogamy	brown
<i>Burhinus vermiculatus</i>	monogamy	brown
<i>Burhinus capensis</i>	monogamy	brown
<i>Burhinus grallarius</i>	monogamy	brown
<i>Burhinus oedicephalus</i>	monogamy	brown
<i>Burhinus senegalensis</i>	monogamy	brown
<i>Haematopus longirostris</i>	monogamy	brown
<i>Haematopus fuliginosus</i>	monogamy	brown
<i>Haematopus palliatus</i>	monogamy	brown
<i>Haematopus moquini</i>	monogamy	blue
<i>Haematopus ostralegus</i>	monogamy	brown
<i>Haematopus unicolor</i>	monogamy	brown
<i>Haematopus bachmani</i>	monogamy	brown
<i>Ibidorhyncha struthersii</i>	monogamy	blue
<i>Himantopus himantopus</i>	monogamy	brown
<i>Himantopus novaezealandiae</i>	monogamy	blue
<i>Himantopus leucocephalus</i>	monogamy	brown
<i>Pluvialis squatarola</i>	monogamy	brown
<i>Pluvialis apricaria</i>	monogamy	brown
<i>Pluvialis fulva</i>	monogamy	brown
<i>Pluvialis dominica</i>	monogamy	brown
<i>Eudromias morinellus</i>	variable	brown
<i>Anarhynchus frontalis</i>	monogamy	blue
<i>Charadrius pecuarius</i>	monogamy	brown
<i>Elsayornis melanops</i>	monogamy	white
<i>Charadrius alexandrinus</i>	variable	brown
<i>Charadrius rubricollis</i>	monogamy	white
<i>Charadrius pallidus</i>	monogamy	brown
<i>Charadrius obscurus</i>	monogamy	brown
<i>Charadrius marginatus</i>	monogamy	brown
<i>Charadrius forbesi</i>	monogamy	brown
<i>Charadrius montanus</i>	variable	brown
<i>Charadrius vociferus</i>	monogamy	brown
<i>Charadrius dubius</i>	monogamy	brown
<i>Charadrius hiaticula</i>	monogamy	brown
<i>Charadrius tricollaris</i>	monogamy	white
<i>Charadrius melodus</i>	monogamy	white
<i>Charadrius asiaticus</i>	monogamy	brown
<i>Charadrius bicinctus</i>	monogamy	blue
<i>Peltohyas australis</i>	monogamy	brown
<i>Thinornis novaeseelandiae</i>	monogamy	brown
<i>Vanellus melanopterus</i>	monogamy	brown
<i>Vanellus coronatus</i>	monogamy	brown
<i>Vanellus vanellus</i>	variable	brown
<i>Vanellus albiceps</i>	monogamy	brown
<i>Vanellus senegallus</i>	monogamy	brown
<i>Vanellus superciliosus</i>	monogamy	brown
<i>Vanellus lugubris</i>	monogamy	brown
<i>Vanellus tectus</i>	monogamy	brown
<i>Vanellus tricolor</i>	monogamy	brown
<i>Vanellus armatus</i>	monogamy	brown
<i>Vanellus spinosus</i>	monogamy	brown
<i>Vanellus miles</i>	monogamy	brown
<i>Vanellus crassirostris</i>	monogamy	brown

offspring. The cost of parasitism has provoked an evolutionary arms race between parasite and host, in which hosts evolve defences to avoid becoming victimized and parasites counterattack by evolving strategies to outwit their hosts (Davies, 2000). Most of these evolutionary battles are waged at the egg stage of the nesting cycle (but see Langmore, Hunt & Kilner, 2003), and they are likely to have affected the evolution of egg colouring and patterning.

For example, species that are potential victims of brood parasites often protect themselves against exploitation by recognizing and rejecting any odd-looking eggs that are added to their clutch. Some hosts select the alien egg for removal from the nest, while others will abandon the entire parasitized clutch (Davies, 2000). Hosts learn to recognize the appearance of their eggs, and can be induced to learn the wrong appearance if egg colour is experimentally manipulated during their first breeding attempt (Lotem, Nakamura & Zahavi, 1995). Eggs can be selected for rejection by reference to this memorized image alone, because hosts will reject entire clutches of foreign-looking eggs, removing them one by one from the nest (Victoria, 1972; Lahti & Lahti, 2001). West African Village Weaverbirds (*Ploceus cucullatus*), which are host to cheats of their own species as well as Diederik Cuckoos (*Chrysococcyx caprius*), distinguish their own eggs by their colouring first and then by their pattern of speckling (Lahti & Lahti, 2001).

The remarkable powers of discrimination exhibited by hosts have, in turn, selected parasites whose eggs are sufficiently mimetic (or cryptic) that they escape detection and rejection by hosts (Davies, 2000). The degree of mimicry need only be good enough to beat the hosts' skills at recognition. Dunnocks (*Prunella modularis*) do not reject even very odd eggs that are added to their nest (Davies & Brooke, 1989a) and the Common Cuckoo gens (*Cuculus canorus*) that exploits this host does not lay a mimetic egg (Brooke & Davies, 1988).

The co-evolutionary interactions between parasites and their hosts become especially interesting once the parasite evolves the ability to lay a good mimic of the hosts' eggs. How can a host then refine its ability to detect an alien egg? One possibility is that hosts develop personal signatures for their eggs, that are far too complex to be forged by a parasite, and that are far more outlandish than the patternings seen in species which are not victims of brood parasites (Swynnerton, 1918; Davies & Brooke, 1989b). Perhaps this can account for the evolution of egg colours that do not obviously enhance crypsis. The evidence, however, suggests otherwise. Eggs taken from a British population of Pied Wagtails (*Motacilla alba*) in sympatry with the Common Cuckoo, and an Icelandic population with no history of cuckoo parasitism were equally spotty, as were those obtained from two equivalent populations of Meadow Pipits (*Anthus pratensis*; Davies & Brooke, 1989b). Similarly, the egg speckling patterns of Greek Great Reed Warblers (*Acrocephalus arundinaceus*), which are not currently exploited by the Common Cuckoo, were similar to those of a heavily parasitized Hungarian Great Reed Warbler population (Moskát, Szanpéteri & Barta, 2002). Comparative analyses

yield the same null result. Davies & Brooke (1989b) found no difference in the distinctiveness of the egg markings of seven hosts of the Common Cuckoo, and five species which are unlikely to have had evolutionary interactions with the cuckoo. Therefore there is no indication that brood parasitism causes specific directional change towards more conspicuous egg colouring or more spectacularly complex patterning as hosts attempt to outwit the parasite's skills at egg mimicry.

(2) The evolution of diversity in egg appearance

(a) Selection by predators

Nests commonly contain one egg that stands out from the rest of the clutch, either because its shell is more richly coloured (Newton, 1893), or paler in colouring (Verbeek, 1990) or differently patterned (Preston, 1957; Chamberlin, 1977; Hockey, 1982). Often this is the last egg laid and its colouring may be the non-adaptive consequence of pigment glands becoming depleted (Nice, 1937), or emptying themselves entirely with the completion of the clutch (Lowther, 1988). Alternatively, the last-laid egg may be differently coloured for one of several different adaptive reasons. The first possibility is linked to the observation that last-laid eggs are less valuable than the rest of the clutch. They can be smaller and undernourished in comparison with other eggs in the nest, and produce nestlings with a poor chance of survival. Verbeek (1990) argued that conspicuous last-laid eggs are sacrificed for the good of the clutch. He found that the clutches of Northwestern Crows (*Corvus caurimus*) were vulnerable to attack by conspecifics, who were in the habit of taking just one egg. In 12 out of 17 cases of depredation, the palest egg of the clutch disappeared. However, there is no evidence yet to suggest that the fitness of clutches that include a pale egg is greater than those that do not.

Furthermore, Hockey's (1982) observations of African Black Oystercatchers (*Haemotopus moquini*) are not consistent with Verbeek's idea. In their clutches of two eggs, the oystercatcher's second egg was covered in smaller blotches than the first, but was no more likely to be taken by a predator. Hockey (1982) reasoned that the pattern differences between the two eggs functioned instead to promote the crypsis of the clutch, because two differently coloured eggs would be harder to spot than two eggs of the same appearance. Although Hockey (1982) presented no evidence to test this idea, it is supported by observations of Namaqua Sandgrouse (*Pterocles namaqua*), because nests of this species that contained eggs of greatest diversity in colour and patterning were most likely to survive (Lloyd *et al.*, 2000). However, clutches which have been experimentally manipulated to contain odd-looking eggs are no less likely to succumb to predators than those containing eggs of more uniform appearance (Mason & Rothstein, 1987; Davies & Brooke, 1988).

A further suggestion is that birds invest heavily in colouring their eggs to conceal them from predators, and that the benefit of this investment is felt most during egg-laying when the incomplete clutch is left unattended. The

female can afford to skimp on the expense of disguising her final egg because she will attend her clutch much more closely once she has started incubating (Ruxton, Broom & Colegrave, 2001). This hypothesis has not yet been tested directly. However, the assumption that nest attendance reduces the vulnerability of the clutch does not match observations that parental activity at the nest can increase the likelihood it will be found by a predator (e.g. Martin, Scott & Menge, 2000).

It is therefore unlikely that predators have led to the evolution of conspicuous last-laid eggs. There is no experimental evidence that conspicuous last-laid eggs reduce the vulnerability of the clutch to predators. It is also unclear whether egg pigmentation is costly to produce, and whether birds are capable of strategically allocating shell pigments among their eggs.

(b) *Selection by brood parasites*

(i) *Selection for odd-looking last eggs within the same nest (increased intraclutch variation).* The odd colour of last-laid eggs might instead be a signal to intraspecific brood parasites that the clutch is complete and that incubation has begun (Yom-Tov, 1980). A key assumption here is that the advertisement of clutch completion is beneficial for host and parasite alike. It would pay parasites to take note of this information, because any egg added to the clutch after the start of incubation may be doomed never to hatch. Even if the egg hatches, the parasitic chick is then likely to fail in the competition for food with its older, larger nestmates. Hosts, meanwhile, clearly gain by avoiding parasitism. However, if hosts potentially make themselves vulnerable to exploitation by signalling that they have completed their clutch, then this idea cannot work. For example, rather than leave the nest alone to search for a more profitable host, the parasite may instead choose to destroy a completed clutch, thus farming that host for future parasitism (N. B. Davies, *personal communication*).

