Imperfectly camouflaged avian eggs: artefact or adaptation?

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ABSTRACT

For many birds, the fight for survival begins at the egg stage: avoiding predation is paramount. At a broad phylogenetic level, selection by predators for egg camouflage appears to be the primary driver of variation in egg colouration and patterning. Despite this, experiments at fine-scale taxonomic levels have largely failed to find support for adaptively camouflaged egg appearance. How are we to resolve this baffling contradiction? Here we present and evaluate five explanations which are not mutually exclusive and which may explain why eggs appear imperfectly camouflaged at the genus or species level. First, imperfect camouflage may be an artefact of imperfect measurements. In studies of egg camouflage, researchers have consistently neglected to account for predator vision, and only rarely have egg appearance and camouflage been quantified carefully and objectively. Recalibrating our assessment of egg camouflage may answer many questions, but it is unlikely to wholly explain why many eggs do not appear seamlessly cryptic. Instead, imperfect camouflage may stem from mechanistic constraints on pigment production in some avian lineages or may be a consequence of selection for anti-microbial protection. Or perhaps the manifold demands of the egg and selection for functions other than protective concealment have tugged the egg phenotype away from an ideally cryptic appearance. Finally, imperfect egg camouflage may occur if other forms of defence are simply more effective, or if a diverse brigade of predators imposes different selective pressures on egg appearance. A combination of these factors is likely involved. Avian eggs provide an excellent model system for investigating animal camouflage, and recent advances in numerous fields make this area particularly ripe for future research.

1. INTRODUCTION

In the animal kingdom, birds are exceptional in their capacity to lay pigmented eggshells, a feat long considered to have evolved as an anti-predator defence. Unlike many non-avian reptiles that bury their eggs, almost all birds lay and incubate their eggs above ground, making them vulnerable to detection by predators. A few species thwart predators by nesting in burrows (*e.g.* shearwaters) or by burying their eggs in heaps of rotting vegetation, [*e.g.* Brush Turkeys (*Alectura lathami*)]. However, for many birds the threat is substantial: the risk of predation at the nest is higher than 50% in most species (Ricklefs, 1969). Wallace (1889) hypothesised that the ancestral avian egg was white, a condition retained only by birds safe from attack, particularly those nesting in protected holes or sufficiently capable of fending off intruders. Wallace reasoned that as birds colonised more exposed nest environments, selection for camouflaged egg appearance gave rise to tremendous colour and pattern diversity. Since Wallace, a range of adaptive hypotheses has been proposed to explain variation in eggshell appearance, including selection

by brood parasites and their hosts (reviewed in Davies, 2000), thermoregulation (Montevecchi, 1976; Bertram and Burger, 1981), eggshell strength (Gosler *et al.*, 2005), and sexual signalling (Moreno and Osorno, 2003; but see Reynolds *et al.*, 2009). Recent reviews on the adaptive value of these forces (Underwood and Sealy, 2002) and their relative evolutionary importance (Kilner, 2006) conclude that a "hierarchy of selective factors" (Kilner, 2006) has influenced the diversification of egg colour and patterning. Among these, selection by predators for egg camouflage appears to be the predominant driver of variation in egg appearance (Kilner, 2006), just as Wallace predicted, and indeed seems to have produced remarkably camouflaged eggs in many lineages (*e.g.* Figures 1 and 2).

Despite its evolutionary potency, selection for egg camouflage remains poorly understood, partly because it is more complex than it might at first appear. In fact, the collected results of comparative and empirical studies on egg camouflage to date present us with a troublesome paradox: at a broad phylogenetic level, selection for egg camouflage appears to have been a crucial driver of egg colour
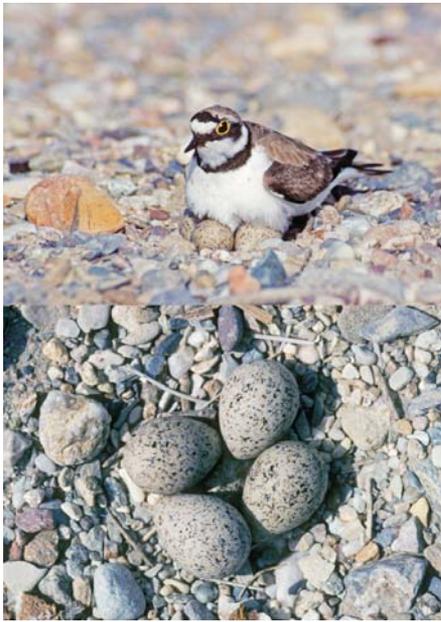
Figure 1 When a predator approaches, incubating Little Ringed Plovers (*Charadrius dubius*) often flee the nest, sometimes feigning injury to lure predators away. The eggs (below) are left exposed but appear (to human eyes) to be remarkably camouflaged against the background of pebbles, sand, and grit. Photo credits – D. Kjaer.

Figure 2 In Eurasian Curlews (*Numenius arquata*), camouflage may function at many different levels. Both the adult's plumage (above) and eggs (below) seem to be concealed in the tall grasses of the breeding grounds. Adults are often aggressive toward predators, offering an additional line of protection. Photo credits – D. Kjaer.

and pattern diversity (Kilner, 2006) yet at the species or genus level, experimental work does not uniformly demonstrate that egg appearance serves to protect eggs from predators (Underwood and Sealy, 2002; Kilner, 2006; Cherry and Gosler, 2010).

How are we to resolve this apparent contradiction? Previous reviews have emphasised the difficulties associated with experimental techniques for testing egg camouflage, such as the use of artificial eggs and nests (*e.g.* Underwood and Sealy, 2002). Here we present and evaluate five explanations which are not mutually exclusive and which may explain why eggs appear imperfectly camouflaged at the genus or species level. First, imperfect camouflage may largely stem from imperfect assessments: we may have grossly mismeasured egg camouflage. Most studies to date have relied on human assessments, although many visually oriented predators, including birds themselves, have superior vision in many respects. Researchers have consistently failed to account for predator vision and only rarely have egg appearance and camouflage been quantified objectively. Second, some birds may be mechanistically constrained by the pigments they are able to make and therefore are unable to produce a perfectly camouflaged egg with the materials available to them. Third, brown pigmentation may not have evolved for camouflage but instead to provide antimicrobial protection to the egg and the developing embryo within. Fourth, the multiple functions of egg colouration may require that camouflage is compromised in many cases, particularly if the threat posed by predators is outweighed by other dangers (*e.g.* overheating) or necessities (*e.g.* egg mimicry). Fifth and finally, egg camouflage may be relatively unimportant if other forms of defence more effectively deter predators. Moreover, effective egg camouflage may be complicated when a suite of avian, mammalian, and reptilian predators endanger the same nest. We argue that these five hypotheses can explain why camouflage is apparently imperfect at fine-scaled levels of phylogenetic resolution despite evidence that anti-predator strategies have driven egg colour and pattern evolution at a broader phylogenetic scale.

