



Figure 8-5 Clark's Nutcracker, a seed-caching bird with extraordinary spatial memory.

Avian Vision

Birds are highly visual animals. They have large eyes, with which they search visually for food and detect predators at great distances. They also engage in complex, colorful courtship displays, matched it seems by an exceptional system of color vision. The true nature of avian vision, however, remains to be determined. Experiments have not yet confirmed historical beliefs of extraordinary visual acuity—the ability to resolve fine

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detail at distance. Passerines and raptors, believed to have the keenest sight of all birds, can resolve details at 2.5 to 3 times the distance humans can, not 8 times as was once thought (Pearson 1972). One of the distinctions of avian vision may lie in the ability to capture at a glance a whole picture rather than to piece a scene together after a laborious scan, as humans do.

Avian eyes are large, prominent structures. The European Starling's eyes account for 15 percent of its head mass. The eyes of eagles and owls are as big as human eyes. Unlike the uniformly round, rotating eyes of mammals, the eyes of birds vary in shape from round to flat to tubular. They fill the orbits fully but are capable of only limited rotation, mostly toward the bill tip.

Because birds' eyes are generally set on the sides of their heads, birds see better to the side than to the front. Penguins and passerines, for example, examine nearby objects with one eye at a time. The resulting image is relatively flat because monocular vision does not achieve depth perception with the same accuracy as binocular vision. To compensate, birds bob their heads quickly, viewing an object with one eye from two different angles in rapid succession. Some birds, such as swallows, nightjars, hawks, and owls, restrict lateral monocular vision to close objects and use forward binocular vision for distant viewing. Generally, binocular vision is atypical. Among ducks, only the Blue Duck of New Zealand can stare forward; other ducks use one eye at a time. Parrots have a binocular field of only 6 to 10 degrees (Walls 1942). Bitterns stare forward with binocular vision while pointing their bills skyward. Quite the opposite are woodcocks, whose huge eyes are set far back on the head allowing broad rearview binocular vision.

Eye Anatomy

A cross section of the avian eye reveals a small anterior component that houses the cornea and lens and a larger posterior component that is the main body of the eye (Figure 8-6). The two sections are separated by a scleral ring composed of 12 to 15 small bones—called ossicles. Two striated muscles—Crampton's muscle and Brucke's muscle—attach to these ossicles and are responsible for focusing on objects. The lens is large and conspicuous. The pecten, a distinctive and intriguing feature of the avian eye whose function remains unclear, projects from the rear surface of the eye near the optic nerve into the large cavity filled with vitreous humor—the clear substance that fills the eye behind the lens.

Cornea and Lens

In birds, both the cornea and the lens change their curvature while focusing; only the lens does this in mammals. Contraction of Crampton's

optic nerve. This central fovea is deeper and more complex in its cell structure in visually acute passerines, woodpeckers, and raptors than it is in pigeons and Domestic Chickens. Whether deep foveae enhance avian visual acuity is not clear. They may, however, aid in detection of the movements of small images. Fast-flying birds that must judge distances and speeds accurately, such as hawks, eagles, terns, hummingbirds, kingfishers, and swallows, have temporal as well as central foveae. These birds also have forward-directed eyes and, therefore, good binocular vision, which projects images onto the temporal foveae. Images of their peripheral or lateral monocular vision fall on the central foveae. Although cones are most abundant in the foveae, high cone densities also occur in horizontal, ribbonlike strips around the retina in albatrosses, grebes, plovers, and other birds. These ribbons apparently increase a bird's ability to perceive the horizon and work in concert with the semicircular canals of the inner ear to achieve proper body orientation.

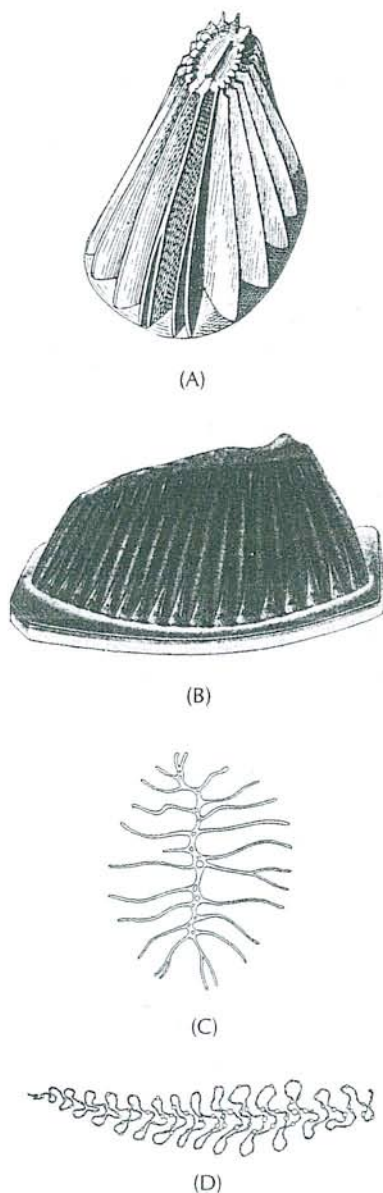


Figure 8-8 Structure of the pecten of (A) an Ostrich and (B) most modern birds. (C) Basal cross section of the structure of A, including central web and lateral vanes. (D) Dorsal view of the typical pleated structure of avian pectens. (Adapted from Walls 1942)