Even when the signalling of clutch completion is mutually beneficial, selection for dishonesty persists because any potential host that laid an odd-looking first egg would escape parasitism altogether. In theory, stable advertisement of clutch completion can evolve if the production of odd-looking eggs is costly, and if this cost is prohibitively high for first-laid eggs but less than the cost of parasitism for last-laid eggs (Ruxton *et al.*, 2001). Empirical tests of this idea have yet to be carried out, though.

(ii) *Selection for reduced intraclutch variation within species and increased interclutch variation.* We return now to the arms race between brood parasites and hosts that we encountered earlier, in which hosts defend themselves against parasitism by rejecting odd-looking eggs from their nests and in which parasites breach host defences by laying eggs that closely mimic the host's clutch. How can hosts improve their chances of detecting a parasitic egg? One option might be to reduce intraclutch variation in egg colouring and appearance. It won't change the mean difference in appearance between parasite and host eggs, but providing there is greater variation in the appearance of parasitic eggs it will, in theory, improve the chance of correctly identifying the

foreign egg hidden amongst the victim's clutch (Davies & Brooke, 1989*b*; Jackson, 1998).

A second means by which individual hosts can identify foreign eggs, is to produce eggs that look unlike the cuckoo's. As long as hosts are unconstrained in their possible direction of mutational change, this will have the effect of increasing the variation in egg appearance between clutches laid by a parasitized population (Swynnerton, 1918; Davies & Brooke, 1989*b*; Jackson, 1998; Takasu, 2003).

These two hypotheses have spawned a cottage industry of empirical testing, both at the species level and with comparative analyses. The prediction that intraclutch variation in egg appearance should decrease in response to parasitism rests on a key assumption: that foreign-looking eggs are easier to spot amidst a clutch of uniform host eggs. Experimental evidence in support of this assumption is, however, rather mixed. Standing against this idea is the finding that Red-backed Shrikes (*Lanius collurio*) which lay uniform clutches are no more likely to reject odd-looking eggs than those which lay more variable eggs (Lováski & Moskát, 2004). Avilés *et al.* (2004) even report that Magpie (*Pica pica*) hosts of the Great-Spotted Cuckoo (*Clamator glandarius*) were more likely to reject model cuckoo eggs from the nest if their own clutch was highly variable than otherwise. Evidence in support of this assumption comes from the behaviour of Reed Warblers (*Acrocephalus scirpaceus*) who are more likely to reject foreign eggs if they lay a more uniform clutch (Stokke *et al.*, 1999). However, the foreign eggs used in this experiment were immaculate and blue, quite unlike the Reed Warbler's greenish speckled eggs. On average, the difference between the appearance of the foreign eggs and the Reed Warblers' own eggs was so great that it probably exceeded the variation in egg appearance seen within one clutch. Arguably, then, the foreign eggs were readily detectable even amongst a highly variable clutch (Karcza *et al.*, 2003). A uniform host clutch would therefore do little to increase the relative discordance of the foreign egg. Perhaps instead the birds which laid clutches of identical eggs had a more clearly memorized image of their own eggs and this improved their ability to distinguish and remove foreign eggs from the nest.

In a further attempt to test the assumption that reduced intraclutch variation increases the chance of detecting a foreign egg, clutches of Great Reed Warblers were manipulated to be highly variable and the incidence of model egg rejection was then compared with that seen at less variable control clutches (Karcza *et al.*, 2003). Unfortunately, the Great Reed Warblers were just too good at recognizing foreign eggs for this treatment to have much of an effect on the rate of egg rejection; about 80% of model eggs were rejected in both treatments. The Great Reed Warblers even managed sometimes to reject conspecific eggs added to their nests (Karcza *et al.*, 2003). Two more studies, this time with Common Whitethroats (*Sylvia communis*) and with Chaffinches (*Fringilla coelebs*), provide further evidence that intraclutch variation itself has little influence on the incidence of egg rejection. The key predictor of egg rejection instead was found to be the degree of contrast between host and foreign eggs (Procházka & Honza, 2003; Stokke

et al., 2004), which is more likely to depend on the extent of interclutch variation.

Furthermore, there is indirect experimental evidence that hosts do not compare the appearance of eggs within a clutch when choosing one for rejection but, instead, rely entirely on the mental image of their eggs that they have memorized. The incidence of egg rejection by Village Weaverbirds is no greater when their own eggs are present in the nest for comparison, than when they are absent (Lahti & Lahti, 2001). Collectively, these studies suggest that the most plausible function of a uniform clutch is to sharpen the imprinted image of the host's own egg appearance.

A different set of analyses compares the clutches laid by populations of the same species, but with contrasting histories of parasitism, to test whether parasitism has caused changes in egg appearance. Davies & Brooke (1989*b*) examined the variation in egg appearance within and between clutches belonging to Icelandic and British populations of Meadow Pipits or Pied Wagtails, but were unable to demonstrate an effect of parasitism on either characteristic. However, subsequent studies have found that a history of parasitism can both reduce intraclutch variation and increase interclutch variation. Avilés & Møller (2003) also compared the clutches of Meadow Pipits from Iceland and the Faeroe Islands with those from England, this time measuring small patches of shell colour with a reflectance spectrophotometer. They report that a history of parasitism reduced variation within the clutch in the relative amount ultraviolet reflectance, but did not affect any other aspects of the eggs' appearance. Moskát, Szenpéteri & Barta (2002) quantified and compared the appearance of Great Reed Warbler clutches from Greece and Hungary using computer images of egg photographs. They found that the ground colour of eggs, and their degree of spotting, varied more between clutches in the Hungarian population parasitized by the cuckoo than in the unparasitized Greek birds. However, the populations did not differ in the extent to which eggs varied within clutches. Finally, Lahti (2005) quantified egg colour and patterning in two island populations of Village Weaverbirds, now free from cuckoo parasitism, but founded by birds introduced from Africa, where this species is host to Diederik Cuckoos. Weaverbirds on Hispaniola have bred for roughly 200 years without selection imposed by cuckoos and the appearance of their eggs has changed correspondingly, with lower interclutch variation in the ground colour and brightness of eggshells than in the source African population. Within clutches, eggs laid by the Hispaniola population were more variable in colour, brightness and spotting than those laid by their parasitized counterparts in Africa. The weaverbirds introduced to Mauritius have been separated from cuckoos for about 100 years. Their egg appearance is similarly starting to diverge from that of the source population, but the contrast between populations in egg colour and patterning is far less marked (Lahti, 2005). In summary, these studies suggest that brood parasites exert strong selection on the appearance of eggs laid by their hosts, resulting in increased interclutch variation and decreased intraclutch variation.

The results of these comparisons within species are broadly similar to those obtained by comparative analyses

across species. Stokke, Moksnes & Røskaft (2002) compared the appearance of clutches laid by victims of the common cuckoo in Europe, where the parasite often lays a mimetic egg, with the appearance of clutches produced by hosts of the Brown-Headed Cowbird (*Molothrus ater*) in North America, a parasite which lays non-mimetic eggs (Davies, 2000). Amongst European passerines, an escalated arms race of recognition and mimicry has led to a greater divergence in the appearance of clutches laid by hosts than is seen amongst the more passive North American cowbird victims. However, eggs are similarly variable within clutches laid by both types of hosts (Stokke *et al.*, 2002).

Øien, Moksnes & Røskaft (1995) scored egg variability in a sample of suitable and unsuitable cuckoo host species from Europe. They found greater egg variability among clutches laid by suitable hosts, but this effect disappeared when the unsuitable cavity-nesting hosts were removed from the comparison, which suggests that the hole-nesting species had lower interclutch variation (Davies, 2000). The hole-nesting species in this analysis laid white or blue eggs, some were speckled and some were not. Their colour and patterning were therefore not so uniform as to limit the possible extent of variation in shell pigmentation between clutches. One interpretation of this result is that a nest's vulnerability to predators has a greater influence on the variation observed among clutches than does a history of brood parasitism. In open-nesting species, perhaps variability in nest sites maintains variation among clutches because no single egg colour or style of patterning can then be universally cryptic (Davies & Brooke, 1989*b*). Øien *et al.* (1995) also found that the degree of variation among clutches was greater in species that were very good at finding and removing odd-looking eggs from their nests, even when cavity-nesting species were excluded. Perhaps the evolutionary arms race between cuckoo and host secondarily increases any variation among clutches that is already present through selection for crypsis.

Øien *et al.*'s (1995) data were reanalysed by Soler & Møller (1996), who attempted to control for the possibility that some species may produce highly variable clutches as a non-adaptive by-product of their evolutionary history, rather than in specific response to brood parasitism. They, too, found that variation among clutches in egg appearance increased with the likelihood with which hosts removed odd-looking eggs from the nest. In addition, they discovered that eggs within each clutch were more alike in species which were good egg-rejectors. Neither result was confounded by the vulnerability of the nest to predators, because both effects persisted when hole-nesting species were dropped from the analysis.