2. THE PARADOXICAL STATE OF PLAY

For over a century, biologists have puzzled over the paradoxical nature of eggshell colours. In his great tome "Darwinism", Wallace (1889) affirmed that "the colours of birds' eggs have long been a difficulty on the theory of adaptive colouration" because eggs were often so "bright and conspicuous that they seem intended to attract attention rather than to be concealed." Yet he concluded that egg colouration

was protective in "a great number of cases" and attributed inexplicably showy egg colouration to historic artefact: "we may suppose that it has been protective in some ancestral form, and, not being hurtful has persisted under changed conditions which rendered the protection needless." Wallace's ideas were widely accepted until Swynnerton, an English-born naturalist who emigrated to Africa, proposed an alternative. He suggested that bright egg colours were aposematic (see Speed and Ruxton, 2007), warning predators about the egg's unpalatability. Swynnerton (1916) predicted that brightly coloured eggs would be considerably less savoury than plainer ones, but the preferences of his test subjects, which included a rat, a lemur, an Indian Mongoose, and assorted human house guests, did not support such a relationship. Cott (1948) revived Swynnerton's idea during the Second World War. A panel of wartime taste-testers rated 81 different varieties of scrambled eggs. Chicken (*Gallus gallus domesticus*) eggs were the clear favourite, with Great Tit (*Parus major*) and Wren (*Troglodytes troglodytes*) eggs the least delectable. Cott (1948) concluded that delicious eggs tended to be more camouflaged, while less tasty ones appeared more conspicuous. Lack (1958) disputed Cott's (1948) rationale, arguing that (1) many eggs Cott categorised as conspicuous were actually cryptic, and (2) Cott's findings were an artefact of the strong correlation between egg size and palatability. Importantly, neither Swynnerton nor Cott considered how eggs tasted to relevant predators or the extent to which unpalatable eggs were actually unprofitable (as opposed to simply unpleasant). In the following decades, the aposematic colouration hypothesis faded away, with subsequent work identifying a number of physiological factors which would prohibit the evolution of egg toxicity (*e.g.* Orians and Janzen, 1974).

Cott's legacy was not his work on egg palatability but his milestone book, "Adaptive colouration in animals" (1940). Working as a camouflage instructor in the Second World War, Cott harnessed his knowledge of military camouflage to make inferences about protective colouration and patterning in animals. He advanced several theories on protective concealment, disruptive colouration, and obliterative shading in nature. His ideas, along with those about camouflage and countershading promoted by the American artist Abbott Thayer (1909), provided a framework for animal camouflage research in the twentieth century. Building on these ideas, Endler (1978) promoted the concept that a predator's view of animal colour patterns was pivotal for questions of animal camouflage.

Experimental tests of Wallace's (1889) egg-crypsis hypothesis were pioneered by Tinbergen *et al.* (1962). Working in a colony of Black-headed Gulls (*Chroicocephalus ridibundus*), Tinbergen and his colleagues painted a number of gull eggs white and determined that these eggs suffered higher predation than natural brown speckled eggs. In two accompanying experiments, the researchers painted eggs to make them appear (to human eyes) either camouflaged or white. In these tests, white eggs were no more vulnerable than the camouflaged eggs, leading Tinbergen to conclude that "we had underrated the eye-sight of the predators … we were astonished to see how easily particularly the Carrion Crows found even 'camouflaged' eggs." Clearly, eggs painted to appear camouflaged to humans in fact looked very different to avian predators. Despite this early word of caution, the use of painted eggs persisted in subsequent tests of the egg-crypsis hypothesis. The general approach has been to paint real eggs or plasticine models, endowing them with varying degrees of camouflage, and to chart their survival when placed in artificial scrapes or nests. Using this experimental paradigm, results have been mixed. In their review of 19 studies investigating egg crypsis, Underwood and Sealy (2002) discovered that only six found an effect of egg colouration on predation rate. Studies relying on uncalibrated painted eggs for camouflaged treatments were far less likely to find an effect of egg colouration than those which used natural eggs instead, adding further proof that painted eggs far fall short of replicating camouflage as seen by predators. Specifically, artificial pigments are unlikely to mimic real egg colours (Westmoreland, 2008; Major and Kendal, 1996), and painted eggs both fail to account for predator vision (Cherry and Gosler, 2010) and are often mismatched in size and shape to those laid by the species in question. An added complication is that paints may alter odour cues used by olfactory-hunting mammals. Consequently, predators often attack plasticine eggs at a higher rate than natural eggs (Rangen *et al.*, 2000). When they considered only studies using naturally coloured or minimally altered eggs (*i.e.* the addition of painted spots only), Underwood and Sealy (2002) determined that more than half found an effect of egg camouflage on predation rate.

Relatively weak experimental support for the egg-crypsis hypothesis led researchers to consider an alternative: perhaps effective egg camouflage is crucial among ground-nesters but less so for arboreal-nesters. If predators search for nests rather than eggs (nest-crypsis hypothesis; see Götmark, 1992), then selection for camouflaged eggs will be strong among birds with weakly concealed or non-

existent nests but weak among birds building conspicuous nests. In a comparative study, Götmark (1993) showed that among non-passerines, subtle nests tend to contain highly camouflaged eggs while conspicuous nests tend to contain eggs lacking in camouflage. Weidinger (2001a) tested Götmark's (1992) nest-crypsis hypothesis with a field experiment, which was designed to tease apart the adaptive value of egg crypsis and nest crypsis by exposing artificial nests and eggs to potential attack by predators. White, blue, and brown-spotted artificial eggs were placed in three types of artificial nests designed to mimic those of a Song Thrush (*Turdus philomelos*), which is conspicuous and arboreal, a Blackcap (*Sylvia atricapilla*), which is cryptic and arboreal, or a Yellowhammer (*Emberiza citrinella*), which is cryptic and placed on the ground. Weidinger (2001a) found that whereas egg colouration had little influence on the likelihood of attack by predators, nest type and location were much more important, results that are seemingly consistent with Götmark's (1992) nest-crypsis hypothesis. Intriguingly, however, the nest type which offered most security from predators differed between years. These results are not easy to interpret at face value, and the use of artificial nests in this experiment makes the task even harder because they may attract predators more readily than real ones (Major and Kendal, 1996; Ortega *et al.*, 1998) and can lead to inaccurate assessments of natural nest survival (Weidinger, 2001b). This problem was remedied by Westmoreland (2008) in a subsequent experiment. He placed real eggs laid by Red-winged Blackbirds (*Agelaius phoeniceus*), Brewer's Blackbirds (*Euphagus cyanocephalus*), and Yellow-headed Blackbirds (*Xanthocepahalus xanthocephalus*) in large conspicuous nests built by American Robins (*Turdus migratorius*). Eggs of the Red-winged Blackbird, which are the most conspicuous (to human eyes at least), were discovered earliest by predators. This suggests that, counter to the nest-crypsis hypothesis, cryptic egg colours can be beneficial even in conspicuous nests. Westmoreland (2008) used natural eggs in randomly allocated natural nests, so the results are particularly convincing and suggest that cryptically coloured eggs provide protection to ground-dwellers and nest-builders alike. The general conclusion is that while egg colouration can serve a camouflage function regardless of nest type, experimental studies do not always reveal this to be the case.

In contrast to the mixed results of experimental tests are the more straightforward results of a recent comparative phylogenetic analysis, which strongly suggest that selection for egg camouflage has greatly influenced the evolution of egg appearance (Kilner,

Figure 3 Vivid blue eggs laid by a Gray Catbird (*Dumetella carolinensis*). The evolution of blue eggs in diverse avian lineages remains a mystery. One hypothesis is that blue eggs may appear camouflaged in nest environments surrounded by green vegetation, although this idea requires further testing. Photo credit – T. Seeley.