The Pecten

The pecten, a remarkable feature of the avian eye, is a large, pleated, vascularized structure attached to the retina near the optic nerve. Protruding conspicuously into the vitreous humor and, in some birds, almost touching the lens, the large, elaborate avian pecten is unique among vertebrates. In most birds the pecten has 20 or more accordion-pleated fins, giving it a superficial resemblance to an old-fashioned steam radiator (Walls 1942) (Figure 8-8). Nocturnal birds have fewer folds. The pectens of owls, nightjars, and the Kakapo have only four to eight folds, and the simple, reptilelike pecten of kiwis has no folds at all; it probably represents an evolutionarily degenerate condition (Sillman 1973).

The avian pecten has fascinated scientists for centuries. At least 30 theories have been proposed to explain its existence. Some researchers believe the pecten is involved in the regulation of internal eye temperatures and hydrostatic pressures; some suggest it reduces glare; others hypothesize that it might be a sextant for navigation or a dark mirror for indirectly viewing objects near the sun. The majority opinion, however, holds that the avian pecten functions primarily as a source of nutrition and oxygen for the retina. Unlike its mammalian counterpart, the avian retina has no embedded blood vessels. The assumption is that, instead, the vascular supply system is concentrated in a single structure, the pecten, which interferes less with visual functions than would a complex network of blood vessels.

Color Vision

The richness of avian color perception is probably beyond that of human experience (Goldsmith 1980). We speculate that primitive mammals, including the ancestors of primates, were night creatures that lost the retinal

oil droplets. The density of human pigments is not that high. The retina is not that dense.

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oil droplets associated with sensitive color vision. Once lost, these droplets did not evolve again in placental mammals. Instead, the color vision of humans and other primates reevolved on a different basis, without pigmented oil droplets. Very likely, the avian retina—with its high cone densities, deep foveae, near-ultraviolet receptors, and colored oil droplets that interact with several cone pigments—is the most capable daylight retina of any animal.

The presence of large numbers of cone receptors, which contain the visual pigments, suggests that diurnal birds have well-developed color vision. By contrast, the retinas of nocturnal owls contain mostly rods, which are simple light receptors important in black-and-white (and hence night) vision. Color vision is based on visual pigments, which convert the electromagnetic energy of light into neural energy. In addition to visual pigments, the cones of diurnal birds often contain colored oil droplets. Carotenoid pigments (Chapter 4) in the oil act as red–yellow filters, but their contribution to color vision is not understood. Perhaps the yellow oil droplets enhance the contrast of objects seen against the sky by filtering out much of the blue background. Similarly, red oil droplets may enhance the contrast of objects against green backgrounds, such as fields and trees, by filtering out the prevailing green background. The yellow oil droplets are concentrated in the central and lower retina, where distant images such as those in the sky usually fall. Red oil droplets are concentrated in cones of the peripheral and upper retina, where nearby images such as those on land usually fall.

Unlike humans, birds are sensitive to light in the near-ultraviolet spectrum. The lenses of the human eye absorb ultraviolet light; in birds, the lenses transmit ultraviolet light to the retina, where some cones have peak sensitivity in the near-ultraviolet spectrum (Chen et al. 1984). Melvin Kreithen and Thomas Eisner (1978) demonstrated that homing pigeons, in addition to having the normal vertebrate sensitivity to blues and greens (at 500 to 600 nanometers), are sensitive to the near-ultraviolet spectrum (325 to 360 nanometers). Black-chinned Hummingbirds, Belted Kingfishers, Mallards, and several passerines also are sensitive to ultraviolet light (Goldsmith 1980; Parrish et al. 1984). Given the taxonomic diversity of species tested, the majority of birds probably possess this trait.

Detection of Natural Magnetic Fields

Birds use magnetic information for navigation. (See Chapter 13 for a detailed discussion of this topic.) Tiny crystals of magnetite near the olfactory nerves between the eyes of pigeons discovered by Charles Walcott and his colleagues (1979) were initially thought to be the basis of a directional sensory system for the detection of magnetism. Similar crystals exist in bacteria and honeybees that respond to magnetism.

More recent research, however, points to an entirely different reception mechanism (Semm and Demaine 1986; Wiltschko and Wiltschko 1988;