COVER ILLUSTRATION

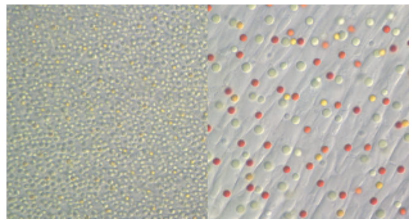
Halcyon days

In classical Greek mythology, Halcyone, daughter of Aeolus, was married to Ceyx, King of Thessaly. On a voyage at sea, Ceyx fell overboard and drowned. Halcyone turned into a kingfisher when she saw his corpse. Her lamentations awakened the gods who then turned Ceyx into a kingfisher, and Ceyx and Halcyone mated. Their nest of bones and shells floated on the open sea as Halcyone brooded over her young. Aeolus, her father and the god of wind, quieted the sea for seven days on either side of the winter solstice to protect this union. Milton immortalised these ''Halcyon'' days in the *Hymn of the Nativity* when he wrote ''While birds of calm sit brooding on the charmed wave.''

In reality, only one species of kingfisher is pelagic and none nests on the sea, but they have evolved other interesting traits, most notably ocular adaptations that are deserving of recognition.

Evolution has found specialised adaptations to fit specialised niches. Coloured oil droplets, located in the inner segments of cones, can be found in lungfish, diurnal reptiles, turtles, and birds. Amphibians, snakes, crocodiles, and placental mammals have lost these structures, presumably because of an extended period of nocturnality during evolution. All species with coloured oil droplets also have different types of visual pigment; many avian species have four such pigments, so the function of coloured droplets cannot be to add colour to a black and white world. However, coloured oil droplets function as long pass filters and will absorb photons below a specific wavelength. Coloured oil droplets decrease overall photon capture, shift the peak sensitivity of the cones to wavelengths longer than the peak absorbance of the visual pigments they contain, and narrow their spectral bandwidth. Current evidence suggests that oil droplets not only enhance colour vision (by increasing both discrimination and the number of discriminable colours in the animal's ''colour space''), but also reduce chromatic aberration and glare (Vorobyev M, *Proc R Soc Lond B* 2003;**270**:1255).

The aquatic kingfishers, as represented by the green and rufous kingfisher (left half of cover), have a



preponderance of red oil droplets in their retinas. Many avian species that must look through water for their prey, such as kingfishers, have a preponderance of red oil droplets. The reason red droplets predominate is not understood, but the droplets may help with the glare or the dispersion of light from particulate matter in the water. A woodland kingfisher, the kookaburra (right half of cover) has five different types of oil droplets in each of the four types of single cones and one type of double cone. Centrally coincident with the nasal fovea, the cones become thinner and the oil droplets lose much of their colour (fig, left) compared to the thicker cones at the periphery (fig, right). This distribution pattern is also seen in another woodland species, the sacred kingfisher (*Todiramphus sanctus*) but its function is not completely understood (Hart NS, *J Comp Physiol A* 2001;**187**:685–97).

As with many avian predators, kingfishers have two foveae in each eye. As previously discussed in the February 2001 *BJO* cover essay, bifoveate birds have a monocular fovea and a binocular fovea, but this species has a real twist. The temporal fovea is at the ora and shares the binocular field with its compatriot in the contralateral eye even if the neural integration is not understood. This temporal fovea is shallow and surprisingly inferior anatomically. The ganglion cell density around the monocular nasal fovea is much higher than the cell density around the binocular temporal fovea, suggesting that the acuity is significantly higher at the nasal fovea (Moroney MK, Pettigrew JD, *J Comp Physiol A* 1987;**160**:137–49). This would not be a surprise. Presumably, a kingfisher will sight its prey with the higher acuity nasal monocular fovea and, if aquatic, hover above it. As the bird drops towards its prey, acuity becomes less critical but the ability to see prey movement especially in the three dimensional world of water becomes paramount. The infula or visual streak which connects the two foveae allows the image to swing temporally as the bird drops onto the prey, and if the prey moves, the temporal fovea senses the difference in position and the kingfisher can adjust accordingly.

When hovering 12–15 metres above their prey, aquatic kingfishers are presented with an unusual problem. The simultaneous movement of the fish and of the bird as it hovers would create a neurological nightmare. The solution produces a dramatic real life aerial dance for those who have witnessed it. The pied kingfisher is the only species that is pelagic, and during its hover before the plunge-dive it keeps its head rock steady relative to the movements of wing and body. Curiously, the depth of the prey will vary the form of the plunge-dive. The deeper the prey, the steeper the dive angle (with achieved speed as high as 4.5 m/s), perhaps to reduce the effects of refraction on the apparent position of the prey.

The position of the monocular fovea tends to be fairly constant in all bifoveate birds, but the temporal fovea is different. The two foveae in kingfishers have very large angles of separation which measure up to 52° compared to 15° in eagles and kites. This anatomical separation means that the binocular foveae are sighted along the beak much like laser sighting a gun.

Even the imagination of Greek mythology cannot match the reality of this bird's evolutionary creativity, although birds of calm may not be the best name for them.

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Cover photographs by the author. Retinal photographs by Nathan Hart, PhD, of the Vision Hearing and Touch Center, University of Queensland, Australia.

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Br J Ophthalmol 2004 88: 613
doi: 10.1136/bjo.2004.045492