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COVER ILLUSTRATION

With just a quiver

Nutrition is expensive. There is a price to pay to nourish any cell, and this is especially true of the eye. Evolution has had to be creative to nourish portions of the eye so as not to interfere with vision. If the retina is relatively simple and is thinner than about 150 μm, diffusion from the choroid is sufficient. But, if the ecology demands better vision, the retina must thicken to permit more amacrine and horizontal cells to increase retinal processing. To assure inner retinal cells have adequate nutrition and proper cellular metabolism, evolution has found creative and seemingly contradictory mechanisms.

Primates have intraretinal vessels, and must actually look through these vessels and the oxygen carrying pigment of the red blood cells that degrades the image, however slightly. Some animals, though, demand the best possible vision and have shunned any obscurations from vascularisation—birds! Yet, even though birds do not have obvious inner retinal nourishment, they must somehow provide nutrients and oxygen to the high concentration of amacrine, horizontal, and ganglion cells present in the inner retina. How can this be done?

Nocturnal birds bring to mind owls or nightjars, but there are others. The bush stone curlew (*Burhinus grallarius*) is a primarily nocturnal, ground dwelling bird found throughout Australia. It has an eerie call that betokens fear and foreboding at night. It is an omnivore but feeds principally on lizards, amphibians, and small mammals—indeed almost anything it can catch and swallow. Birds, including the bush stone curlew, do not have any retinal vascularisation, but rather have a collection of vessels projecting from and attached to the optic nerve head. This vascular collection is the pecten and it is homologous to the central retinal artery in other mammals. The pecten projects into the inferior vitreous and in some species nearly touches the lens. The vessels in the pecten are permeable to nutrients and oxygen, yet its purpose has remained a mystery until recently.

Casey Wood (1856–1942) was a consummate ophthalmologist who spent most of his life in North America and served as editor to three ophthalmic journals, including the *American Journal of Ophthalmology*. His educational pedigree reads as one of the classics of the times—New York Eye and Ear Infirmary, University of Berlin, various London hospitals, including Moorfields and the Middlesex. When he settled in Chicago in 1890, he was one of the best educated men in ophthalmology in America. A prolific writer, he wrote several ophthalmic texts as well as *An Introduction to the Literature of Vertebrate Zoology*. But, his magnum opus is entitled *The Fundus Oculi of Birds*. This classic may never be repeated as much of the material is, or soon will be, lost to science. In this large format book, he documents, with written descriptions and full page drawings, the fundi of many different species of birds. Having no fundus camera, he had an artist draw them following ophthalmological examination, and he carefully documented the pecten of each species he recorded. Since each species has a specific pecten and, conceivably, one could identify the bird by its pecten, his extraordinary skill and attention to detail is on display in this book. He described the pecten and speculated on its function, as many others have since. This book is the first and most comprehensive study of the avian pecten.

Normal pecten

The pecten projects its vascular net into the vitreous with multiple macroscopic and microscopic pleats to increase the surface area. Pleating in this manner is reminiscent of the stomach of the puffer fish as a mechanism to increase surface area in an enclosed space (*BJO* cover essay, October 2002). Although most observers have believed that it is primarily a nutritive tissue, there has been much speculation. Some investigators have thought the pecten to be a sunshade, an azimuth, or a magnetosensor, although these are unlikely. Others have thought that the tissue could be used to assist accommodation, and it may do that. It has been thought to be a mechanism to warm the interior of the eye in high flying geese and similar birds to prevent degradation of the optics due to cooling.

It remained for the bush stone curlew, among others, to help investigators document the primary function for this organ. The pecten is permeable to small molecules including fluorescein which will diffuse out of the pecten after injection. Fluorescein will remain pooled in the inferior vitreous immediately adjacent to the pecten until the bird performs a saccade. In birds, and only in birds, each saccade has an associated oscillation of the globe that includes a pronounced cyclotorsion or rotary component. Each saccade will create plumes of fluorescein rising from the inferior vitreous, billowing like steam rising off the spout of a kettle. These oscillations occur with each saccade to spread nutrients with the pecten acting as an agitator to allow diffusion of oxygen to the inner retina (Pettigrew JD, *et al*, *Nature* 1990;**343**:362–3). Saccades would not be otherwise particularly necessary or helpful since the extraocular muscles are rudimentary and such movements would not improve the visual fields greatly.

These saccadic oscillations allow for inner retinal nutrition without intraretinal or epiretinal vascularisation, This extraordinary nutritive mechanism allows for significant retinal thickening. In some birds, the retina may be 300 μm thick allowing for amacrine concentration that is three times our own. So, the pecten has been a requisite evolutionary innovation assisting birds to have the best vision on earth—with just a quiver.

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