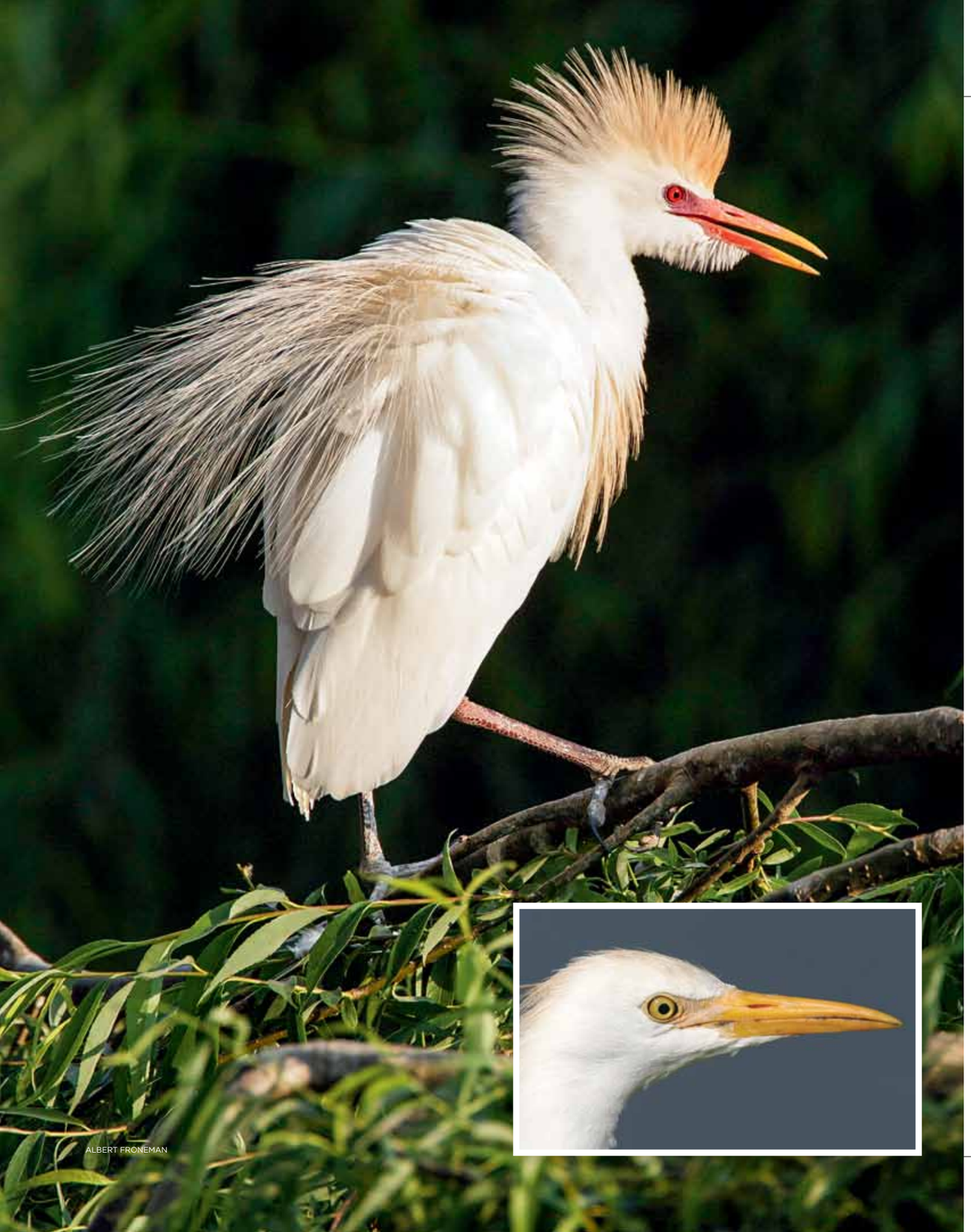
THE eyes HAVE IT

TEXT & PHOTOGRAPHS
PETER RYAN

RELATIVE TO THEIR size, birds have the largest eyes of any animal, at least in part because they need excellent vision for flight. As a result, birds set the standard for visual acuity. We know a considerable amount about the structure and function of their eyes and we're starting to learn how birds see their environment, but less attention has been given to the appearance of their eyes.