2006). In an extensive analysis involving 132 bird families, Kilner (2006) demonstrated that the ancestral egg was probably white and has been retained (or secondarily regained) by birds nesting in cavities and holes safe from attack. Brown eggs probably evolved as an adaptation for camouflage, first appearing some 30–100 million years ago when birds diversified their nesting habits. Among living birds, ground-nesters typically have brown, speckled eggs, and speckled eggs are more common in nests that are susceptible to predators. Blue eggs remain a puzzle, but the phylogenetic analysis indicated that they rarely occur in cavity nests and may therefore have some cryptic value, particularly in nest environments rich with green vegetation (Figure 3).

This leaves us with a new and baffling puzzle: Why have experiments yielded such feeble support for adaptively camouflaged egg appearance when the comparative results so compellingly suggest that selection for egg camouflage has been paramount? Why do empirical tests at the species or genus level tell a drastically different story than phylogenetic patterns at the family level? To resolve this paradox, we now turn to five explanations that could unravel the current contradiction and revitalise our understanding of egg camouflage.

3. FIVE RESOLUTIONS FOR THE CURRENT PARADOX

3.1 Mismeasure of camouflage

Our first explanation for the current paradoxical state of play speaks to earlier criticisms of experimental

techniques (Underwood and Sealy, 2002) but here explicitly focuses on the measurement of camouflage itself. Egg camouflage is in the eye of the beholder; it should thus be adapted to the expected visual observer – the predator. Despite this, many studies investigating the visual camouflage conferred by egg colour and patterning have ignored two crucial points. First, there is more than one way to hide an egg, and it is crucial to determine which concealment strategy is at work before quantifying the extent of camouflage. Second, the main egg predators – birds, mammals, and snakes – each have dramatically different visual systems from one another (and, importantly, from humans). Clearly, our subjective human impression of how well eggs are hidden is severely flawed. Yet even recent studies of egg camouflage have continued to rely on human vision, overlooking available methods for studying egg colour and luminance (brightness) from the perspective of the correct receiver (for methods, see Avilés, 2008; Cassey *et al.*, 2008; Langmore *et al.*, 2009; Stoddard and Stevens, 2010, 2011; Spottiswoode and Stevens, 2010). Moreover, the added challenge of capturing complex spatial patterns, which likely play a crucial role in egg camouflage, has greatly hindered efforts to understand how egg speckling protects eggs from predators. Overall, we lack a fundamental understanding of how camouflage works to conceal eggs. Camouflage and crypsis generally have been poorly defined, and egg camouflage studies in particular have failed to make a distinction between different forms of concealment. Throughout this paper, we primarily stick to the term 'camouflage,' which refers to all strategies involved in concealment. Later (Section 4) we make a clear distinction between two forms of camouflage: crypsis (which reduces detection) and masquerade (which reduces recognition).

What appears to be imperfect egg camouflage could thus be an artefact introduced by subjective assessments and inadequate measurements. To determine whether this is the case, egg camouflage must be quantified through the eyes of the appropriate visual receiver. We devote the latter sections of this paper to a detailed discussion of how future research might accomplish this. Only then can fine-scale variation at the species level be properly quantified.

3.2 Mechanistic constraints

The second possibility is a variant of evolutionary lag. We suggest that the evolution of the nest microhabitat has outpaced the evolution of egg pigmentation; perhaps some bird species are simply physically incapable of producing a perfectly camouflaged egg with the colour-producing pigments currently available to them. Remarkably, just two pigments appear to be responsible for the great colour diversity observed in all bird eggs. The pigments are porphyrins, a group of endogenous pigments with nitrogen-containing pyrrole rings. Protoporphyrin IX is responsible for the rusty or brown colouration of egg ground colour or speckling, while biliverdin produces blue, green, and olive hues (Kennedy and Vevers, 1976; McGraw, 2006; Gorchein *et al.*, 2009; Igic *et al.*, 2010). Eggs can possess uniform, immaculate ground colouration or can be maculated with protoporphyrin-based speckles, blotches, streaks or elaborate scrolls which spiral round the eggshell. Both protoporphyrin and biliverdin can be produced simultaneously to create intermediate colours. Pigment-mixing appears to be the rule in birds: the only avian eggshells thought to contain pure biliverdin are the vividly blue eggs of the American Robin (Kennedy and Vevers, 1976). In the same way that some theoretically visible feather colours are impossible to produce with existing pigmentary and optical mechanisms (Stoddard and Prum, 2011), many eggshell colours may be unattainable with the available pigments – which could limit the extent to which eggs appear camouflaged in certain contexts. In a recent evaluation of eggs laid by 251 taxonomically diverse bird species, Cassey *et al.* (2010) found that egg background colours tend to be relatively constrained, with the greatest colour variation occurring in the bird-visible range between red-brown and blue – which likely corresponds to varying mixtures of protoporphyrin and biliverdin, respectively.

Constraints like this could explain why vulnerability to predators accounts for egg colouration at a broad phylogenetic level but does not do so consistently at the finer taxonomic levels. At the species and genus levels, perhaps some lineages have the colour palette required to camouflage their eggs while other lineages do not. Although both pigments appear to be widespread in Aves and phylogenetically labile (Kennedy and Vevers, 1976; Kilner, 2006; Cassey *et al.*, 2010), it is possible that the optimally camouflaged egg just cannot be made for some nest microhabitats. In short, protoporphyrin and biliverdin may offer eggs some crude level of protection against predators but are insufficient to generate perfectly camouflaged eggs in every nest microhabitat.

3.3 Anti-microbial function of brown pigmentation

We turn now to three adaptive explanations for the current paradoxical state of play. The first of these challenges the long-standing assumption that brown pigmentation evolved to enhance egg camouflage. A new study suggests that brown protoporphyrin

pigmentation may instead function to protect the egg from anti-microbial attack. Ishikawa *et al.* (2010) exposed brown hen eggs to two types of gram-positive bacteria and two types of gram-negative bacteria. Avian eggshells are typically contaminated by millions of bacteria present in the nest environment; gram-positive bacteria, which are resistant to desiccation, tend to be more prevalent on eggshells than gram-negative bacteria. When subjected to light, more than 99% of the gram-positive bacteria on brown eggshells were killed. In contrast, gram-negative bacteria did not decline; in general, gram-negative bacteria appear to resist photodynamic inactivation. The authors repeated the experiment using brown, white, and green eggshells. Brown eggshells had the best anti-microbial properties when exposed to light, with bacterial survival decreasing considerably. Though less effective than brown eggshells in reducing microbial invasion, green eggshells fared better than white. These effects disappeared in the dark, where bacterial survival was consistently high on all eggshell colours. The strong photodynamic action of brown pigments suggests that against gram-positive bacteria, protoporphyrin acts as an effective photosensitiser, reacting with light to trigger a bacteria-killing chemical cascade. The substantial photodynamic action exhibited by pigments on green eggshells implies that the blue-green biliverdin pigment may also serve an anti-microbial function. Both avian eggshell pigments are porphyrins, which have long been recognised for their potency as pathogen-destroying photosensitisers and are commonly used in photodynamic therapy to kill cancer cells.