These studies raise some interesting questions. First of all, which has the greater influence on the likelihood of egg rejection: intraclutch variation or interclutch variation? And just how much does phylogeny constrain the evolution of egg appearance and rejection? Using the data Soler & Møller (1996) present in Table 3, I repeated their analyses, this time using multiple regressions with species as independent datapoints, and obtained qualitatively identical results. Variation among clutches in egg appearance (multiple regression: $F_{2,33} = 19.44$, $P < 0.0001$, $R^2 = 0.53$)

Table 2. The incidence of egg polymorphisms in some interspecific brood parasites and their hosts ('Polymorphism' means produces eggs which fall into at least two of the categories described in Section IV (1a))

Nature of polymorphism	Parasite	Host(s)	Source	
Neither parasite nor host lays polymorphic eggs	Great-spotted Cuckoo <i>Clamator glandarius</i>	Various corvid and starling species e.g. Magpie <i>Pica pica</i> , Pied Starling <i>Spreo bicolor</i>	Soler <i>et al.</i> (2003)	
	Chestnut-winged Cuckoo <i>Clamator coromandus</i>	<i>Garrulax</i> spp.	Baker (1913)	
	Horsfield's Bronze-cuckoo <i>Chalcites basalis</i>	<i>Malurus</i> spp.	Brooker & Brooker (1989)	
	Shining Bronze-cuckoo <i>Chalcites lucidus</i>	<i>Acanthiza</i> spp.	Brooker & Brooker (1989)	
	Greater Honeyguide <i>Indicator indicator</i>	Cape Glossy Starling <i>Lamprotornis nitens</i> , Plum-coloured Starling <i>Cinnyricinclus leucogaster</i> , Little Bee-eater <i>Merops pusillus</i>	Tarboton (2001)	
	Lesser Honeyguide <i>Indicator minor</i>	Black-collared Barbet <i>Lybius torquatus</i> , Striped Kingfisher <i>Halcyon chelicuti</i>	Tarboton (2001)	
	Sharp-billed Honeyguide <i>Prodotiscus regulus</i>	Lazy Cisticola <i>Cisticola aberrans</i>	Tarboton (2001)	
	Brown-headed Cowbird <i>Molothrus ater</i>	100 or more N. American passerines e.g. Yellow Warbler <i>Dendroica petechia</i> , Red-winged Blackbird <i>Agelaius phoeniceus</i> *, Song Sparrow <i>Melospiza melodia</i>	Baichich & Harrison (1997)	
	Host lays polymorphic egg but parasite does not	Pallid Cuckoo <i>Cuculus pallidus</i>	Eastern Yellow Robin <i>Eopsaltria australis</i>	Slater <i>et al.</i> (1989)
		African Cuckoo <i>Cuculus gularis</i>	Fork-tailed Drongo <i>Dicrurus adsimilis</i>	Tarboton (2001)
Black Cuckoo <i>Cuculus clamosus</i>		Crimson Breasted Shrike <i>Laniarius atrococcineus</i>	Tarboton (2001)	
Sharp-billed Honeyguide <i>Prodotiscus regulus</i>		Tinkling Cisticola <i>Cisticola rufilata</i> , Neddicky <i>C. fulvicapilla</i> , Grey-backed Bleating Warbler <i>C. subruficapilla</i> , Drakensberg Prinia <i>Prinia hypoxantha</i>	Tarboton (2001)	
Parasite lays polymorphic egg but host does not	Jacobin Cuckoo <i>Clamator jacobinus</i>	e.g. Black-eyed Bulbul <i>Pycnonotus barbatus</i> , Common Fiscal Shrike <i>Lanius collaris</i> , Golden-Breasted Bunting <i>Emberiza flaviventris</i>	Tarboton (2001)	
	Common Cuckoo <i>Cuculus canorus</i>	Various hosts e.g. Reed Warbler <i>Acrocephalus scirpaceus</i> , Great Reed Warbler <i>A. arundinaceus</i> , Meadow Pipit <i>Anthus pratensis</i> , Pied Wagtail <i>Motacilla alba</i>	Brooke & Davies (1988)	
	Lesser Cuckoo <i>Cuculus poliocephalus</i>	<i>Phylloscopus</i> spp., <i>Prinia</i> spp.	Baker (1923)	
	Large Hawk Cuckoo <i>Cuculus sparverioides</i>	Spiderhunters and <i>Garrulax</i> spp.	Baker (1923)	
	Oriental Cuckoo <i>Cuculus saturatus</i>	<i>Phylloscopus occipitalis</i>	Higuchi & Sato (1984)	
	African Emerald Cuckoo <i>Chrysococcyx cupreus</i>	Green-backed Bleating Warbler <i>Camaroptera brachyura</i> , Collared Sunbird <i>Antheptes collaris</i>	Tarboton (2001)	
	Diederik Cuckoo <i>Chrysococcyx caprius</i>	Southern Red Bishop <i>Euplectes orix</i> *	Tarboton (2001)	
	Klaas's Cuckoo <i>Chrysococcyx klaas</i>	Grey Sunbird <i>Nectarinia veroxii</i>	Tarboton (2001)	
	Shiny Cowbird <i>Molothrus bonariensis</i>	Brown-and-yellow Marshbird <i>Pseudoleistes virescens</i>	Mermoz & Reboreda (1999)	
	Parasite lays polymorphic eggs and so does host	Common Cuckoo <i>Cuculus canorus</i>	<i>Prinia</i> Warblers, Crow Tit <i>Paradoxornis webbiana</i>	Baker (1923); Kim <i>et al.</i> (1995)
Red-chested Cuckoo <i>Cuculus solitarius</i>		Natal Robin <i>Cossypha natalensis</i> , Heuglin's Robin <i>C. heuglini</i>	Tarboton (2001)	
Diederik Cuckoo <i>Chrysococcyx caprius</i>		Village Weaver <i>Ploceus cucullatus</i> *, Southern Masked Weaver <i>P. velatus</i> *, Golden Weaver <i>P. xanthops</i> *, Yellow Weaver <i>P. subaureus</i> , Spectacled Weaver <i>P. ocularis</i> *	Tarboton (2001)	
Klaas' Cuckoo <i>Chrysococcyx klaas</i>		Bar-throated Apalis <i>Apalis thoracica</i> , Yellow-breasted Apalis <i>A. flavida</i> , White-bellied Sunbird <i>Nectarinia talatala</i>	Swynnerton (1918); Tarboton (2001)	
Cuckoo Finch <i>Anomalospiza imberbis</i>		<i>Cisticola</i> spp. and <i>Prinia</i> spp.	Tarboton (2001)	

* Known to have intraspecific brood parasitism (from Yom-Tov, 2001).

Table 3. The data used in the comparative analyses, showing family measures of mass and clutch size (taken from Bennett & Owens, 2002); the number of species sampled per family for these analyses, and the number of species that: build their nest on the ground; build their nest in cavities; are interspecific brood parasite hosts; are intraspecific brood parasite hosts; are obligate brood parasites; lay white eggs; brown eggs; blue eggs or spotted eggs together with the number of egg types laid by each family and the number of nest types built by each family

Family	Mass (g)	Clutch size	Species sampled	Ground nesters	Cavity nesters	Inter-specific brood parasite hosts	Intra-specific brood parasite hosts	Obligate brood parasites	White egg	Brown egg	Blue egg	Spots	No. egg types	No. nest types
Struthionidae	1 000 000	12.0	1	1	0	0	1	0	1	0	0	0	1	1
Rheidae	23015.0	4.0	2	2	0	0	0	0	2	0	0	0	1	2
Casuariidae	34950.0	7.5	4	4	0	0	1	0	0	0	4	0	1	1
Apterygidae	2620.0	1.7	3	0	3	0	0	0	3	0	0	0	1	2
Tinamidae	886.0	4.0	21	21	0	0	2	0	0	12	9	1	3	1
Cracidae	1409.0	2.4	50	4	0	0	1	0	50	0	0	0	1	1
Megapodidae	1218.0	15.6	16	6	10	0	5	0	2	14	0	0	2	3
Odontophoridae	200.0	9.8	19	19	0	0	1	0	17	2	0	11	2	1
Numididae	1588.0	7.3	4	4	0	0	4	0	2	2	0	1	3	1
Phasianidae	996.0	7.2	66	63	0	0	0	0	42	24	0	44	2	2
Anhimidae	3972.0	5.5	3	3	0	0	0	0	3	0	0	3	1	3
Anseranatidae	2000.0	7.5	1	0	0	0	0	0	1	0	0	0	1	3
Dendrocygnidae	709.0	10.2	5	5	0	0	0	0	4	1	0	2	3	1
Anatidae	1423.0	7.4	105	76	27	0	74	1	75	11	19	0	3	2
Turnicidae	63.8	4.0	9	9	0	0	0	0	9	0	0	9	1	2
Ramphastidae	329.0	3.7	20	0	20	0	0	0	20	0	0	0	1	2
Lybiidae	30.0	2.8	30	0	30	0	13	0	30	0	0	0	1	1
Megalaimidae	119.0	3.1	15	0	15	0	0	0	15	0	0	0	1	2
Indicatoridae	26.7	4.0	8	0	0	0	0	8	7	0	1	0	1	1
Picidae	86.9	3.8	140	0	140	0	7	0	140	0	0	0	1	1
Bucconidae	32.8	2.4	14	0	14	0	0	0	14	0	0	0	1	2
Galbulidae	24.2	3.0	7	0	7	0	0	0	7	0	0	0	1	1
Upupidae	66.0	7.0	1	0	1	0	0	0	0	0	1	0	1	2
Phoeniculidae	64.0	3.4	6	0	6	0	3	0	0	0	6	4	2	1
Bucorvidae	3412.0	1.8	2	0	2	0	0	0	2	0	0	0	1	1
Bucerotidae	856.0	2.7	47	0	47	0	0	0	47	0	0	0	1	1
Trogonidae	63.3	2.7	30	0	30	0	0	0	26	0	4	0	2	3
Leptosomidae	196.0		1	0	1	0	0	0	1	0	0	0	1	1
Coraciidae	149.0	3.5	11	0	11	0	0	0	11	0	0	0	1	1
Meropidae	39.3	4.1	24	0	24	0	1	0	24	0	0	0	1	1
Momotidae		3.4	4	0	4	0	0	0	4	0	0	0	1	2
Todidae	6.8	2.8	5	0	5	0	0	0	5	0	0	0	1	1
Alcedinidae	44.0	6.7	20	0	20	0	0	0	20	0	0	0	1	1
Cerylidae	128.2	4.6	8	0	8	0	0	0	8	0	0	0	1	2
Dacelonidae	109.5	4.1	38	0	38	0	0	0	38	0	0	0	1	1
Coliidae	52.3	2.8	5	0	0	0	0	0	5	0	0	2	1	1
Crotophagidae	110.0	4.3	4	0	0	0	0	0	0	0	4	0	1	1
Neomorphidae	44.0	4.0	8	0	0	0	0	3	7	0	2	2	3	2
Opisthocomidae	810.0	3.0	1	0	0	0	0	0	1	0	0	1	1	2
Coccyzidae	71.7	2.6	20	0	0	1	1	1	10	0	10	0	2	1
Centropodidae	204.0	3.6	21	0	0	0	0	0	21	0	0	0	1	1
Cuculidae*	91.7	3.0	72	0	0	0	0	55	43	14	15	31	6	1
Psittacidae	246.0	3.7	218	2	215	0	0	0	218	0	0	0	1	1
Apodidae	40.5	2.6	65	0	59	0	0	0	65	0	0	0	1	1
Hemiprocnidae	60.0	1.0	4	0	0	0	0	0	4	0	0	0	1	2
Trochilidae	4.3	2.0	221	0	15	2	0	0	221	0	0	0	1	2
Musophagidae	424.0	2.3	21	0	0	0	0	0	18	0	3	0	2	1
Strigidae	600.0	3.6	111	10	91	0	0	0	111	0	0	0	1	1
Tytonidae	351.0	3.5	9	2	7	0	0	0	9	0	0	0	1	1
Aegothelidae			2	0	2	0	0	0	2	0	0	0	1	1
Podargidae		2.0	3	0	0	0	0	0	3	0	0	0	1	1
Batrachostomidae		1.5	7	0	0	0	0	0	7	0	0	0	1	1
Nyctibiidae	355.0	1.0	3	0	0	0	0	0	3	0	0	3	1	1
Steatornithidae	418.0	3.0	1	0	1	0	0	0	1	0	0	0	1	2
Eurostopodidae		1.0	4	4	0	0	0	0	1	2	1	3	4	2
Caprimulgidae	60.2	1.8	62	61	0	0	0	0	48	14	0	58	3	2
Columbidae	257.0	1.6	159	11	7	1	9	0	147	12	0	1	3	2
Rallidae	296.0	6.1	83	60	0	2	7	0	33	50	0	73	2	1

