

Avian Vision: A Review of Form and Function with Special Consideration to Birds of Prey

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Abstract

More so than any other terrestrial vertebrate, birds rely most heavily on their ability to assess their visual environment. High visual acuity is not only necessary to find and acquire food, but also to navigate surroundings, to identify conspecifics and potential mates, and to quickly identify and escape from predators. This article aims to help the reader understand how birds, particularly birds of prey, see by reviewing pertinent anatomy and physiology of the eye, color vision, visual fields, visual acuity, accommodation, and flicker-fusion frequency. For more information on specific disease conditions of the avian eye, the reader is encouraged to review any number of avian medical and surgical texts. Copyright 2007 Elsevier Inc. All rights reserved.

Key words: avian; eye; ocular; raptor; vision

Birds, with some exceptions, are incredibly visual animals. The avian globe, in relation to the size of the skull, is very large, which is advantageous for species relying heavily on their ability to interpret and respond to their visual environment. A large eye allows a larger image to be projected onto the retina, thus contributing vastly to visual acuity.¹ In birds, approximately 50% or more of the cranial volume of the skull is occupied by the eye, whereas in humans, the eye occupies less than 5% of the skull's volume.² Some owls and hawks even have eyes that are larger than human eyes. Among terrestrial vertebrates, the ostrich (*Struthio camelus*) has the largest eye, which measures 50 mm in diameter, twice that of the human eye.^{2,3}

Although the avian eye varies in size, it also varies tremendously in shape. One commonality, however, is that in most cases, the nearly hemispheric posterior region of the globe is disproportionately larger than the anterior segment.^{4,5} The anterior and posterior segments of the globe are united by a variably shaped intermediate region based on the scleral os-

sicles.⁶ The asymmetry between the anterior and posterior segments is also present on the horizontal plane, with the temporal aspect (area nearest the ears) of the globe being more extensive than the nasal aspect (area nearest the beak).^{6,7} Avian eye shapes are either flat, with a short anteroposterior axis, flat or concave intermediate (ciliary) region, and convex cornea—typical of most diurnal birds with narrow heads (e.g., domestic fowl); globose, with the concave ciliary region sloping backward at

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Figure 1. Juvenile goshawk (*Accipiter gentilis*) demonstrating the pronounced superciliary ridge.

varying angles to meet the posterior segment—typical of many diurnal birds requiring high-resolution distance vision (e.g., diurnal raptors); or tubular, in which a concave intermediate segment is elongated anteroposteriorly, forming a tube before joining the posterior segment, at a sharp angle, and the cornea positioned anteriorly—typical of owls.¹⁻⁵

The Orbit

The orbit is formed by the frontal, prefrontal, sphenoid, ethmoid (mesethmoid), palatine, quadrate bones, and the jugal arch.³⁻⁷ The dorsal and temporal aspects of the globe are unprotected by the bony orbit, but the rest of the globe fits very snugly within the orbit. In woodpeckers, the tight fit of the globe within the orbit, in addition to extensive fascial connections between the orbital rim of the globe and the narrowed orbital entrance compared with the size of the posterior segment, protect their eyes from acceleration deceleration-induced ocular trauma as they forage.⁸ In many species, the globe's equatorial diameter is larger than the anterior bony orbital rim.⁴ In most birds, the large size of the eyeballs has compressed the bone at the depth of the orbit into a thin, interorbital bony septum.³

In most raptors (e.g., eagles, hawks, and falcons), a distinctive eye ridge, formed by a well-developed superciliary ridge and the feathers in the region, extends above and in front of the eye (Fig 1).⁸ This “eyebrow” gives raptors their distinctive, piercing stare. The super-

ciliary ridge also functions to shield the eye from excessive glare resulting from the sun passing through the iris and causing a dazzle reflex (blinking elicited by bright light shone in the eye) of the retinal surface, and to physically protect the eye from wind, dust, and debris.⁸ Ospreys (*Pandion haliaetus*) lack this superciliary ridge; however, the arrangement of the feathers above the eye serves a similar function.⁸ Interestingly, the osprey also possesses dark feathers in front of the eye, and these black feathers probably serve to reduce the glare from the surface of the water as they attempt to capture fish.⁸ Raptor species such as peregrine falcons (*Falco peregrinus*), American kestrels (*Falco sparverius*), prairie falcons (*Falco mexicanus*), and the aplomado falcon (*Falco femoralis*) have very distinctive malar stripes (dark feathers in front and below the eye) that may also help to reduce glare from the sun when searching for or pursuing fast-moving prey (Fig 2).

Extraocular Muscles

Extraocular muscles in avian species are reduced to thin bands, and torsional movement of the globe in many species is limited to between 2° and 5°.⁹ These limitations are due to the largeness of the globe and its fit within the orbit. The extraocular muscles consist of the medial, lateral, dorsal, and ventral rectus muscles, and the dorsal and ventral oblique muscles. Eye movements, which are of small amplitude, have been described as (1) impulses and oscillations, (2) tremors, (3) flicks, and (4) drifts.⁷ The retractor bulbi muscle

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