If brown eggshell pigments evolved to protect the developing embryo from microbial attack, then the observed phylogenetic patterns of eggshell evolution may not be associated with camouflage at all but with susceptibility to bacterial contamination. This could account for the association between brown eggs and a ground-nesting habit, for example, assuming that nests built on the ground are more likely to be infested with microbes. It also explains why white eggs are typically found in darker nests: in these darkened environments, protoporphyrin lacks any anti-microbial function and so could not serve a useful role. Excitingly, this hypothesis may provide an adaptive explanation for the evolution of blue egg colouring, a trait that has long baffled ornithologists (Kilner, 2006), although the question remains of why blue pigmentation should evolve in place of brown, which apparently offers superior anti-microbial protection. If egg pigments function primarily to protect eggs from microbes, rather than predators, then it is unsurprising that experimental studies of egg camouflage have produced such mixed results. Nevertheless, it seems unlikely that all shell markings serve an exclusively anti-microbial function: why spotting and speckling should evolve rather than uniform colouration remains unclear. As far as we know, the generality of this idea has yet to be tested, but it does lend itself to comparative analysis. For example, it could be tested by incorporating susceptibility of nests to microbial attack into phylogenetic models and searching directly for an association with brown egg pigmentation.

3.4 Multiple functions of pigmentation

In the medley of selective forces influencing egg appearance, camouflage is a key player – but it is not the only one. Perhaps the broad significance of camouflage in determining egg colour and patterning shows itself in the association between vulnerability to predation and egg colouring at the family taxonomic level (Kilner, 2006). At the genus or species level, however, the multiple functions of egg colouration may tug the egg phenotype in several different directions at once, with the result that some eggs are imperfectly camouflaged. For example, egg colouration may be affected by brood parasites and their hosts (reviewed in Davies, 2000), thermoregulation (Montevecchi, 1976; Bertram and Burger, 1981), eggshell strength (Gosler *et al.*, 2005), and sexual signalling (Moreno and Osorno, 2003, but see Reynolds *et al.*, 2009). These adaptive hypotheses have been reviewed extensively elsewhere (Underwood and Sealy, 2002; Kilner, 2006) and here we discuss a few specific cases where selection for certain functions may preclude perfect camouflage.

One possibility is that egg colouration represents a trade-off between camouflage and thermoregulation. Pigments may endow eggs with a cryptic appearance, but they also increase their risk of overheating in direct sunlight. Classical experiments showed that egg pigments increase the internal temperature of the egg, sometimes to levels that can be fatal to the developing embryo (Montevecchi, 1976; Bertram and Burger, 1981). The fact that eggshells must often mitigate the dual threats of predation and overheating may explain why some eggs – like the lustrous white eggs of the Ostrich (*Struthio camelus*) – appear puzzlingly conspicuous. If the hazards posed by predators are outweighed by the risk of overheating, then eggs may reduce or altogether sacrifice cryptic pigmentation to optimise thermodynamic function. However, both protoporphyrin and biliverdin pigments may have built-in properties to mitigate the effects of sunlight exposure, much of which is in the near-IR range; in this part of the spectrum, pigments

reflect 90% of light, which substantially reduces heat by the sun (Bakken *et al.*, 1978). In keeping with this, a recent study by Westmoreland *et al.* (2007) suggests that eggs need not compromise pigmentation to improve thermodynamic function, at least not in species whose nests are mostly shaded from direct sunlight. Using real eggs – as opposed to the artificial pigments applied earlier (Montevecchi, 1976; Bertram and Burger, 1981) – Westmoreland *et al.* (2007) showed that pigmentation had no effect on heat gained by different coloured eggs laid by three species of blackbird (*icterid*). However, where eggs are directly exposed to the sun, like those laid by herons nesting in treetops or shorebirds nesting along the coast, and yet also vulnerable to predators, we might expect the tradeoffs between camouflage and thermoregulation to be more pronounced. Shorebirds typically lay brown speckled eggs, suggesting that selection for camouflage often trumps selection for thermoregulation. Interestingly, herons often lay blue eggs, which reflect more light in the visible range than do dark eggs (Westmoreland *et al.*, 2007). Thus, blue eggs could be a compromise between effective heat management and camouflage if the blue colouration helps eggs blend into the microenvironment of the nest.

When else might cryptic colouration be compromised? In brood parasite – host systems, selection pressure imposed by hosts on the appearance of the brood parasitic egg is likely to be far stronger than selection for camouflage. As a result, many brood parasites have evolved eggs that precisely mimic those laid by their target hosts. If the brood parasite egg is a poor match, it will often be rejected by the host (Davies, 2000). Whether the egg is camouflaged is initially irrelevant, although crypsis could be secondarily important, particularly if super-parasitism by female cuckoos is common (Brooker *et al.*, 1990). In at least one brood parasitic species, however, selection for camouflage appears to trump selection for mimicry. Little Bronze-cuckoos (*Chalcites minutillus*) lay cryptic eggs that are clearly non-mimetic in dark host nests (Figure 4), which could help prevent discovery and removal by the host or a second female cuckoo (Langmore *et al.*, 2009).

Just as hosts affect the parasite's egg colouration, so parasites, in turn, can influence the colour of the host's clutch and this too can lead to eggs that are less than optimally camouflaged. Hosts can escape mimicry by brood parasites if individuals diversify their clutches, with each host female effectively laying her own distinctive egg type so that she can more readily spot any foreign egg within her clutch. The Tawny-flanked Prinia (*Prinia subflava*) dramatically illustrates the process in action: to escape egg

Figure 4 Brood parasitic Little Bronze-cuckoos (*Chalcites minutillus*) lay dark, cryptic eggs in dark host nests, which could reduce detection and removal by the host or a second female cuckoo. Here is a triple-parasitised Large-billed Gerygone (*Gerygone magnirostris*) clutch, showing the white speckled host egg (top) and three olive brown Little Bronze-cuckoo eggs. Photo credit – G. Maurer.

mimicry by the brood parasitic Cuckoo Finch (*Anomalospiza imberbis*), these hosts now lay at least eight different morphs of egg (Spottiswoode and Stevens, 2011). Yet Tawny-Flanked Prinias construct nests using a single design (a woven grassy dome) and the diverse egg morphs they now lay cannot all be camouflaged in what amounts to a single microhabitat. Brood parasitism by the Cuckoo Finch has therefore caused egg colouration to radiate in diverse directions away from an optimally camouflaged form.

These three case studies each illustrate an important general point. Ultimately, an egg's appearance depends on the myriad functions it serves. The relative potency of the various threats to the egg, and the way in which each is mitigated by eggshell pigmentation, determines the egg's appearance. As a consequence, perfect egg camouflage is probably compromised in many cases.

3.5 Multiple lines of defence and defence against diverse predators

An essential but often overlooked consideration is the fact that camouflage functions at many levels, with egg camouflage typically the last line of defence. To begin, let us imagine a single type of predator. What draws the predator to the nest? Predators typically rely on visual, olfactory, and auditory cues to locate nests. These cues can come from parents, chicks, or the eggs themselves. To protect their nests, birds usually employ multiple defence strategies. First, bird parents

might exhibit aggressive behaviour or purposely lure predators away from the nest. Šálek and Cepáková (2006) compared anti-predator defence strategies of Little Ringed Plovers (*Charadrius dubius*) (Figure 1) and Lapwings (*Vanellus vanellus*), both of which lay camouflaged eggs. Both species routinely depart the nest in the presence of an avian predator, yet neither species relies exclusively on egg camouflage. Lapwings, which are larger and more capable of defending themselves against predators, are far more likely to remain on the nest than smaller Plovers (Figure 1), which quickly flee. But Plovers are armed with an arsenal of defence strategies: they pretend to incubate fake clutches and feign injury to lure predators away from the nest. These distraction tactics are less common in Lapwings, though the authors describe one occasion where a brave Lapwing parent feigned injury to deceive a small herd of roe deer.