Table 3 (cont.)

Family	Mass (g)	Clutch size	Species sampled	Ground nesters	Cavity nesters	Inter-specific brood parasite hosts	Intra-specific brood parasite hosts	Obligate brood parasites	White egg	Brown egg	Blue egg	Spots	No. egg types	No. nest types
Eurypygidae	200.0	2.0	1	0	0	0	0	0	1	0	0	1	1	2
Cariamidae	1750.0	2.0	1	0	0	0	0	0	1	0	0	1	1	1
Rhynochetidae	500.0	1.0	1	1	0	0	0	0	0	1	0	1	1	3
Psophiidae	1160.0	3.0	3	0	3	0	0	0	3	0	0	0	1	1
Heliornithidae	558.0	4.5	2	0	0	0	0	0	2	0	0	2	1	2
Gruidae	5036.0	2.0	11	11	0	0	0	0	1	7	3	9	4	1
Pteroclididae	240.0	2.8	16	16	0	0	0	0	0	16	0	16	1	1
Jacaniidae	177.0	3.9	8	8	0	0	0	0	0	8	0	7	2	1
Rostratulidae	140.0	3.0	2	2	0	0	0	0	0	2	0	2	1	1
Pedionomidae	75.0	4.0	1	1	0	0	0	0	0	1	0	1	1	2
Scelopacidae	164.0	3.8	53	53	0	0	0	0	0	43	10	53	2	2
Charadriidae	190.0	3.3	38	38	0	0	8	0	4	29	5	38	3	1
Burhinidae	625.0	1.9	5	5	0	0	0	0	0	5	0	5	1	1
Chionidae	420.0	2.5	2	0	2	0	0	0	2	0	0	2	1	1
Glareolidae	156.0	2.3	15	15	0	0	0	0	0	15	0	15	1	1
Laridae	482.0	2.0	110	89	14	0	8	0	31	74	5	100	4	1
Falconidae	463.0	3.2	49	1	19	0	1	0	0	49	0	49	1	2
Sagittariidae	3605.0	2.5	1	0	0	0	0	0	1	0	0	0	1	1
Accipitridae	1471.0	2.3	103	7	4	0	0	0	92	4	7	82	4	2
Podicipedidae	431.0	4.4	22	22	0	6	0	0	22	0	0	0	1	1
Phaethontidae	550.0	1.0	3	0	3	0	0	0	0	3	0	3	1	2
Sulidae	1986.0	1.6	9	7	0	0	0	0	1	0	8	0	2	1
Anhingidae	1334.0	4.0	2	0	0	0	0	0	0	0	2	2	1	2
Phalacrocoracidae	1477.0	3.4	36	26	6	0	0	0	0	0	36	0	1	1
Ardeidae	793.0	3.7	49	7	0	0	3	0	4	4	38	2	6	3
Scopidae	470.0	5.0	1	0	0	0	0	0	1	0	0	0	1	1
Phoenicopteridae	2055.0	1.0	5	5	0	0	1	0	5	0	0	0	1	1
Fregatidae	1317.0	1.0	5	1	0	0	0	0	5	0	0	0	1	3
Threskiornithidae	1230.0	3.0	15	2	1	0	1	0	8	1	6	9	1	1
Ciconiidae	2516.0	2.8	23	1	4	0	1	0	23	0	0	1	2	2
Pelecanidae	6165.0	2.3	8	4	0	0	0	0	8	0	0	0	1	1
Spheniscidae	3135.0	1.9	17	17	0	0	0	0	17	0	0	0	1	2
Gaviidae	3233.0	2.0	4	4	0	0	0	0	0	4	0	4	1	2
Procellariidae	2813.0	1.0	95	12	83	0	2	0	95	0	0	8	2	1
Acanthisittidae	7.5	4.0	3	0	3	0	0	0	3	0	0	0	1	1
Eurylaimidae		3.8	12	0	0	2	0	0	12	0	0	12	1	1
Pittidae	62.8	4.7	25	6	0	0	0	0	25	0	0	25	1	2
Furnariidae	34.6	2.1	135	4	82	11	0	0	119	0	16	0	2	1
Formicariidae	64.0	2.0	10	3	0	0	0	0	0	3	7	5	3	2
Conopophagidae		2.0	3	0	0	0	0	0	0	3	0	3	1	1
Rhinocryptidae			13	0	10	1	0	0	13	0	0	1	2	3
Thamnophilidae	23.6	2.0	83	13	4	3	0	0	81	1	1	83	3	1
Tyrannidae	45.0	2.6	93	0	10	17	0	0	63	30	0	86	3	3
Climacteridae	27.5	2.5	6	0	6	0	0	0	5	1	0	6	2	1
Ptilonorhynchidae	144.0	1.4	15	0	1	0	0	0	8	5	2	7	5	1
Maluridae	10.5	2.8	19	0	0	13	0	0	19	0	0	19	1	1
Menuridae	950.0	1.0	4	1	0	0	0	0	2	2	0	4	2	3
Meliphagidae	33.5	2.0	71	0	0	35	0	0	35	36	0	71	2	2
Pardalotidae	12.0	4.0	48	11	5	37	0	0	41	7	0	43	4	1
Petroicidae	15.0	2.7	22	1	3	15	0	0	5	2	15	22	3	1
Irenidae	29.0	2.0	2	0	0	0	0	0	2	0	0	2	1	1
Orthonychidae			2	1	0	0	0	0	2	0	0	0	1	1
Pomatostomidae	71.0		4	0	0	1	0	0	0	4	0	4	1	1
Laniidae	40.5	4.6	15	0	0	2	0	0	13	2	0	15	2	2
Vireonidae	14.9	3.5	11	0	0	11	0	0	11	0	0	11	1	3
Corvidae	137	3.4	131	4	3	33	3	0	56	13	62	128	4	1
Bombycillidae	45.8	3.5	3	0	0	2	0	0	1	0	2	3	2	3
Cinclidae	60.7	4.9	2	0	2	0	0	0	2	0	0	0	1	1
Muscicapidae	37.1	4.4	147	13	57	27	5	0	36	8	103	123	6	3
Sturnidae	84.8	3.7	49	0	34	11	5	0	3	0	46	36	4	1
Sittidae	19.0	6.1	11	0	11	1	0	0	11	0	0	11	1	1
Certhiidae	13.8	4.6	16	0	6	7	0	0	12	0	5	16	3	2

Table 3 (cont.)

Family	Mass (g)	Clutch size	Species sampled	Ground nesters	Cavity nesters	Inter-specific brood parasite hosts	Intra-specific brood parasite hosts	Obligate brood parasites	White egg	Brown egg	Blue egg	Spots	No. egg types	No. nest types
Pycnonotidae	34.2	2.6	34	0	0	6	0	0	20	13	1	34	3	2
Paridae	14.0	7.2	33	0	26	2	2	0	33	0	0	25	2	1
Aegithalidae	7.0	6.5	2	0	0	0	0	0	2	0	0	1	2	1
Hirundinidae	20.1	3.9	73	0	73	0	7	0	73	0	0	12	2	1
Regulidae	5.8	9.0	4	0	0	4	0	0	4	0	0	4	1	2
Cisticolidae	10.4	4.4	54	0	0	18	0	0	29	2	23	46	6	2
Zosteropidae	10.6	3.2	9	0	0	3	0	0	4	0	5	0	2	1
Sylviidae	23.8	4.5	109	14	0	22	0	0	60	3	46	93	6	2
Alaudidae	27.8	3.4	60	57	2	0	0	0	55	0	5	60	2	1
Nectariniidae	9.0	2.0	64	0	0	14	1	0	37	14	13	61	5	3
Passeridae	18.9	4.4	220	21	14	50	30	17	153	10	57	112	6	2
Fringillidae	29.5	3.6	240	58	12	96	12	3	130	1	109	193	5	3

* Scored egg types of different races within each species (data taken from $N=38$ brood-parasitic species and 21 non-brood-parasitic species).

was positively related to both egg rejection rates (partial $t=5.11$, $P<0.0001$) and the extent of egg variability within clutches (partial $t=4.10$, $P=0.0003$), while the extent of intraclutch variation in egg appearance (multiple regression: $F_{2,33}=8.68$, $P=0.001$, $R^2=0.32$) was negatively related to both the rate of egg rejection (partial $t=-2.91$, $P=0.0065$) and positively related to the extent of inter-clutch variation (partial $t=4.10$, $P=0.0003$) (cf. Table 2 in Soler & Møller, 1996). Over evolutionary time, species can apparently modify the appearance of their eggs directly in response to attack by brood parasites, with relatively little constraint on either clutch diversity (but see below) or egg rejection behaviour imposed by their evolutionary past.