Peter Ryan describes the diversity of birds' eyes, and explores why they are so variable. >

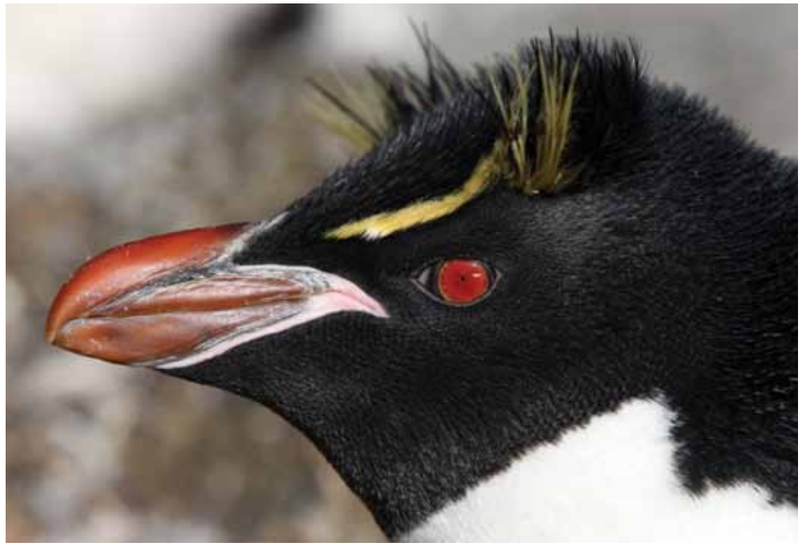


ALBERT FRONEMAN

EYES ARE FAMOUSLY described as being 'windows to the soul'. When we stare into someone's eyes we see the pupils, which let light into the eye; the iris, which expands and contracts to control the size of the pupil; and, in some species, the sclera that forms the tough outer sheath around the eye. Birds' eyes are so large that they are relatively immobile within their skulls. A bird can't roll its eyes at you, although species such as cormorants, herons and albatrosses can move their eyes slightly to improve their binocular vision while hunting. This immobility means that the iris typically covers the visible portion of a bird's eye, so you don't see the whitish sclera that surrounds the iris in human eyes. The appearance of a bird's eyes thus depends on the coloration of the iris and the size and shape of the pupil.

Like bird feathers and skin, the iris is coloured by a combination of chemical pigments and structural colours. The inner side of the iris typically comprises two layers of pigmented epithelial cells, and the overlying stroma can contain pigmented cells, including melanophores and several types of chromatophores. Bright colours result from carotenoids, purine and pteridine crystals, or occasionally from collagen fibres or blood-filled venous sinuses. Simply put, birds have evolved lots of ways to colour their eyes. I'll explore quite why they might do so towards the end of the article.

Most birds have a dark brown iris – a result of high concentrations of the pigment melanin – which helps to block stray light from entering the eye. Some people have argued that this mechanism explains the dominance of dark eyes in birds, but there is no evidence that pale eyes are less effective in this regard. All birds seem to have a dark-pigmented basal layer to their iris, which in birds with brightly-coloured eyes is masked by other pigments in the stroma. The eye needs to be well lit to discern the black pupil against a dark brown iris, but the pupil contrasts with the iris in birds with paler eyes, making the eye's appearance depend as much on pupil size and shape as it does on iris coloration.



THE OTHER EXCEPTION TO THE RULE OF ROUND PUPILS IS THE PENGUINS, WHICH HAVE **TINY SQUARE OR STAR-SHAPED PUPILS IN BRIGHT LIGHT**

The size of the pupil is determined by the iris, which expands or contracts to control the amount of light entering the eye, just as a camera's aperture controls the amount of light reaching its sensor. The pupil is small in bright light and larger in dim light. This is readily observed in owls with a yellow iris: their pupils are much larger at dawn and dusk than during the middle of the day. Humans' pupils also dilate slightly when viewing something arousing or disturbing. Birds have greater control over their pupillary response than mammals, and some birds such as crows, starlings and parrots are known to change the size of their pupils in social interactions. For example, Adrian Craig observed how dominant Pied Starlings contract their pupils to emphasise their white iris when they approach a subordinate bird.