A second defence may involve camouflaged plumage of the incubating parent. Some evidence suggests that conspicuous plumage of incubating adults has been strongly selected against in ground-nesting birds (Haskell, 1996). However, camouflage was measured using artificial ''cones of stiff paper'' made of either dull brown or bright red paper, which likely appear very different when modelled from the appropriate predator's perspective. Even if the incubating parent is not particularly camouflaged, parental behaviour can reduce the risk of predation (Martin et al., 2000). Kreisinger and Albrecht (2008) found that in mallards, the presence of a female enhanced nest survival even though nests guarded by females were more readily spotted by human observers than those with females absent. Furthermore, in a remarkable case of olfactory camouflage, several ground-nesting birds switch the preen wax they use in their feathers right at the beginning of the breeding season (Reneerkens et al., 2005). The scent of the new preen wax appears to be less detectable by mammalian predators. When the incubating parent is the female exclusively, only the female exhibits the change in preen wax composition.

Third, parents can modify the nests to make them appear more camouflaged. Concealing the nest with vegetation can substantially reduce predation rate (e.g. Kreisinger and Albrecht, 2008). Finally, it is interesting to note that many chicks have cryptic colouration (see Kilner, 2006b), suggesting that different camouflage strategies function in different phases of the breeding season. The Eurasian Curlew (*Numenius arquata*) exemplifies the idea that camouflage may function at many different levels (Figure 2). Nests, eggs, chicks, and adults are well camouflaged in the grassy meadows where curlews typically breed. Additionally, adults are often aggressive toward

predators, providing another line of protection (Berg, 1992).

Considering egg camouflage in isolation presents a misleadingly myopic view of much more sophisticated defence strategies employed by bird parents (Martin, 1995; Martin et al., 2000), who can sometimes assess nest predation risk and alter their reproductive strategies accordingly (Fontaine and Martin, 2006). Evaluating egg camouflage alone may be sufficient to detect broad levels of association with the nest's vulnerability to predation (e.g. Kilner, 2006), but it is too narrow a measure of anti-predator defence to account for variation in egg pigmentation at the species level.

The above examples address multiple defence strategies against a single predator. Now let us consider multiple predators in the same system: in reality, eggs are often vulnerable to attack from a diverse array of species. Only birds tend to be primarily visual hunters (Castilla et al., 2007). Nocturnal mammals typically rely on odour to find nests (Rangen et al., 2000), while snakes often use a combination of olfactory and visual stimuli to target nests (Greene, 1997). At a given nest site, the battalion of local predators can be surprisingly diverse: one study of Black-tailed Godwit (*Limosa limosa*) and Lapwing nests (Teunissen et al., 2005, reviewed in MacDonald and Bolton, 2008) reported predation by 80 foxes, 20 stoats, four crows, three beech martens, two hedgehogs, two marsh harriers, one polecat, one goshawk, one oystercatcher, and 16 unknown animals. In a system as complex as this one, what constitutes effective egg camouflage? When both avian and mammalian predators are present, different egg colours may provide different degrees of protection. In South American Terns (*Sterna hirundinacea*), which lay polymorphic eggs, egg survival depended on the relevant local predators: green eggs fared best in mainland colonies, where both mammalian and avian predators were present, whereas white eggs survived best on island colonies, which had no mammalian predators (Blanco and Bertellotti, 2000). Terns are nomadic and breed in different locations each year, so the high degree of egg polymorphism is maintained by the presence of different local predators in highly variable nest sites. In this system, mammalian predators appear to rely, at least in part, on visual cues, but other studies have shown that egg colouration has no effect on mammalian predation even when the effect on avian predation is strong (Castilla et al., 2007). If mammals primarily rely on non-visual cues, selection for camouflaged egg appearance will be reduced in the absence of avian predators. This might explain the apparent paradox of conspicuously coloured Great

Figure 5 Selection for camouflaged eggs may be reduced if predators rely on different cues or have poor vision. Great Tinamou (*Tinamus major*) nests are primarily targeted by dichromatic mammals, which do not detect the eggs themselves but rely on behavioural cues from incubating parents to locate nests. The brightly coloured eggs may be an intraspecific signal to other Tinamou females to promote communal egg-laying. Photo credit – R. Fournier.

Tinamou (*Tinamus major*) eggs (Figure 5), which are vibrantly coloured in glossy shades of turquoise. Brennan (2010) determined that mammalian predators pose the greatest threat to Tinamou eggs, yet these predators do not detect the eggs themselves when locating nests but rely on behavioural cues from incubating parents. The bright egg colours (Figure 5) might be irrelevant to mammals but important to conspecifics, perhaps as a signal to other females to promote communal egg-laying (Brennan, 2010). Predator-specific visual models could be used to determine the degree to which Tinamou eggs are conspicuous to avian females but cryptic to mammals, raising the intriguing possibility of a 'deer hunter' effect in egg colouration. The blaze orange vests worn by deer hunters are purposely conspicuous to trichromatic humans but camouflaged to dichromatic deer and other large game (Von Besser and Gutting, 2011). The opposing influences of conspecific and predator vision on animal colouration have been well documented in many taxonomic groups including fish (Endler, 1991), birds (Håstad *et al.*, 2005) and reptiles (Stuart-Fox *et al.*, 2003; Macedonia *et al.*, 2009), but whether similar concepts apply to egg camouflage remains to be seen.

Clearly, different predators impose different selective pressures on egg appearance. Unless we account for this critical fact, studies on egg camouflage are doomed to fail, particularly when considering variation at the species or genus level. We predict that visual egg camouflage should be stronger where

visually oriented birds are the primary predators and that selection for camouflage will be relaxed if the main mammalian predators rely on non-visual cues. When both mammalian and avian predators rely on visual cues, egg colouration might be selectively optimised to provide camouflage against: (1) the most prevalent visually oriented predator, (2) the predator with the best vision, or (3) a mix of predators, such that egg appearance is a compromise to provide decent protection overall (see Sherratt, 2002). To our knowledge, these fundamental ideas have never been tested. Evaluating these predictions will likely reveal that aspects of egg appearance are more nuanced and complex than we assumed.

Taken together, the five explanations presented here indicate that imperfect egg camouflage at fine-scale taxonomic levels may be an artefact of experimental mismeasurement, a by-product of mechanistic constraint, or an adaptive outcome resulting from selection for different purposes (anti-microbial protection, multiple functions for egg colouration, or defence against multiple predators). Most likely, a combination of these factors is involved. We now return to the crucial problem of camouflage mismeasurement. With the eventual aim of eliminating this experimental artefact, we must rigorously define egg camouflage and account for predator perception of egg colour and pattern.