Next, I determined the extent to which intraclutch or interclutch variation could explain the likelihood of egg rejection, confining my analysis to the species with a history of victimization by cuckoos. When both types of variation were included in the model (multiple linear regression: $F_{2,25}=5.28$, $P=0.013$, $R^2=0.26$), the incidence of egg rejection was positively related to variation in egg appearance among clutches alone (partial $t=3.24$, $P=0.0037$). The results imply that cuckoo hosts can better refine their egg recognition skills by producing eggs that look unlike the average cuckoo egg rather than by laying clutches of eggs which look alike.

(iii) *Polymorphisms in egg colour and patterning.* If the response of a parasitized population is to produce clutches of greater diversity, how does evolution proceed next? A theoretical analysis by Takasu (2003) suggests that, no matter how continuous the variation in egg diversity at this stage, the arms race will come to a stable conclusion with the production of polymorphic eggs by parasite and host alike (see below and Table 2). Polymorphic cuckoo eggs evolve as parasites become increasingly specialized on their various hosts, while egg polymorphisms evolve among hosts as they attempt to outpace the evolution of egg mimicry by parasites. Takasu's (2003) analysis formalizes the verbal arguments made previously concerning the evolution of polymorphic eggs laid by cuckoo hosts (Swynnerton, 1916;

Collias, 1993), as well as earlier suggestions that intraspecific brood parasitism may have driven the evolution of polymorphic weaver eggs (Collias, 1993; Jackson, 1998). It also explains why so many of the southern African *Cisticola* warblers have egg polymorphisms. I related the incidence of egg polymorphisms to brood parasitism, conservatively defining a polymorphism as one species laying at least two of the following six egg types: white, white with spots, brown, brown with spots, blue, blue with spots. Of the thirteen southern African *Cisticola* species which lay polymorphic eggs, 11 are parasitized by either the Sharp-billed Honeyguide (*Prodotiscus regulus*) or the Cuckoo Finch (*Anomalospiza imberbis*) or both. The four remaining species all lay monomorphic eggs and are not known to be parasite hosts (Tarboton, 2001; Fisher Exact $P=0.0063$).

The particular egg morphs produced by the different polymorphic *Cisticola* species are quite similar. Typically there are four morphs: immaculate white, speckled white, immaculate blue, and speckled blue. By contrast, the polymorphisms seen among the closely related *Prinia* warblers involve the laying of speckled eggs with either a white, blue or brown background (Tarboton, 2001). The difference in egg colouring is unlikely to result from differences in nest design because species of both genera build nests that are ovoid, with an entrance hole near the top (Tarboton, 2001). These observations suggest that although species may not be constrained in the diversity of their response to brood parasitism (see above), the precise colouring of their eggs might be limited by the scope for mutational change and hence by their evolutionary history.

Village Weaverbirds have a further variety of polymorphism, laying eggs with a background colour of white, emerald or turquoise, with or without a sprinkling of speckles on top. By analysing the outcomes of 20 different crosses among captive birds, Collias (1993) showed that individual females lay just one egg type throughout their lives. She concluded that the pattern of inheritance of the ground colouring was best explained by Mendelian inheritance of two autosomal loci, one for emerald and one for

turquoise, each with a pair of alleles (recessive and dominant). According to this scheme, white eggs are laid by females that are double recessive at both loci, females that are double recessive at a single locus (e.g. emerald) produce eggs of the opposite phenotype (e.g. turquoise), and females that have dominant alleles at both loci lay emerald-turquoise eggs. Thus, mothers and fathers contribute equally to the phenotype of their daughters' eggs, which suggests that females can have no prior knowledge of the appearance of their eggs, and might explain why this must be learnt (Lotem *et al.*, 1995; Lahti & Lahti, 2001). Perhaps there are parallels here with the major histocompatibility complex and its role in protecting mammals against pathogens. It would be interesting to investigate whether individuals which are heterozygous at the egg colouring loci are more successful because their grand-offspring emerge from a greater diversity of egg colours and, if so, whether this influences patterns of mate choice (*cf.* Wedekind *et al.*, 1995).

Summarizing this section, increasing the vulnerability of the nest site to predators (and implicitly the variety of nest sites used by a species) has apparently increased variation among clutches in egg appearance suggesting that this aspect of egg colouring must, at least partly, be due to selection for crypsis. Brood parasitism further increases the diversity of egg colouring and spotting within species, secondarily exaggerating existing variation between clutches and ultimately causing the evolution of discrete egg morphs. In addition, parasitized populations and species show markedly reduced variation in egg appearance within clutches. Although increased interclutch variation directly improves the likelihood of detecting and rejecting a parasitic egg, the selective advantage to hosts of a laying a more uniform clutch is less clear. Perhaps low intraclutch variation functions to sharpen the mental image of the host's egg, which is imprinted during the first breeding attempt and used as a reference in subsequent egg rejection decisions.

(c) Selection by brood parasite hosts

The co-evolutionary arms race of egg recognition and egg concealment played out between hosts and parasites has also influenced the diversity of egg appearance among the obligate brood parasites. It is likely that discrimination by cuckoo hosts has resulted in distinct female races (*gentes*) in the Common Cuckoo, each recognizable by the different colour of their eggs and each preferring to exploit a different host (Davies, 2000). However, not all host-parasite co-evolutionary interactions end this way. Parasites may switch to new hosts or hosts may face such high costs of egg rejection that acceptance of the parasitic egg becomes the more profitable strategy (Marchetti, 1992; Davies, Brooke & Kacelnik, 1996; Takasu, 1998; Davies, 2000). Either of these endpoints may be reached long before the evolution of polymorphic eggs in the parasite.

If hosts acquire egg polymorphisms first, parasites are placed at a distinct disadvantage. For example, in southern Africa, the African Cuckoo (*Cuculus gularis*) lays only one of the three egg morphs that are produced by its Fork-tailed Drongo (*Dicrurus adsimilis*) host. Any cuckoo eggs that are

laid in nests containing a different egg morph are immediately rejected by the host (Tarboton, 2001). Parasites might respond by switching hosts or by exploiting several alternative hosts simultaneously (Davies, 2000), and so may never acquire egg polymorphisms themselves (which may have happened with the Pallid Cuckoo (*Cuculus pallidus*) or Sharp-billed Honeyguide, see Table 2).

Furthermore, the benefit to the parasite of acquiring an egg colour polymorphism appears to vary from species to species. The Shiny Cowbird (*Molothrus bonariensis*) parasitizes a range of hosts in South America, and its egg appearance is highly variable. The most common form is a white spotted egg, but immaculate white eggs are produced too, as well as an intermediate morph. In the Argentinian pampas, most hosts accept each of the three parasitic morphs added to their nest. An exception is the Brown-and-yellow Marshbird (*Pseudoleistes virescens*), which rejects white cowbird eggs. However, there is no indication that female Shiny Cowbirds have adjusted their choice of host species accordingly. Females that lay white eggs continue to parasitize the Brown-and-yellow Marshbird, at a similar rate to that seen by the Yellow-winged Blackbird (*Agelaius thilius*), which accepts white eggs (Mermoz & Rebores, 1999). In addition, there is no evidence that white eggs are more likely to be accepted by other host species than those of the spotted morph (Davies, 2000). Why, then, does the white morph persist? One possibility is that hosts have only recently acquired the ability to recognize and reject white cowbird eggs. Perhaps the white morph is the ancestral phenotype in this species, and is in the process of going extinct and being replaced by the more successful spotted morph. The incidence of the white morph varies between regions (Mermoz & Rebores, 1999) and it would be interesting to relate its prevalence to the likelihood that hosts in that area can discriminate against white cowbird eggs.

The existence of the intermediate morph is consistent with the possibility that egg colouring and patterning is controlled by an autosomal locus with two alleles, one for spotting (S) and one for no spotting (s), where heterozygotes (Ss) lay eggs with the intermediate phenotype. According to this scheme, fathers can determine the patterning of their daughter's eggs. Unless there is assortative mating by egg type, it means that cowbirds cannot anticipate the appearance of their own eggs. Perhaps individuals persist in parasitizing hostile hosts because they are unaware of their own egg colour. This suggests that even if an egg polymorphism does arise in the parasite, its evolutionary stability depends on inheritance of egg colouration in the female line alone, as appears to be the case in the Common Cuckoo (Marchetti, Makamura & Gibbs, 1998; Gibbs *et al.*, 2000). Selection for disguise in brood parasitic species may not only change egg colouration, therefore, but its mode of inheritance as well.

(3) Summary

From the preceding review of the literature, the following conclusions can be drawn. In general, it is hard to account for the evolution of egg pigmentation and difficult to judge the extent to which pigmentation is constrained by

phylogeny. There is little indication that specific egg colours evolved primarily to signal their noxiousness to predators, or female quality to birds that will assist with chick rearing, though it is possible that particular egg colours have been co-opted secondarily by individual species to serve these functions. Nor does it seem likely that brood parasitism favours the evolution of either specific egg colours or elaborate patterning. The most plausible general explanation for egg pigmentation remains Wallace's (1889) hypothesis, that deviations in egg colour and patterning from the ancestral white have been selected primarily for their cryptic appearance. The incidence of egg speckling may additionally be explained by a structural role for porphyrins in maintaining eggshell strength and flexibility.

