Evolutionary Biology: Arms Races in the Eye of the Beholder

Perceptual models of the avian visual system accurately predict the egg-rejection ability of species subject to the costly trickery of cuckoos and other brood parasites.

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To the human eye, the eggs of brood parasitic birds, including many cuckoos, look to match the colours of their hosts remarkably. Yet some but not all species parasitized by cuckoos and other brood parasites are able to spot and reject the odd one among the crowd. The European cuckoo (*Cuculus canorus*) presents a special challenge for researchers as selection for the recognition of their eggs by hosts — who lose all of their own offspring to this parasite — should be particularly strong, but acceptance of cuckoo eggs is perplexingly common [1,2]. Perhaps the most fascinating aspect of this arms race between European cuckoos and their hosts is that individual females belonging to different races of this parasite specialize on one or a few of the host species, and do so by laying eggs that, to the human observer, match the particular host egg to near perfection (Figure 1). But how good is this match, really, when viewed by the host itself, and why does rejection behaviour remain so variable even in cases where the match — to our eyes — seems less than perfect? New research and application of methodology by Avilés [3] now provides an insight into this conundrum.

Although the advent of objective, physical measures of avian colours, including eggs, using reflectance spectrometry [4,5] has reshaped colour research for the past decade or so, it is only recently that physical measurements of colour have been incorporated into perceptual modeling studies [6,7] to approximate what the recipients of colour-based communication signals perceive. These studies provide an explanation for the differences between the accuracy of physical measures of colour and how the sensory system of the avian observer processes and perceives ambient colours, including its own emphasis on certain wavelengths and, in turn, its lower sensitivity at other regions of the perceivable spectrum [8].

In the common, but costly, absence of rejection behaviour, it is not known whether acceptance of a foreign egg is truly due to issues related to visual recognition. Recent studies, including the paper by Avilés [3] on host discrimination behaviour of cuckoo eggs, and by Cassey *et al.* [7] on song thrush (*Turdus philomelos*) discrimination of experimentally painted conspecific eggs (Figure 1), revolutionize the investigation of host–brood parasite relationships by their use of physiological modeling of the avian perceptual system to test the ability of hosts to distinguish parasitic eggs. Importantly, both studies found that egg-rejection behaviour is indeed more predictable and less puzzling when avian-appropriate sensory modeling techniques are employed than when viewed from a human perspective.

In the work of Avilés [3], the extent to which parasitic cuckoo eggs could be discriminated from the hosts' own eggs by the passerine visual system was estimated using perceptual models [9,10] that classify the degree of dissimilarity in chromatic (hue) and achromatic (contrast) characteristics of eggs. This study was based on perceptual differences in eggs of favorite cavity-dwelling hosts of the European cuckoo in southern Finland, an area rich with cuckoos, different host races, and many suitable host species. Avilés [3] specifically focused on redstarts (*Phoenicurus phoenicurus;* Figure 1) and pied wagtails (*Motacilla alba*) using host and cuckoo eggs housed in the Zoological Museum in Helsinki (Finland). He recorded the visual contrast between host eggs and six local races of cuckoos, including those that specialize on redstarts and wagtails. Importantly, to incorporate the importance of the light conditions in which discrimination takes place [11], he examined egg colouration under varying light levels characteristic of cavity and open cup nests.

Avilés [3] found that the eggs of redstarts and parasitic *Phoenicurus*-cuckoos are similar in both chromatic and achromatic characteristics visible to hosts, and indeed, as would be predicted, very few *Phoenicurus*-cuckoo eggs are rejected by redstarts. The eggs of another specialist cuckoo, the *Motacilla*-cuckoo, were much less similar to the eggs of their host, the pied wagtail. Rates of parasitic egg rejection in this species are much higher than in the redstart, and show a strong correlation with the results predicted by Avilés' models of avian perceptual abilities. These comparative results are in strong agreement with the experimental approach of Cassey *et al.* [7] who used previously published behavioural rejection and physical reflectance data from painted song thrush eggs [12] to generate a perceptual model-based discrimination score between painted and own eggs. Their model accurately predicts behavioural rejection of perceivably dissimilar eggs, especially when differences in colour included the UV and short-wave length spectra. In contrast, for both cuckoo hosts in the Avilés study [3], discrimination based on achromatic characteristics appears to be more reliable than the use of chromatic cues in the low light conditions typical of these cavity-nesting birds.

A surprising finding reported by Avilés [3] is that the eggs of several cuckoo races are more closely matched to pied wagtail eggs than those of the apparent wagtail specialist, the *Motacilla*-cuckoo. These results suggest that the categorization of specialists based on human visual

systems may inaccurately portray the degree of host specialization, and may require revision.

Collectively, these findings highlight the importance of taking into account both what birds actually see — rather than what their human investigators perceive — and the light environment in which they have to make behavioural decisions when addressing questions involving discrimination and the role of visual signaling. Importantly, the results [3,7] indicate that the discriminatory capabilities predicted by perceptual models more closely match the behavioural outcome of egg discrimination, providing compelling proof that perceptual models furnish accurate information about the visual acuity of these species. As such, both recent studies highlighted here [3,7] underscore the importance of using perceptual models to more precisely predict the dynamics of host-parasite arms races.

In other areas of evolutionary and behavioural ecology, perceptual modeling [9,10] has become state-of-the art for understanding the use of colourful signals, not only limited to egg colour as described here [3,6,7], but also plumage colouration [8,13,14]. These retinal function models have now become widespread in use, and overall suggest very strongly that human perceptual differences are not sufficient for understanding the behavioural and evolutionary dynamics related to colourful signals of all kinds. Additionally, these methods require only non-invasive sampling techniques.