4. THE SEMANTICS OF CAMOUFLAGE AND CRYPSIS

A key challenge in studying egg camouflage, and animal camouflage more generally, lies in generating a standard vocabulary for the various modes of concealment. Unfortunately, there has been very little effort to distinguish between different forms of camouflage and to test how they may function to conceal an egg. As a consequence, the lack of strong experimental support for adaptive egg camouflage may stem from a gross misunderstanding of how different predators detect nests and the relevant perceptual tasks involved.

Animals employ camouflage to make detection or recognition more challenging to predators. Generally speaking, camouflage refers to visual perception, but many examples of non-visual camouflage exist in nature (Ruxton, 2009) and other sensory modalities may indeed be relevant in egg concealment. Olfactory camouflage appears to be employed by Common Waxbills (*Estrilda astrild*; Schuetz, 2005) and possibly Burrowing Owls (*Athene cunicularia*; Martin, 1973, but see Smith and Conway, 2007), which smear their dwellings with mammal manure to reduce nest detection. In this section, we consider multiple camouflage strategies in the context of

Figure 6 The colour and markings of Heermann's Gull (*Larus heermanni*) eggs on Isla Isabel, Mexico, may provide camouflage via background matching, when the egg matches aspects of the background, or via disruptive colouration, when contrasting markings help to break up the outline of the egg. It is also possible that gulls nest near objects that increase the visual complexity of the clutch in order to enhance egg camouflage (complexity crypsis). Photo credit–H. Drummond.

Figure 7 Stone Curlews (*Burhinus oedicnemus*) may maximise egg camouflage by choosing nest sites that optimally match their egg colours. Stone Curlews often nest in shallow scrapes in open farmland, making their eggs vulnerable to a diverse suite of mammalian and avian predators. An important goal of future research will be to incorporate specific models of predator vision to evaluate a "predator's eye-view" of egg colour and pattern camouflage. Photo credit–D. Kjaer.

cryptic egg appearance. For our purposes, we consider visual crypsis only and follow definitions proposed by Stevens and Merilaita (2009a).

Camouflage refers to all strategies involved in concealment. Crypsis, a term often used interchangeably with camouflage, refers to strategies that reduce detection. By contrast, other strategies, such as masquerade, reduce recognition. For eggs, the most relevant forms of crypsis are likely background matching and disruptive colouration (*e.g.* Figures 1, 2, 6), although self-shadow concealment and obliterative shading may be important in some contexts. Finally, we point to one intriguing case in which eggs might masquerade as other natural objects, thereby reducing recognition rather than detection.

4.1 Background matching

Background matching occurs when the subject's appearance generally matches aspects of the colour, brightness, and pattern of the background (Stevens and Merilaita, 2009a). It was this form of crypsis Wallace (1889) had in mind when he described, rather poetically, the close match between shorebirds' eggs (*e.g.* Figures 1 and 6) and their backgrounds: "Here are two birds which nest on sandy shores, the lesser tern and the ringed plover, and both lay sand-coloured eggs, the former spotted so as to harmonise with coarse shingle, the latter minutely speckled like fine sand, which are the kinds of ground the two birds choose respectively for their nests. The common sandpipers' eggs assimilate so closely with the tints

around them as to make their discovery a matter of no small difficulty, as every oologist can testify who has searched for them. The peewit's eggs, dark in ground colour and boldly marked, are in strict harmony with the sober tints of moor and fallow, and on this circumstance alone their concealment and safety depend." A number of studies have attempted to quantify background matching. In a direct test of egg-to-background matching, Westmoreland and Kiltie (1996) photographed eggs of three blackbird (icterid) species and devised a computer vision method to compare subsamples of the eggs to subsamples of the nest background. Across species, eggs were equally cryptic in terms of pattern but differed in terms of brightness; the study did not investigate hue. In terms of clutch survival, nests with high egg-to-nest background matching were no more successful than those with low egg-to-nest background matching, indicating that patterning and brightness could be neutral traits in blackbird eggs, in accordance with the nest-crypsis hypothesis (but see Westmoreland and Kiltie, 2007; and Westmoreland, 2008). Stone Curlews (*Burhinus oedicnemus*; Figure 7; Solís and Lope, 1995), Black-tailed Gulls (*Larus crassirostris*; Lee *et al.*, 2010), and Snowy Plovers (*Charadrius nivosus*; Colwell *et al.*, 2011) apparently maximise camouflage by choosing nest sites that optimally match their egg colours. In a rare evaluation of egg pattern, Nguyen *et al.* (2007) used digital images to compare egg background colour and marking shape to randomly selected regions of Semipalmated Plover (*Charadrius semipal-*

matus) nests. Egg crypsis did not influence nest predation rates, though – as in many of these studies – it should be noted that the images were not calibrated to account for predator vision.

An organism can match a specific background (specialist) or several backgrounds (compromise). An important part of camouflage theory involves making predictions about where the optimal colouration is likely to be a compromise in heterogeneous environments with more than one kind of background (Merilaita *et al.*, 1999). Eggs are stationary: each egg need only match the background on which it is laid. It might therefore seem obvious that eggs exhibit specialist background matching exclusively, yet many species have polymorphic eggs, raising the interesting possibility that compromise background matching is relevant among species nesting in heterogeneous environments (see for example Blanco and Bertellotti, 2000). Note that these instances of egg polymorphisms are unrelated to those resulting from brood parasite – host arms races.

Another intriguing idea is that increased diversity within the clutch enhances crypsis by reducing regularity. In a study of African Black Oystercatchers (*Haematopus moquini*), Hockey (1982) suggested that within-clutch differences in egg markings increase crypsis by creating a more complex, heterogeneous clutch. This notion is intuitively appealing: a clutch of identical, immaculate eggs would appear large, uniform, and conspicuous, while increased complexity within the clutch would disrupt the regular and repeating appearance of an otherwise obvious target. Hockey (1982) observed that first-laid eggs tended to have larger blotches than second-laid eggs. Moreover, Oystercatchers preferred to nest near three-dimensional objects which enhanced the visual diversity of the nest site. Hockey's complexity crypsis idea has been extended to nest construction and breeding site selection, where increasing visual complexity is thought to make eggs more cryptic (Westmoreland and Kiltie, 1996), perhaps by obscuring the predator's traditional search image. Some empirical support for the complexity crypsis idea comes from the ground-nesting Namaqua Sandgrouse (*Pterocles namaqua*), which lays highly variable eggs. Visually complex clutches, *i.e.* those exhibiting high variation in egg background colour and patterning, survived better than clutches with uniformly coloured and patterned eggs (Lloyd *et al.*, 2000).

4.2 Disruptive colouration

Disruptive colouration occurs when highly contrasting shapes or markings on the edge of the

Figure 8 The distinctive markings on eggs laid by the Common Murre (*Uria aalge*) might serve as an identity signal to help parents discriminate their own eggs from those of neighbours, or they might disrupt the outline of the egg and help prevent detection by predators. These functions are not mutually exclusive. Photo credit – M.C. Stoddard © University Museum of Zoology, Cambridge, UK.

body outline create the appearance of false edges, thereby breaking up the outline of an object and reducing its detection (Cott, 1940; Cuthill *et al.*, 2005; Stevens and Merilaita, 2009b). Several authors have remarked that elaborate scrolling and squiggles likely function in disruptive colouration (Montevecchi, 1976; Collias and Collias, 1984), but this idea has never been tested. Many eggs, particularly passerine eggs, are known to have a 'corona' ring, a dense ring of speckles around the bottom shoulder of the egg (Lack, 1968; Davies and Brooke, 1989; Gosler *et al.*, 2005). It is possible that such patterning is particularly effective in breaking up the outline of an egg. Guillemots and murres nesting in high-density colonies lay eggs with fantastic scrolls (Figure 8) which have long been thought to help individuals locate their nests, but evidence that these markings aid in clutch recognition has been lacking (see Avilés *et al.*, 2004). Instead, these markings could be disruptive and help eggs blend into the jagged cliff edges on which they are laid.