The broad diversity we see in egg pigmentation and patterning is easier to explain. For example, variation in nest sites may account for some of the variation in passerine egg appearance and the habit of exploiting the parental care of other birds appears to have increased diversity in egg appearance between individuals, in hosts and parasites alike. In some species, diversity is enhanced by increasing the assortment of the shell's ground colouring among individuals, while in others the extent of diversity depends more on the extent and nature of egg speckling. It is not yet clear whether these differences between species are adaptive or simply due to phylogenetic constraints. In addition variation in egg speckling may be related to variation in egg strength, at least in one species (Gosler *et al.*, 2005). However, the relative importance of predators, brood parasites and structural strength in determining the appearance of bird eggs has yet to be established (see also Soler *et al.*, 2005).

Three questions thus remain unanswered: (1) is the ancestral egg colour white, and does a white egg shell typically confer no adaptive benefit, as Wallace (1889) suggested? (2) Can the risk of attack by predators or brood parasites account for the evolution of egg colour and patterning, and its diversity, or are they merely by-products of structural pigments in the shell, serving no signalling function at all? (3) What is the relative importance of predators, brood parasites and shell structural strength in explaining the evolution of egg appearance? In Section IV, I use comparative analyses to try to provide some answers.

IV. COMPARATIVE ANALYSES

(1) Methods

The results of the comparative analyses come with the caveat that they are only as accurate as the phylogeny I have used. Furthermore, my measures of egg colouring do not include ultraviolet reflectance and are rather basic. The enormous diversity in shell pigmentation is cast into six categories, which are based on genetic analyses of the colour and patterning of bird eggs.

(a) Scoring egg colour

Punnett's classical genetic work on chicken egg shell colouring (described by Collias, 1993), and subsequent

analyses by Collias (1993, described above) on the egg polymorphisms of Village Weaverbirds, suggest that the bluish and brownish components of shell ground colouration are under independent genetic control, although both may be expressed simultaneously to create green or olive eggshells. Both traits involve several genes, and both are dominant to white. The genes for blue shells are autosomal, while those for brown shells may be sex linked as well as autosomal (Collias, 1993). Analysis of Great Tit egg patterning over several generations suggests that egg speckling is regulated by a further suite of genes, whose expression is limited by genes on the sex chromosomes (Gosler, Barnett & Reynolds, 2000, but see Gosler *et al.*, 2005). Taken together, these results suggest that egg colouring might result from one or more of three evolutionary innovations: the production of a shell with a ground colour that is either brown or blue, and the patterning of the shell with speckling. A white shell is either ancestral or might arise through secondary loss of externally visible shell pigmentation. Thus eggs can reasonably be classified into three categories, based on the ground colour of the shell: white (or cream), brown (ranging from buff to red to dark chocolate brown) and blue (including shades of grey or green or violet), which can then be further subdivided into eggs which are speckled and those which are not, giving six egg types in all.

(b) Data collection

I used Sibley & Ahlquist's (1990) classification and phylogeny of bird families, but incorporated Barker *et al.*'s (2004) amendments to the passeriform phylogeny. I searched the *Handbook of the Birds of the World* Volumes 1–9 (del Hoyo *et al.*, 1992–2004) for descriptions of egg appearance, nest site and incidence of brood parasitism, supplementing this source of information with data from *The Birds of the Western Palearctic* (Cramp, Perrins & Simmons, 1977–1994), *The Birds of Africa* (Fry, Keith & Urban, 1982–2004), *The Handbook of Australian, New Zealand and Antarctic Birds* Volumes 1–6 (Higgins *et al.*, 1990–2002), and the *Guide to the Nests, Eggs and Nestlings of North American Birds* (Baicich & Harrison, 1997). Data on parasitism habits came from Ortega (1998), Davies (2000), and Yom-Tov (2001). Family measures of adult mass and clutch size were taken from Bennett & Owens (2002). For each family, I scored the number of species that: nested on the ground; nested in cavities; are known to be a brood parasite (including intraspecific brood parasites); are known to be a host of an obligate brood parasite; lay white eggs, lay brown eggs, lay blue eggs, lay speckled eggs, and the number of different egg types seen within that family (maximum=6). I included only those species for which there was complete information about their eggs and nest sites. I have probably underestimated the number of species that are intraspecific brood parasites or that are hosts to brood parasites.

I divided these scores by the total number of species sampled per family and so derived a continuous measure of each variable for 132 families (see Table 3), and considered the most common form of egg colouring (white, brown or blue) and patterning (speckled or not) as the typical egg for that family.

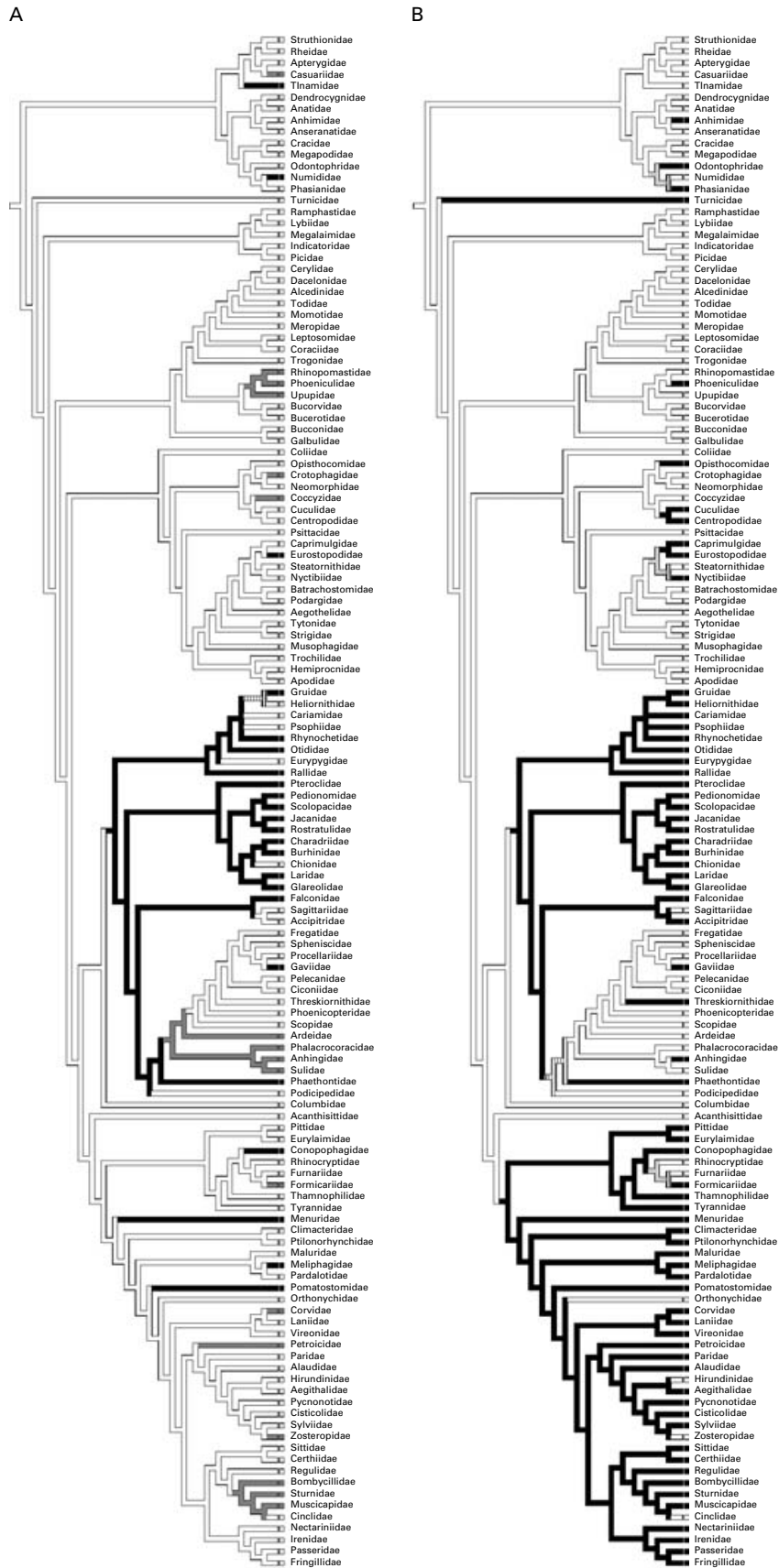


Fig. 1. For legend see opposite page.

(c) Data analysis

Using the application MacClade 3.04 I mapped egg colour and patterning onto the phylogeny to determine which egg colour was ancestral. I also analysed this dataset more formally in two different ways. I began by treating families as independent datapoints. I used simple linear regressions to try to understand variation in the fraction of species producing white eggs, or brown eggs or blue eggs or speckled eggs. The following potential explanatory variables were considered: proportion of ground-nesting species, proportion of cavity-nesting species, proportion of obligate brood parasitic species, proportion of species that are hosts to obligate brood parasites, and the proportion of species that are hosts to intraspecific brood parasites. To test whether (externally visible) pigments function to enhance shell strength when calcium is limiting, I also included female mass and clutch size as explanatory variables. The logic here is that smaller birds, and those laying larger clutches, are more likely to suffer from a limited supply of calcium and therefore may depend more on shell pigmentation for egg strength.

For analyses explaining variation in the incidence of white, brown or blue eggs I considered the fraction of species with speckled eggs to see whether speckling co-varied with one or more of these ground colours. Similarly, in the analyses to account for variation in speckling, I included the three ground colours. After determining how each factor was individually related to the egg trait in question, I tried to assess the relative importance of each variable in explaining egg appearance. I ran a series of multiple regressions, one for each of the four egg characters under consideration, with each of the factors used in the simple linear regressions included as explanatory terms in the initial model. In all cases, non-significant terms were sequentially deleted to yield the minimal model for each dependent variable.