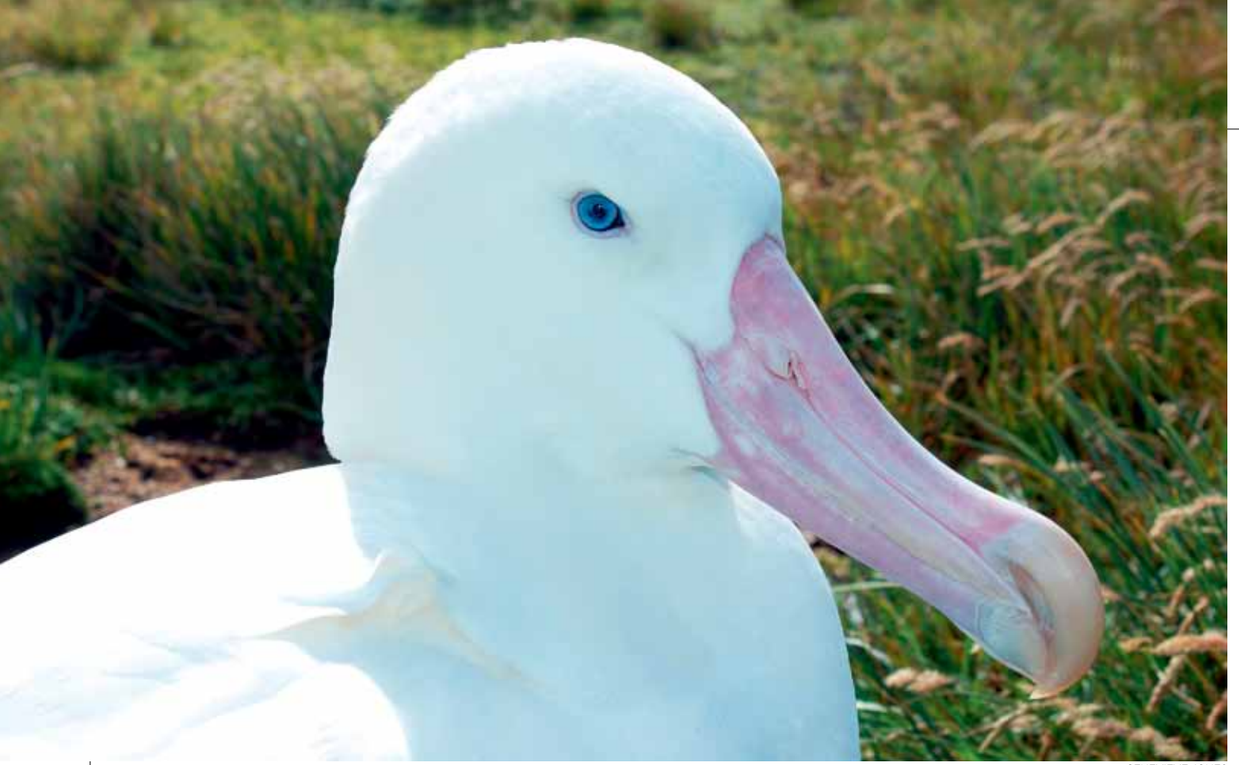
In most birds, like many mammals, the pupil is round. The main exception is the skimmers. Although it is hard to see against their dark brown irises, in bright light they have a vertical, slit-like pupil, resembling that in a cat. It has been suggested that this evolved to allow skimmers to increase the range of their pupillary response, linked to their frequent activity at night. In most birds, a fully open pupil allows about 16 times more light into the eye than when the pupil is at its smallest, roughly the same response as that found in humans. Whether skimmers can increase this range by having a slit-shaped pupil has not been tested. However, other birds that are active by day and night manage with a round pupil, and it is not clear why skimmers differ in this regard.