4.3 Self-shadow concealment and obliterative shading

Self-shadow concealment occurs where light is cancelled out by countershading, *i.e.* darker colouration on the surface directly exposed to light (Rowland *et al.*, 2007). Self-shadow concealment is less likely to occur in eggs, which are routinely turned during incubation, than in dorsal-ventral animals. Yet one could imagine that certain pattern contrasts between the pigments might reduce shadows and even reduce three-dimensional information, which is known as

obliterative shading. Whether this ever happens in nature remains to be investigated. Indeed, the effects of the light environment and the potential influence of shadows on egg crypsis are important areas for future research. As Wallace (1889) described, eggs "lying in the shadow of the nest and surrounded by the many colours and tints of bark and moss, of purple buds and tender green or yellow foliage, with all the complex glittering lights and mottled shades produced by the spring sunshine and by sparkling raindrops" must appear very different than they do when removed from their natural environment. Similarly, Oniki (1985) proposed that blue eggs "may be imitating spots of light on green leaves against a dark background." These intriguing ideas have yet to be tested, and it will be illuminating to see whether vastly different light environments select for different egg appearances. Perhaps some eggs which at first appear to lack crypsis are actually well camouflaged in certain light, just as it was once suggested that the seemingly shocking 'Mountbatten Pink' naval ships used during the Second World War may in fact have appeared camouflaged against the mauve sky at dawn and dusk (Phillips, 1960).

4.4 Masquerade

Another intriguing–but so far unexplored–possibility is that eggs masquerade as more mundane natural objects in the surrounding habitat. Masquerade is different from crypsis *per se* in that it prevents recognition, rather than detection, by providing resemblance to inanimate and inedible objects (Stevens and Merilaita, 2009a). Western Snowy Plovers (*Charadrius alexandrinus nivosus*) often select nest habitats characterised by gravel stones that resemble eggs in size (Colwell *et al.*, 2011); nest survival increased with the number of egg-sized stones in the nest vicinity. Colwell *et al.* (2011) suggest that the presence of egg-sized stones may enhance background matching. This may indeed be the case, but we propose that these stones may confer additional protection if predators fail to recognise real eggs amidst a backdrop of uninteresting egg-like objects. This raises the exciting possibility that some shorebirds may select their nest environments not only to reduce predator detection via background matching (as seen in Solís and de Lope, 1995; Blanco and Bertellotti, 2002; Mayer *et al.*, 2009) but also to reduce predator recognition via masquerade (Figure 9). Future experiments could test this by varying the number of egg-like objects in the microhabitat and measuring subsequent breeding site preference and egg survival rate.

Figure 9 Shorebirds like the Kentish Plover (*Charadrius alexandrinus*) often lay their eggs directly in scrapes on pebble-covered coastline. Like Snowy Plovers, Kentish Plovers may select nest habitats containing gravel stones resembling eggs in size and colour. Nesting near uninteresting egg-like objects may help reduce predator recognition via masquerade.
Photo credit–D. Kjaer.

5. INCORPORATING THE PREDATOR'S PERSPECTIVE

Whichever strategy is used to hide an egg, it is impossible to understand exactly how it works without taking the predator's perspective into account. Nevertheless, most work in this area neglects to take a predator's eye-view of egg camouflage. Why? In recent decades, our knowledge of animal perception has skyrocketed, particularly in terms of vision (Osorio and Vorobyev, 2008; Schaefer, 2010). Advances in our knowledge of photoreceptor sensitivities and photopigment genes across the animal kingdom make it clear that human vision differs profoundly from that of other animals. Many researchers have adopted methods for studying signals in the context of the relevant signal receiver, inspiring new insights into the correspondence between animal sensory systems and communication signals. This has been especially true in bird research, where recent use of avian visual models has greatly informed our understanding of sexual selection, communication, and the visual signals involved in brood parasitism. Moreover, many studies investigating camouflage in systems as diverse as cuttlefish (Hanlon *et al.*, 2009) and spiders (Théry and Casas, 2009) have successfully embraced models of predator perception. In stark contrast, avian egg camouflage research has been very slow to incorporate promising new models of receiver vision. A crucial assumption of the egg camouflage hypothesis is that egg colour and pattern appearance have evolved in response to predator vision (Endler, 1978). Yet almost without exception, assessments of egg camouflage have been based on human perception rather than from

the perspective of visually-hunting predators (or brood parasites), which are typically other birds. Only one study to date has assessed egg camouflage from the perspective of an avian viewer: Langmore *et al.* (2009) employed models of bird vision to demonstrate that Little Bronze-cuckoo eggs are camouflaged in dark nests (Figure 4), potentially preventing detection by hosts or a second cuckoo intruder. To compound the problem, quantifications of egg pattern have been largely based on human-derived scores. These rankings fail to capture intricate spatial patterns on the egg, which likely endow the egg with added protection either by enhancing its match to the background or breaking up its outline and edges.

5.1 Perception of colour and luminance

Animals vary widely in their colour and luminance perception. Most mammals are dichromats, possessing just two colour cone-types. Primates typically enjoy trichromatic vision, with three colour cone-types sensitive to short, medium, and long wavelengths, respectively. Birds have a fourth colour cone that is sensitive to UV wavelengths (reviewed in Cuthill, 2006). Diurnal birds fall into one of two groups, in which the fourth cone is either violet-sensitive (VS) or UV-sensitive (UVS). Luminance refers to the achromatic signal and appears to be involved in pattern, motion, and texture detection (Osorio and Vorobyev, 2005). In humans, luminance perception likely stems from the summed output of the medium and long wavelength-sensitive cones. By contrast, in birds, luminance is likely encoded by double cones and is important in tasks related to texture and pattern discrimination (Jones and Osorio, 2004).

Of the visual nest predators, birds are the most important (Major *et al.*, 1994; Howlett and Stuchbury, 1996; Castilla *et al.*, 2007). In recent years, our understanding of bird colour and pattern perception has greatly improved, and models of bird colour and luminance vision are well described and widely available (comprehensively reviewed in Kelber *et al.*, 2003; Cuthill, 2006). Researchers have successfully incorporated such models in studies on sexual selection and plumage evolution (Vorobyev *et al.*, 1998; Cuthill *et al.*, 1999; Endler and Mielke, 2005; Stoddard and Prum, 2008), egg rejection (Avilés, 2008; Cassey *et al.*, 2008; Spottiswoode and Stevens, 2010; Stoddard and Stevens, 2011), chick mimicry (Langmore *et al.*, 2011), and nestling mouth colouration (Avilés *et al.*, 2008; Tanaka *et al.*, 2011). Yet studies of egg camouflage have categorically neglected models of predator vision despite their widespread and promising use in other studies of animal camouflage. An excellent example is a study by Stuart-Fox *et al.* (2008), which incorporated detailed models of bird and snake vision (see Vorobyev and Osorio, 1998; and Siddqi *et al.*, 2004) to show that chameleons exhibit substantially different colour responses to the two different predators. This approach could easily be adapted to studies of egg camouflage. In addition to bird and snake visual models, dichromatic mammalian models could readily be incorporated (Chiao *et al.*, 2000; Hunt *et al.*, 2009; Jacobs, 2009) to comprehensively evaluate a ''predator's eye-view'' of colour crypsis. Finally, it would be intriguing to test whether avian predators possessing different visual systems (UVS or VS) select for different egg appearances, which would reveal hitherto unnoticed sophistication in egg camouflage. If multiple avian predators possessing different visual systems are present, the predictions made earlier (see 3.5) should still hold.