As well as explaining variation in colour and patterning itself, I was also interested in accounting for the extent of diversity in egg appearance within families. I ran one set of simple linear regressions with the number of egg types per family as the dependent variable and each of the following factors as separate independent variables: the total number of species sampled for that family, the number of nest types (maximum = 3: ground nest, cavity nest, other), the proportion of obligately brood parasitic species, the proportion of species that are hosts to obligate brood parasites, and the proportion of species that are hosts to intraspecific brood parasites as explanatory variables in the initial model. To assess the relative importance of each of these factors in explaining egg diversity, I ran a multiple regression with each variable included as an explanatory

term in the initial model. I then deleted non-significant terms to yield the minimal model.

The review of the literature suggested that there might be phylogenetic constraints on the direction in which the evolution of egg colour might proceed. For example, the Muscicapidae (thrushes, chats and old-world flycatchers) might be saddled with a preponderance of speckled blue eggs, not by adaptive design but through accident of evolutionary history. In an attempt to account for this additional source of variation in egg appearance, I used the CAIC 2.0 application (Purvis & Rambaut, 1995) to calculate statistically independent contrasts in egg colour and the suite of potentially explanatory variables. I assumed that the branch lengths in the phylogeny were equal. Each of the analyses described above was run again, this time using contrasts rather than families as the units of analysis, and using regressions with no intercept term in the model (Purvis & Rambaut, 1995). Just as before, non-significant terms were sequentially deleted from the multiple regression analyses, to yield the minimal model for each aspect of egg appearance.

(2) Results and discussion*(a) White eggs*

Mapping the various traits that make up an egg's appearance onto the avian molecular phylogeny revealed that the ancestral bird egg was white and without speckling (Fig. 1), just as Wallace argued in 1889. At first sight, the analyses also appear to support Lack's (1958) contention that white eggs are an adaptation for offspring care in dimly lit nests because the simple linear regressions revealed that white eggs were significantly associated with cavity nesting (Table 4A; families: $R^2=0.092$, $F_{1,132}=13.30$, $P=0.0004$; contrasts $R^2=0.068$, $F_{1,129}=9.33$, $P=0.0003$). However, once other explanatory variables were incorporated in the analysis, this relationship disappeared. The multivariate analyses of both families and independent contrasts instead suggest that a white eggshell is of relatively little adaptive value in itself, but rather is retained in the species whose nest sites are safe from attack by predators. White eggs were more likely to occur in families that were unlikely to nest on the ground (Table 4A) and families with white eggs were least likely to have speckled eggs (Table 4A). Again, this is consistent with Wallace's (1889) original view.

(b) Brown eggs

Brown eggs, by contrast, are likely to be an adaptation for crypsis because they are most likely to be found in families that construct a ground nest (Table 4B). In addition, brown shell pigmentation was positively associated with egg

Fig. 1. The ground colour (A) and speckling (B) of egg shells, mapped onto a phylogeny of the birds with the application MacClade 3.04. Branch lengths in the phylogeny are arbitrary. (A) White bars depict white shell colours, grey bars show blue eggs and black bars indicate brown eggs. (B) Black bars show eggs with speckling, white bars indicate immaculate eggs. In both cases, hatched bars show cases where the ancestral condition is equivocal. The phylogeny suggests that the ancestral egg was white and immaculate.

Table 4. The results of comparative analyses that searched for correlates of five different aspects of egg appearance. For each egg character, the minimal model is shown, together with the terms that were dropped from the model in the sequence in which they were removed and with their marginal t value just before removal. Terms in bold are significant both in analyses treating families as independent datapoints and in analyses treating contrasts calculated by CAIC as independent datapoints. Asterisks denote the significance of the relationship when simple regressions were run between the egg character and each of the separate terms in the model: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

Egg character	Families as datapoints				Contrasts as datapoints			
	Minimal model	Term	t	P	Minimal model	Term	t	P
(A) White ground colouring	$F_{2,131} = 21.66$ $P < 0.0001$ $R^2 = 0.25$	egg spotting***	-4.14	<0.0001	$F_{2,118} = 10.23$ $P < 0.0001$ $R^2 = 0.15$	egg spotting***	-2.23	0.027
		ground nesting***	-4.31	0.0001		ground nesting***	-3.53	0.0006
		Terms dropped		Marginal t		Terms dropped		Marginal t
			log mass	-0.30		obligate brood parasite	-0.17	
			cavity nesting**	0.25		interspecific brood parasite host	0.33	
			interspecific brood parasite host	0.40		clutch size	-0.55	
			obligate brood parasite	-0.42		log mass	-0.61	
			intraspecific brood parasite host	0.44		cavity nesting**	0.94	
			clutch size	0.50		intraspecific brood parasite host	-1.39	
(B) Brown ground colouring	$F_{3,131} = 30.30$ $P < 0.0001$ $R^2 = 0.42$	egg spotting***	6.23	<0.0001	$F_{2,118} = 14.68$ $P < 0.0001$ $R^2 = 0.20$	egg spotting***	3.53	0.0006
		ground nesting***	5.17	<0.0001		ground nesting***	3.50	0.0007
			interspecific brood parasite host	-2.49	0.014			
		Terms dropped		Marginal t		Terms dropped		Marginal t
			intraspecific brood parasite host	0.048		log mass	0.02	
			log mass	-0.18		obligate brood parasite	0.63	
			obligate brood parasite	0.56		clutch size	0.70	
			clutch size	-0.92		cavity nesting	0.90	
			cavity nesting**	0.95		intraspecific brood parasite	0.98	
						interspecific brood parasite	-1.31	
(C) Blue ground colouring	—	—	—	—	$F_{1,118} = 7.43$ $P = 0.0074$ $R^2 = 0.06$	cavity nesting**	-2.73	0.0074
		Terms dropped		Marginal t		Terms dropped		Marginal t
			clutch size	0.00		clutch size	0.11	
			obligate brood parasite	-0.04		obligate brood parasite	-0.20	
			log mass	0.15		ground nesting	0.32	
			ground nesting	-0.62		egg spotting	-0.61	
			intraspecific brood parasite	0.87		interspecific brood parasite	0.66	
			interspecific brood parasite	1.54		log mass	0.78	
			egg spotting	-0.64		intraspecific brood parasite	1.19	
			cavity nester	-1.42				
(D) Egg spotting	$F_{4,122} = 24.08$ $P < 0.0001$ $R^2 = 0.45$	brown ground colouring***	6.00	<0.0001	$F_{2,118} = 11.81$ $P < 0.0001$ $R^2 = 0.17$	brown ground colouring***	3.74	0.0003
		cavity nesting***	-3.85	0.0002		cavity nesting**	-2.68	0.0085
			interspecific brood parasite host***	2.88	0.0047			
			log mass**	-2.97	0.0036			

Terms dropped		Marginal <i>t</i>
ground nesting*	-0.36	
blue ground colouring	0.60	
white ground colouring***	0.18	
clutch size	-0.77	
interspecific brood parasite host	-1.39	
obligate brood parasite	-1.74	
total number of species sampled***	3.53	0.0006
number of nest types***	2.85	0.005
obligate brood parasite interspecific brood parasite host*	2.06	0.042
	2.29	0.023
Terms dropped		Marginal <i>t</i>
interspecific brood parasite host		1.29

Terms dropped		Marginal <i>t</i>
white ground colouring***	0.044	
interspecific brood parasite host	0.079	
ground nesting	-0.36	
obligate brood parasite	0.42	
clutch size	-0.51	
blue ground colouring	-0.58	
log mass	-0.72	
interspecific brood parasite host	-0.14	
total number of species sampled***	3.41	0.0009
number of nest types***	3.16	0.0020
obligate brood parasite**	3.19	0.0018
Terms dropped		Marginal <i>t</i>
interspecific brood parasite host		0.26
interspecific brood parasite host		1.25

Terms dropped		Marginal <i>t</i>
white ground colouring***	0.044	
interspecific brood parasite host	0.079	
ground nesting	-0.36	
obligate brood parasite	0.42	
clutch size	-0.51	
blue ground colouring	-0.58	
log mass	-0.72	
interspecific brood parasite host	-0.14	
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clutch size	-0.51	
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log mass	-0.72	
interspecific brood parasite host	-0.14	
total number of species sampled***	3.41	0.0009
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obligate brood parasite**	3.19	0.0018
Terms dropped		Marginal <i>t</i>
interspecific brood parasite host		0.26
interspecific brood parasite host		1.25

(E) Egg diversity

$F_{3,129} = 22.83$
 $P < 0.0001$
 $R^2 = 0.35$

$F_{4,131} = 15.38$
 $P < 0.0001$
 $R^2 = 0.33$

spotting (Table 4B), even after controlling for the habit of ground nesting.

(c) Blue eggs

Lack (1958) was baffled by the production of blue bird eggs, and these analyses just add to the confusion, with no clear correlate of the incidence of blue eggs emerging from analyses of the family data (Table 4C). The analyses of independent contrasts, however, showed that blue eggs were least likely to be found among cavity-nesting species (Table 4C) suggesting that blue eggs might somehow enhance crypsis because they were more likely to be found in nests that are vulnerable to attack from predators. However, many more families construct nests in risky sites than have predominantly blue eggs (82 with risky nest sites versus 16 with mainly blue eggs) which may explain why the relationship was not apparent when the family data were analysed. It also suggests that if blue egg pigmentation is adaptively cryptic, it is only for a subset of vulnerable nest types.

(d) Egg spotting

Speckled eggs appear to have evolved in response to selection for crypsis in all vulnerable nests, not just those placed on the ground. Speckled eggs are both more likely to be brown and less likely to be laid in a cavity nest (Table 4D). Egg spots are often brown themselves, which may explain why the incidence of speckling is so closely associated with a brown ground colour to the shell.