The other exception to the rule of round pupils is the penguins, which have tiny square or star-shaped pupils in bright light. This is not easy to see in the African Penguin, which >

above *The tiny, star-shaped pupil of the Southern Rockhopper Penguin is an adaptation to allow it to forage in deep, dark waters.*

opposite *Just before the eggs are laid, Western Cattle Egrets have distinctive red eyes and pink faces (main picture), quite different from the rest of the year (inset).*

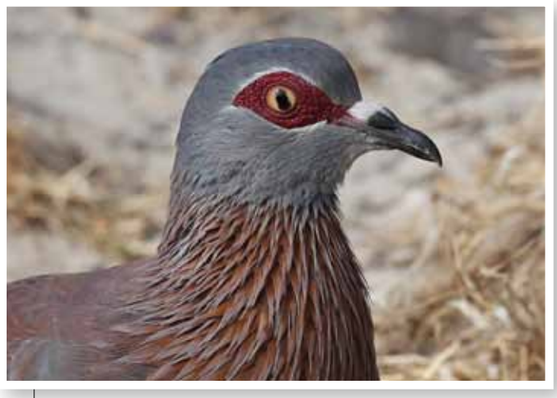
previous spread *Black-bellied Starlings are unique among the pale-eyed glossy starlings in changing their eye colour from yellow to red, apparently in response to their emotional state. However, adult males may have red eyes throughout the breeding season.*



GENEVIEVE JONES

above *Wandering Albatrosses typically have blackish-brown eyes, but a few individuals have one pale blue eye. It is unknown whether such cases of heterochromia are hereditary or caused by a disease or an injury.*

below *Speckled Pigeons appear to have asymmetrical pupils.*



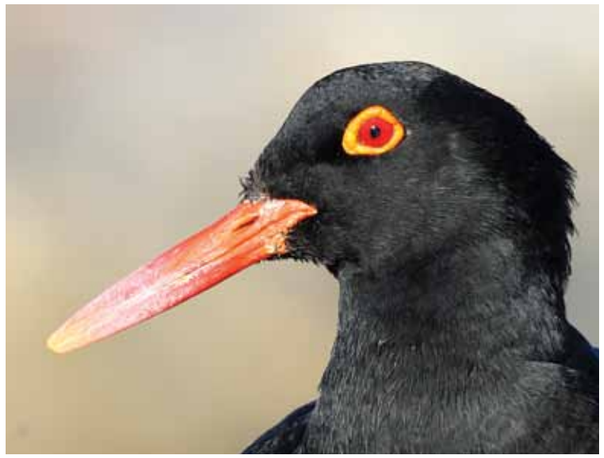
has a blackish-brown iris, but is obvious in the bright red iris of crested penguin species. The importance of a tiny pupil has been studied in the King Penguin by the guru of avian vision, Graham Martin, but I need to digress a little to elaborate on what he found.

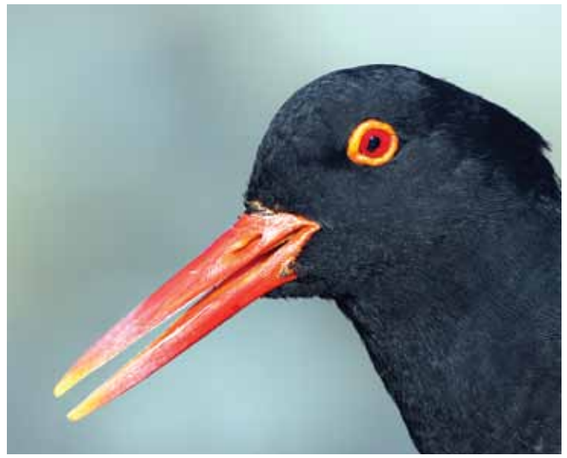
The pupil responds extremely rapidly to changing light levels. When chickens are subjected to a rapid flash, their pupils react within milliseconds, and the maximum contraction occurs within 0.15 seconds. However, the magnitude of the pupillary response in most birds' eyes is only sufficient to cope with modest changes in light intensity, such as those experienced when moving from sun to shade. Night vision depends on the presence of rhodopsin in the eye's receptor cells. This chemical, which is extremely sensitive to light, takes about 10 minutes' exposure to low light levels to build up in the retina. This explains why it takes a while for your night vision to develop when you go into the dark.