5.2 Perception of pattern, shapes, and edges

In vertebrates, pattern perception and edge processing are likely to stem from early-stage visual processes which involve receptive fields, lateral inhibition, and spatial frequencies (Bruce *et al.*, 2003; Troscianko *et al.*, 2009). Understanding how pattern perception works is particularly relevant in studies of eggs, where complex patterns of blotches, squiggles, and streaks probably play a crucial role in crypsis (see above). Unfortunately, most of the methods available for measuring colour and luminance (*e.g.* reflectance spectrometry) fail to capture the spatial structure of chromatic information. As a consequence, although many researchers have started to use receiver-specific models of colour and luminance, studies of animal pattern not based on human vision have been scarce. In terms of egg crypsis, egg pattern quantifications are typically based on human-produced scores of spottiness, dispersion, darkness, or complexity (*e.g.* Avilés *et al.*, 2006) or derived from uncalibrated photographs (Lee *et al.*, 2010). Using uncalibrated cameras is particularly hazardous because it fails to account for the fact that RGB values have nonlinear responses to light intensity. Additionally, many studies have failed to control for light conditions and have inappropriately relied on human-vision-specific colour spaces such as HSB and CIE. To use digital images appropriately, camera-specific RGB values must be mapped to camera-independent RGB values, in which mapping can be tailored to the relevant visual receiver (Stevens *et al.*, 2007). Some researchers suggest that within-photograph comparisons offer a control against changing light conditions (Lee *et al.*, 2010), but without proper calibration and linearisation these

kinds of comparisons are unjustified: in a lighter image, two colours may appear less similar to one another than they do in a darker image.

The good news for research in this area is that new methods for studying egg patterns have been developed (Stoddard and Stevens, 2010), in which specific models of luminance perception can be used in combination with two-dimensional spatial information (see Chiao *et al.*, 2009) derived from calibrated images. In many cases, colour information can also be derived from calibrated images (*e.g.* To *et al.*, 2010). Easy-to-test models of predator spatial vision have been implemented with respect to camouflage in other systems, such as the creation of artificial moth-like targets exposed to bird predation (*e.g.* Cuthill *et al.*, 2005). Additionally, hyperspectral imaging, which incorporates full-spectrum light data and permits simultaneous analysis of colour and pattern, shows great promise for the future study of animal camouflage from the perspective of predators (Chiao *et al.*, 2011).

6. CONCLUSION

For many animals, avoiding predation is the most important factor for survival. For eggs, the situation is even more dire: there is no way to run (nor roll) from predators. Why do not all eggs, then, appear to be perfectly camouflaged? If selection to avoid predation has had a predominant influence on avian egg appearance, as comparative analyses (Kilner, 2006) indicate, then we would expect to find exquisitely camouflaged eggs across the board at the genus and species level. This may be true in some cases–many

eggs certainly appear well hidden to human eyes–but egg camouflage hardly appears to be universal and experimental studies have failed to provide clear evidence that egg colour and patterning commonly afford protection. Perhaps the most parsimonious explanation is that imperfect egg camouflage at fine-scale taxonomic levels is an artefact of experimental mismeasurement. Researchers have long neglected models of predator vision in studies of egg camouflage, have relied on poor measurements of egg colour and pattern, and have failed to consider how different forms of camouflage may actually function. Armed with fresh insights into predator perception and camouflage theory, we are now perfectly poised to revisit fundamental questions about egg crypsis. If imperfect camouflage has merely been an artefact of human error, then future research will expose its true colours.

In many instances, imperfectly camouflaged eggs may be a perfectly sensible compromise between the competing limitations and demands of the egg. If this is true, then imperfectly camouflaged eggs may be optimal in many cases, analogous to the ''jack-of-all-trades'' intermediate phenotype often adopted by Batesian mimics living amidst multiple (harmful) model species (Sherratt, 2002). It will be intriguing to see whether other parallels exist between imperfect egg camouflage and recently developed models of imperfect Batesian mimicry (Sherratt, 2002).

Historically, cryptic colouration has often been dismissed as intuitively obvious and sometimes boring, thereby lacking much of the research vigour applied to other areas of adaptive colouration (Stevens and Merilaita, 2009a). In the last decade, egg camouflage has attracted but a fraction of the research effort devoted to testing flashier hypotheses on the evolution of egg appearance, such as the influence of brood parasites or sexual signalling (Figure 10). We seek to reverse this trend: there has never been a better time to study the evolution of egg camouflage. New advances in fields as diverse as sensory ecology, signal processing, and computer vision have made great strides toward overcoming previous obstacles to studying animal signals. Moreover, camouflage research has recently surged, with exciting studies emerging on topics ranging from facultatively colour-changing chameleons (Stuart-Fox *et al.*, 2008) and flatfish-mimicking cryptic octopi (Hanlon *et al.*, 2010) to caterpillars masquerading as twigs (Skelhorn *et al.*, 2010). This renewed interest in camouflage research, coupled with powerful techniques for
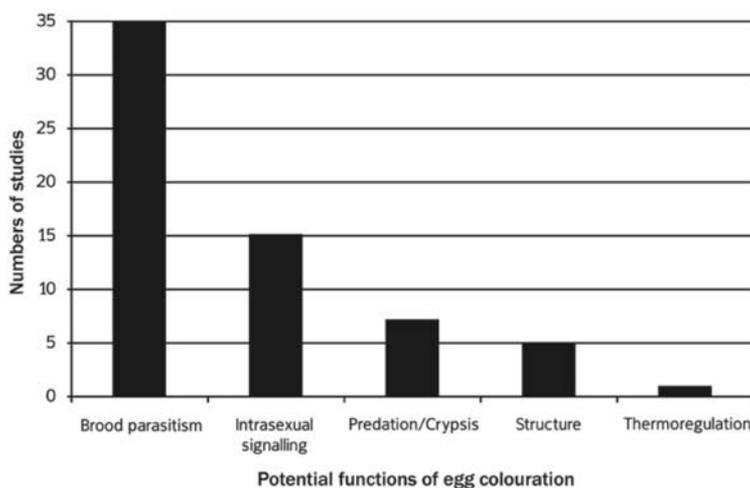
Figure 10 Studies related to egg colouration and pigmentation, as classified according to the functional hypothesis they best addressed, in six journals: *Animal Behaviour, Behavioral Ecology, Behavioural Ecology & Sociobiology, Ibis, Journal of Avian Biology*, and *Journal of Ornithology* from 1996-2011. We used the search term 'egg colour' to identify studies.

modelling predator vision and quantifying pattern, now makes it possible to investigate egg camouflage in a way that has never been done before.

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