While most perceptual models are based on species for whom we have photoreceptor sensitivity data — for example, the blue tit *Cyanistes caeruleus* [3] and the congeneric European blackbird *Turdus merula* [6,7] — it would be fascinating to examine how species-specific costs of parasitism impact the evolution of colour sensitivity between related species. Likewise, for those species where one and not the other sex rejects the parasite eggs [15], studying within-species variation in perceptual abilities [16] could provide additional insight into the foreign egg rejection behaviour of hosts. Finally, it remains to be determined what the visual sensitivity of any cuckoo species is, and if parasite vision plays a role in selecting the best-matching host clutches [17,18].

Figure 1. Finding cuckoos eggs in the nest.
Top left: a redstart (*Phoenicurus phoenicurus*) nest with a parasitic cuckoo egg hatching before the others. Top right: the cuckoo nestling that eventually evicted all of the host's own eggs from this very nest. Bottom left: the redstart female, one of the subjects of Avilés' study. Bottom right: a song thrush *Turdus philomelos* nest with the bird's own egg painted following the methods of Cassey *et al.* [6] to determine which perceptual characteristics induce ejection behaviour. (Redstart and cuckoo photos: Tomas Grim; bottom right photograph: Mark Hauber.)

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Biological Timing: Sheep, Dr. Seuss, and Mechanistic Ancestry

For many animals, knowing the time of year and predicting the forthcoming season is crucial for their survival and that of their offspring. Recent research sheds light on hormonal mechanisms that perform this calendar function in birds and mammals.

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How does our brain know when to wake up in the morning? Dr. Seuss' Chippendale Mupp has an amusing method of timing such daily activities. It has an extraordinarily long (and, presumably, non-myelinated) tail, which it bites just prior to going to sleep. According to Dr. Seuss, its tail is so long that it doesn't feel any pain until the "nip makes the trip" to its brain exactly 8 hours later and causes it to wake up with a yell. This simple, yet effective, biological circuit might allow the Chippendale Mupp to know when it is morning, but how could it tell which season it was in? What are the local environmental conditions going to be like in three months? Should it try and hoard food? Breed? Migrate? Get fat? These are real, life-or-death challenges that wild animals face on an annual basis.

Daily, or circadian, activity in vertebrates is timed by the suprachiasmatic nucleus (SCN) in the brain [1,2] and we now know a great deal about SCN biology. In contrast, timing of seasonal processes is less well understood. In all vertebrates, the hormone melatonin is secreted from the pineal gland at night, so the duration of the night (or day) dictates the duration of melatonin secretion. Thus, the melatonin signal provides organisms with a very accurate measurement of both the length of the day and whether the day lengths are increasing (spring) or decreasing (fall). Knowing this, one can rightly expect that many seasonally breeding animals use the nightly melatonin signal to time seasonally appropriate changes in their reproductive physiology and behavior.

Melatonin is important for timing seasonal processes such as gonadal growth and regression, but not all animals respond to it in the same way. Some mammals (e.g., sheep and deer) mate during short days and their young are born during the lengthening days the following spring. Other mammals with shorter gestation periods (e.g., hamsters and voles) mate and give birth solely during the long days of spring and summer. Melatonin administration to these animals (as an endocrine mimic of short days) has rapid and profound effects on their reproductive status. Short-day breeders, such as sheep, undergo gonadal activation and long-day breeders, such as hamsters, exhibit gonadal inactivation, but they all have one thing in common: melatonin duration provides time of year information to coordinate reproduction. Unlike in mammals, there is little evidence of a direct role for melatonin in the regulation of gonadal function in birds. Removal of the pineal gland and the eyes (the retina is also a significant source of melatonin in birds) does not alter the gonadal response to changing day length in American tree sparrows [3]. In some experiments, melatonin stimulates gonadal growth in birds [4] and, in others, it inhibits gonadal growth [5]. As such, there has been no unifying 'melatonin theme' in terms of a timing mechanism for seasonal breeding in birds and mammals.

Thyroid hormones have also been implicated in seasonal breeding. Removal of the thyroid gland in sheep, deer and several bird species completely disrupts seasonal changes in activity of the reproductive system, often prematurely inducing gonadal growth in birds [6,7], sheep [8,9] and red deer [10]. So, if melatonin and thyroid hormones are important for timing of seasonal breeding, how do they interact?

The pars tuberalis (PT) of the pituitary might be a key component of the interaction between melatonin and thyroid hormones. The first of several recent findings that pointed to such a role for the PT was that, in quail mediobasal hypothalamus, long day lengths induce the gene encoding type 2 iodothyronine deiodinase (Dio2), an enzyme which activates thyroid hormone [11] (Figure 1A). Thus, long days increase conversion of thyroxine (T_4) into its bioactive form, tri-iodothyronine (T_3), to about 10-fold higher than under short-day conditions. In addition, infusion of T_3 into the brain induced testicular growth in quail held under non-stimulatory short days. Activation of *Dio2* is one of the earliest events detected in the photoperiodic cascade. These effects on gene activation are thought to amplify the localized action of thyroid hormones and lead to neuroendocrine changes that cause secretion of gonadotropin-releasing hormone (GnRH) a few hours later. GnRH then causes release of gonadotropins, luteinizing hormone (LH) and follicle-stimulating hormone (FSH) from the anterior pituitary gland, activating the gonads. The mechanism by which thyroid hormones are processed and transferred to the GnRH system is not yet known. Very recently, a wave of thyrotropin (TSH) β-subunit gene expression in the PT