Penguins forage by sight, often at depths where light levels are very low. For example, King Penguins regularly dive to depths of between 200 and 300 metres, where even at midday the light level is similar to that on a starry night. However, penguins don't have the luxury of waiting for their night vision to kick in, because their dives only last a matter of minutes. As a result, they have evolved the largest pupillary response yet measured – a roughly 300-fold change in the amount of light admitted to the eye. By keeping the pupil almost closed at the sea surface, they retain some of their night-vision capacity for when the pupil is fully expanded at depth. The musculature of the iris responsible for accomplishing this feat has not been studied, but it presumably accounts for the irregular shape of the contracted pupil. Cormorant eyes also have a tiny, not-quite-circular pupil in bright light, most probably for the same reason.

SOME OTHER BIRDS APPEAR TO HAVE IRREGULARLY-SHAPED PUPILS... IT IS PARTICULARLY NOTICEABLE IN SPECKLED PIGEONS, WHICH **APPEAR TO HAVE A KEYHOLE-SHAPED IRIS**

Some other bird species appear to have irregularly-shaped pupils, but this is as a result of patchy black coloration of the iris. It is particularly noticeable in Speckled Pigeons, which appear to have a keyhole-shaped iris, and it has been recorded in several other pigeons and woodpeckers. It also occurs in adult oystercatchers, where it is more pronounced in females than males, providing a handy way to distinguish between the sexes. In most cases the dark patch is below the iris and slightly towards the bill, suggesting that the placement is not random, but no one has yet come up with a sensible explanation for why this might be the case in three distinct groups of birds.





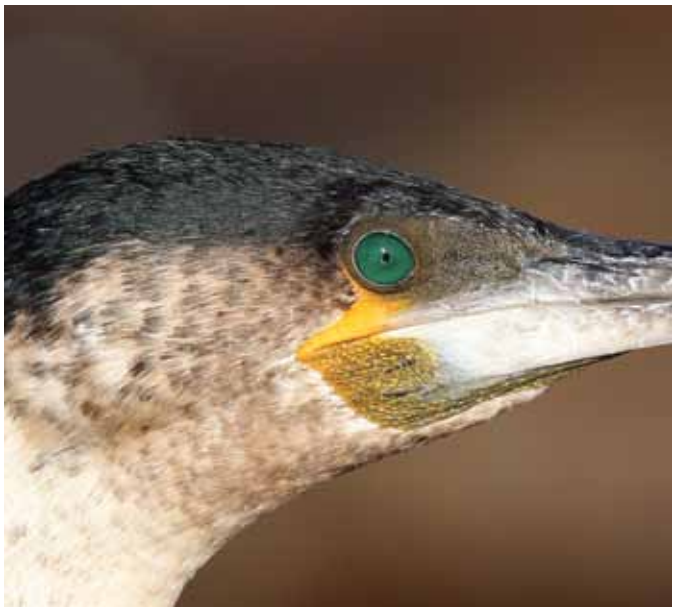
Adult female African Black Oystercatchers typically have an irregular blackish mark on the iris below the pupil (above right), which is either absent or greatly reduced in most males (above left). Note also the fleshy eye-ring that increases the conspicuousness of the eyes.

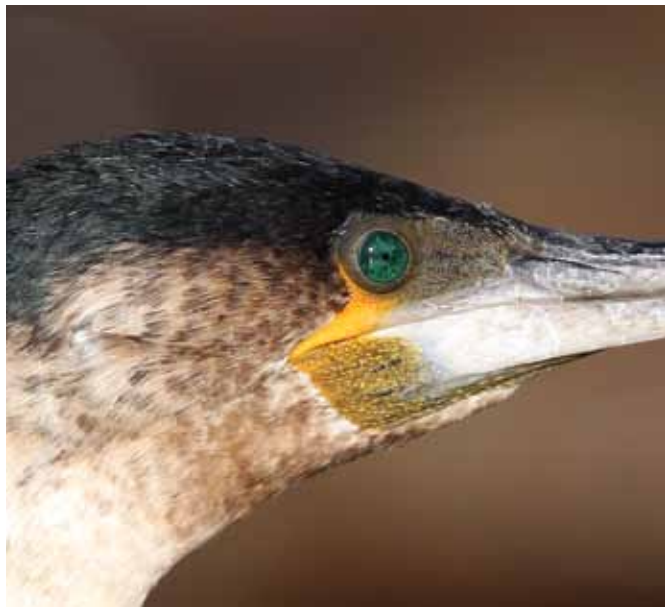
Now let's return to the question of why some birds have strikingly-coloured eyes and others don't. An animal's colour may simply be a consequence of its structure or it might be selected for one of three reasons: to affect its visibility to other animals, to signal information, or to improve the animal's vision (for example, dark eye-stripes reduce glare around the eye). These factors are not mutually exclusive. Bird colour patterns are usually a compromise between the need to signal to potential mates or competitors and to avoid being detected by potential predators or prey. We can infer the factors driving eye colour by examining how colour varies within and among species.