The family data indicated that hosts of interspecific brood parasites are more likely to lay eggs covered in spots (simple linear regression: $R^2 = 0.24$, $F_{1,131} = 42.1$, $P < 0.0001$), but the equivalent relationship could not be found with the analysis using independent contrasts (simple linear regression: $R^2 = 0.008$, $F_{1,129} = 1.04$, $P = 0.31$). Perhaps this is because brood parasites exploit cup-nesting species and their eggs already happen to be speckled as a consequence of a more ancient adaptation to a vulnerable nest location (see Owens & Bennett, 1997). In addition, the family data revealed that smaller birds were associated with speckled eggs (simple linear regression: $R^2 = 0.06$, $F_{1,121} = 7.21$, $P = 0.008$) which is consistent with the suggestion that egg speckling serves a structural function (Gosler *et al.*, 2005). However, the relationship did not persist when independent contrasts were analysed (simple linear regression: $R^2 = 0.003$, $F_{1,121} = 0.371$, $P = 0.54$), perhaps because it was originally driven by the passerines, which are both small-bodied (Table 3) and prone to laying speckled eggs (Fig. 1). There is therefore little indication that egg speckling evolved primarily to add structural strength to shells, although it may have been retained for this purpose secondarily.

(e) Diversity in egg appearance

After controlling for the number of species sampled, the number of egg types produced by each bird family is likely to have been influenced by both selection from brood parasite

Table 5. Selective agents that may explain variation in the ground colour of eggshells, and the phylogenetic level at which their effects are likely to be seen

Ground shell colour	Level of variation			
	Ancestral	Between families	Between species	Between individuals
white	yes		thermoregulation?	
brown	no	predators/nest site	thermoregulation?	predators/nest site
blue	no	predators/nest site?	thermoregulation?	sexual selection?
spotted	no	predators/nest site	thermoregulation? structural strength	predators/nest site; structural strength

hosts and selection from predators. The greater the number of species that are obligate brood parasites within the bird family, the greater the variety of egg types produced (Table 4E). Egg diversity within the family was also positively associated with nest type diversity and presumably, therefore, with variation between species in a clutch's vulnerability to attack by predators (Table 4E). Of the two factors, the range in nest types was the more important in explaining variation in egg diversity.

Analysis of the family data showed that increased egg diversity was associated with a high level of exploitation by interspecific brood parasites, but this relationship did not persist when independent contrasts were assessed (Table 4E). One possibility is that brood parasites habitually exploit families with species that happen to build a diversity of nest types, each in vulnerable locations. Increased egg diversity within the family may therefore be a more ancient adaptation to promote crypsis in a variety of different nest sites.

V. SYNTHESIS

We began with the observation that bird eggs are strikingly diverse in their appearance, from family to family, and from species to species. Examination of the egg-colour literature showed that this variation also persists at a finer level of resolution, between clutches laid by members of the same species and even within clutches laid by the same individual. We can now combine the results of the comparative analyses with the findings of the literature review to see which selective agents account for variation in egg appearance, which account for egg diversity and at which level their effects are likely to be seen.

(1) Egg colour and appearance

Table 5 summarizes the information for traits associated with egg appearance, the ground colour of the shell and the incidence of spotting. It shows that the choice of nest site, and hence the risk that the clutch will be attacked by predators, most successfully explains the evolution of egg appearance, at least for brown eggs. The results at the family level probably reveal ancient adaptations for crypsis, dating

back to between 30 and 100 million years, at least by Sibley & Ahlquist's (1990) molecular clock. This is the period during which birds apparently diversified in their nesting habits, setting in motion a cascade of related life history and mating system adaptations (Owens & Bennett, 1997; Bennett & Owens, 2002). Small wonder, then, that fundamental changes in egg appearance also occurred at roughly the same time. In future work, it would be interesting to quantify the extent to which egg appearance in bird species today can be explained by ancient adaptations, and the proportion of variation in egg colouring and patterning that is attributable to variation in nest location today (see Bennett & Owens, 2002).

Other factors might further account for a bird's egg colour, but these are likely to be modern refinements, turning more anciently acquired egg colourings to a new function. For example, a secondary reversion to a white groundshell, or incorporation of shell pigments that reflect infrared light, might be favoured in birds whose nests are exposed to intense heat from the sun. Similarly, blue eggshells might become a means of signalling female quality to birds that will help in chick-rearing. The retention of egg speckles by species that nest in cavities, and are not exploited by brood parasites, can be explained if eggshell pigments serve a structural role in strengthening the shell.

(2) Egg diversity

Turning now to egg diversity, we find a greater number of selective factors at work (Table 6) with brood parasites and their hosts, as well as predators, influencing the range of egg types seen today. The range of nest sites seen within the family accounts for some of the diversity in egg appearance at the family level, which suggests that eggs are designed to be cryptic in their particular nest. Predators are not alone in exerting an ancient influence on egg appearance. The eggs laid by obligate brood parasites can vary considerably in their appearance, even within the same species, probably as a consequence of discrimination against their eggs by their hosts (Davies, 2000). The effect is most marked for the Cuculidae, whose member species now exploit hosts that can defend themselves against parasitism with fine-tuned egg rejection skills. Cuckoo hosts also construct a wide range of nest types, and so lay diverse eggs themselves. Selection by predators for host eggs that are cryptic in

Table 6. Selective agents that may explain diversity in egg appearance, and the phylogenetic level at which their effects are likely to be seen

Selective agent	Diversity in egg appearance :				
	Among species, between families	Among clutches, between species	Within clutches, between species	Among clutches, within species	Within clutches, within species
Nest type and risk of attack by predators	greater diversity with more nest types	higher diversity within cup-nesting species than within cavity-nesting species	no evidence that cavity nesting influences intraclutch variation		no clear evidence that diversity enhances crypsis
Brood parasites	no effect	brood parasites have increased diversity among clutches	no clear evidence that brood parasites have caused reduced intraclutch variation	egg colour polymorphisms have evolved in response to brood parasitism	brood parasites reduce diversity within clutches of their hosts
Brood parasite hosts	increased diversity is correlated with the lifestyle of an obligate brood parasite	defences mounted by brood parasite hosts can increase diversity between clutches within species		some obligate brood parasites have evolved egg colour polymorphisms	

their particular nest types, followed by selection by hosts for cuckoo egg mimicry, may together account for the extraordinary range in egg types laid by the Old World Cuckoos. Obligate brood parasites whose hosts either do not reject foreign eggs (e.g. cowbirds) or whose hosts are more conservative in their nesting habits (e.g. viduine finches) lay eggs that are correspondingly less diverse. Brood parasites themselves have had a more recent influence on egg diversity, increasing variation in egg appearance between clutches both within and between species (Table 6) and reducing variation within clutches. However, there is little evidence that predators have caused increased diversity within each clutch, and little sign that their victims would benefit anyway.

(3) A hierarchy of selective factors

Taken together, the evidence thus suggests a hierarchy of selective forces at work on the evolution of egg colour and appearance. Predators generate selection for egg crypsis and this accounts for much of the variation in egg colouring, from deep within the evolutionary history of the birds until current times. Brood parasites, and their hosts, play a secondary role in diversifying egg colouring. The degree of exposure to direct sunlight, the risk of weakness in the shell, and partners helping at the nest, may have an even smaller effect.

What arranges the sequence in which these selective agents act? One possibility is that the hierarchy is just an artefact, an unremarkable consequence of a hierarchy in the quality of data used in the analyses presented here. The data on brood parasite hosts in the comparative analyses, for example, are likely to be less accurate than the data on nest types. However, the data on nest types were also rather crude, packing the enormous variety in nest structures and locations onto a simple three-point scale.

The hierarchy may instead be ordered by the number of birds affected by each of the selective influences. The nests of many bird species are potentially vulnerable to attack by predators, but only some are likely to be victimized by brood parasites. Fewer still will benefit from using egg pigments to signal egg quality to their partners, to protect their eggs from lethally high temperatures or to increase eggshell strength. The hierarchy may also be arranged by the magnitude of the benefit associated with an adaptive change in egg appearance. Mutations that more effectively conceal eggs from predators, or that prevent egg rejection by hosts in the case of obligate brood parasites, bring immediate and substantial fitness gains to the clutch. Changes in clutch appearance that facilitate the rejection of a brood parasitic egg are potentially equally valuable, but the benefit will be experienced only if a brood parasite chooses to parasitize that clutch, thus reducing the mean benefit gained. Fine-tuning levels of chick care in response to egg colouring has little direct impact on offspring mortality and so has an even smaller impact on fitness. Perhaps future comparative studies, using more finely resolved data, will be able to quantify the separate influence of each selective agent on the colour and patterning of bird eggs.

VI. CONCLUSIONS

(1) The ancestral bird egg was probably white and without patterning. It has been retained by birds that build their nests in sites that are safe from attack by predators.

(2) Basic differences in egg colouring among bird families can be explained by ancient diversification in nest location. Brown, speckled eggs are typically associated with ground-nesting birds and presumably are adaptations for crypsis. In general, speckled eggs are more likely to be found in nests

that are vulnerable to predators. Even blue eggs might be cryptic in a subset of nests built in vegetation.

(3) Nest site and nest architecture further account for diversity in egg colouring, both among species within families and among clutches within species.

(4) There is no evidence that brood parasites, and their hosts, have caused specific directional change in egg colouring or spotting. Instead, it is likely that each has increased diversity in egg appearance, culminating in the evolution of egg polymorphisms. Their influence on egg diversity is secondary to the effect of nest type. The route by which egg diversity is increased in species or genera may be contingent on phylogenetic history.

(5) Reduced variation in egg appearance within clutches has evolved in response to exploitation by brood parasites, although its function is unclear.

(6) Ancient adaptations in egg colouring might have been adopted for new uses within species, for example in signalling female quality, in protecting eggs from potentially harmful solar radiation, or in adding structural strength when the calcium required to manufacture eggshells is in short supply.

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