In almost all cases, brightly-coloured eyes develop with age and maturity, suggesting that they serve a social signalling function. There are a few cases where young birds have arguably more striking eyes than adults. This is apparent in birds such as the accipiters, in which the pale yellow eyes of juveniles gradually turn red with age in some species (for example, the Gabar Goshawk). However, even these species tend to have dull, grey-brown eyes as chicks. It thus appears that having dark eyes was the ancestral condition among birds.

The level of intensity of brightly-coloured eyes may be an important signal of health, if this is linked to the concentration of carotenoids. This group of compounds, derived from the diet, helps to combat diseases and, in males, offsets the immunosuppressant effects of androgens. In European Sparrowhawks, males with dark red eyes produce more offspring than those with paler eyes, but it is not clear if this simply reflects the effect of greater experience because eye colour tends to darken with age. Such condition signals are likely to be important for males in polygamous species, where females choose among a suite of potential partners. This probably explains >

Adult Pied Starlings have a striking white iris, which they use to signal social status. When a dominant bird feeds a subordinate, it contracts its pupil, emphasising the white eye, while the subordinate bird expands its pupil to make its eye appear darker, more closely resembling the dark eye of a juvenile bird.





The uniform green eye of a White-breasted Cormorant develops darker shadows when viewed at an angle, possibly due to light scattering effects caused by the fibres of the stroma. Note the tiny pupil, similar to a penguin's.

why all weavers in which the males have distinctively coloured eyes are polygamous.

Eye colour tends to vary among bird groups. For example, almost all swallows and thrushes have dark eyes, whereas a disproportionately large number of starlings and all oystercatchers have red or pale eyes. And among plovers, most lapwings have bright eyes, whereas most *Charadrius* plovers have dark eyes. At a regional scale, the incidence of passerines with brightly-coloured eyes is higher in Australia (35 per cent) and southern Africa (26 per cent) than in the Neotropics (12 per cent) or the north-temperate zone (10 per cent). The significance of these patterns, if any, is not clear.

In addition to age- and sex-related variation, eye colour can vary geographically, and even be polymorphic within a population (for example, Bearded Reedlings).

Eye colour also can change quite rapidly as a result of fluctuating hormone levels. The first time you see a pre-breeding Western Cattle Egret with its scarlet eye and pink face you might be forgiven for thinking it is an entirely different species. Allen's Gallinules also acquire much brighter eyes when breeding.

The conspicuousness of a bird's eyes can be enhanced by contrasting with skin or feathers around the eye. Bare eye-rings have the advantage of being easier to modify than feathers, whose appearance can only be changed by moulting. Many birds develop larger, brighter eye-rings or bare facial skin during the mating season. By linking these features directly to the hormonal status of the bird, they accurately signal availability to potential mates. And some species, such as the African Harrier-Hawk, can even change the colour of their facial skin in minutes to indicate their level of arousal or distress.

Finally, the colour of the eyelids might be selected to contrast with that of the eyes. A recent paper showed how ducks with pale eyes have dark eyelids, and those with dark eyes typically have pale eyelids, irrespective of sex-linked differences in eye colour. The authors suggest that this signals who is asleep to other members of the flock, so they can modify their vigilance level accordingly. It all goes to show that there's a lot more going on in the bird world than first meets the eye. ◆

The Bank Cormorant is unique among birds in having an asymmetrical colour pattern move progressively down its eye with age. Juveniles have dark grey-brown eyes, which turn green in their second year, and then an orange wash descends from the top of the eye. A few, presumably old birds, have almost fully orange eyes.