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Eye Marks in Vertebrates: Aids to Vision

Abstract. *Lines leading forward from the eye may function as aiming sights in many small vertebrates. The chief evidence is the correlation of distribution and positions of eye-lines in various vertebrate groups with predatory feeding habits. Dark patches around the eye may serve to reduce glare in species in bright environments. Facial patterns often have multiple functions.*

Several functions have been suggested for the characteristic colors and markings of species, including camouflage (*1*, *2*), social signals (*3*), mimicry (*4*), and thermoregulation (*5*). We suggest that, in addition, the patterns of circles and lines about the eyes of vertebrates may enhance their vision and enable predaceous species to locate and capture prey more effectively.

Eye-lines are well-defined marks, usually very dark and narrower than the eye. The dorsal borders are usually more or less straight and uninterrupted (Fig. 1A). The ventral margins may be straight, but some are curved, demarcating a facial patch. The eye-lines extend from the margin of the eye or, more rarely, from or through an eye circle (Fig. 1B) toward, above, or below the bill tip or snout; sometimes they become narrower along their path. Some are positioned so that the line of sight is along the upper edge of the eye-line. However, often a line from the center of the pupil bisects the dark eye-line. Another frequent pattern is that of light over dark lines, which could be used as a line of sight in at least two ways; either the dark line or the line margins could be followed (Fig. 1B). The area above the eye-line might regulate light falling on the eye-line. Many birds lift the feathers above the eye-line forming an eye-brow (Fig. 1C). In birds with eye-lines the area above the line is frequently light in color. Increased light falling on the dark line from this area might increase visual acuity.

If the eye-lines serve as lines of sight in tracking and capturing swiftly moving prey, their presence, position, and type should be related to feeding habits. These lines should occur more frequently in species that feed on rapidly moving prey. We grouped North American songbirds by feeding habits in six categories, ranging from rank 1 in which more than 50 percent of the diet consisted of flying insects or other swiftly moving animal life. There was a + .94 rank-difference correlation between the presence of eye-lines and feeding on swiftly moving prey [see (*6*)]. Also we compared 50 species of insectivorous vireos and warblers with 44 species of granivorous and insectivorous sparrows (Emberizinae, closely related to warblers). We assigned all 94 species to categories based on the complexity of eye markings. We considered a dark line, as shown in Fig. 1A, simple; light over dark stripes with a broken or unbroken eye circle we considered complex (Fig. 1B). The most complex eye markings, as depicted in Robbins *et al.* (*7*), were found in all North American vireos and 32 out of 36 northeastern North American warblers, but in only four North American sparrows ($P < .01$).

Many species of birds having eye-lines show variations in the direction of the eye-line which are apparently adaptive. As a general rule (Fig. 1), bird eye-lines point just below the tip of the bill. Some grebes (Fig. 1D) and mergansers (*Mergus* sp.) have a line slanting downward from the eye to the tip of the opened lower mandible. They may use the lines in sighting on prey before diving or when swimming under water. The birds probably open their bills and look down the eye-line toward their prey. Many sandpipers have eye-lines which point below the bill tip or, in the case of some with decurved bills, to it (Fig. 1E). These birds have medium to very long bills which would probably interfere with direct sighting on the very small invertebrates on which they feed. On the other hand, it is possible that the upward angle of the eye-line in herons is used as a line of sight that helps them correct for light refraction by the water. They strike at the apparent image, but they hit the fish (*6*).

If eye-lines serve as sighting devices it would be expected that smaller members of a group would be more likely to have such lines than larger members because the prey-capturing apparatus of the former is relatively smaller and the prey moves more swiftly in relation to their size. Among the North American frogs depicted in Conant (*8*) and Stebbins (*9*), almost all ranids and hylids longer than 2½ inches lack eye-lines, whereas almost all below this size have them ($P < .01$). Among eastern North American salamanders (*8*) there is a similar trend, smaller species more frequently having eye-lines ($P < .01$); however, such eye-lines are relatively uncommon in salamanders. Do predaceous young have eye-lines more often than the much larger adults? This seems to be the case among some ambystomid salamanders; the lines are present in the young of some species and absent in adults. The same trend occurs in certain lizards (for example, skinks).

The eye-line or groove (or both) in fishes is almost always unicolored and typically leads from the eye to the snout. If predation is broadly defined as feeding on discrete objects and includes biting of seaweed, then eye-lines or grooves occur only in predaceous species of fish, although only a minority of such fish have eye-lines. In general, nonpredatory species such as filter feeders, suckers, and grazers (but not browsers) do not have eye-lines (*10*). The pickerels (*Esox* spp.), which have a teardrop mark (Fig. 1F), typically wait for prey by maintaining steady postures near the water surface where they probably sight down the teardrop on small species of fish in submerged aquatic vegetation beneath them; then they plunge downward and snap up a victim. The pigmented eye grooves of the northern pike (*Esox lucius*), which converge toward the tip of the spatulate snout, may enhance binocular vision and function as aiming sights (*11–13*). These sighting grooves also occur in the American chameleon (*Anolis carolinensis*), and Polyak (*11*) suggests that the black stripes around and in front of the eyes of purple martins (*Progne subis*) resemble these sighting grooves.

Refinement of the accurate strike faculty increases with the probability of missing prey and may reach a zenith in the tree snakes. For example, the vine snake (*Oxybelis aeneus*) has a very precise eye-line in a very narrow groove, which tapers to a point (Fig. 1H). The narrow head in this and other arboreal forms increases binocularity in aiming along such a path; as far as we know, such features are never this precise in terrestrial snakes. Vine snakes probably have the opportunity for comparatively fewer strikes at prey than terrestrial snakes since they are partially anchored to limbs and, more important, living where prey can easily drop away through space. Another species of tree snake (*Dryophis mycterizans*) not only has a pigmented groove but is further specialized for accurate striking by the addition of a keyhole-shaped pupil and a temporal fovea (*14*).

Several functions might be served by eye-lines and grooves exclusive of, or in addition to, aiming at prey. The

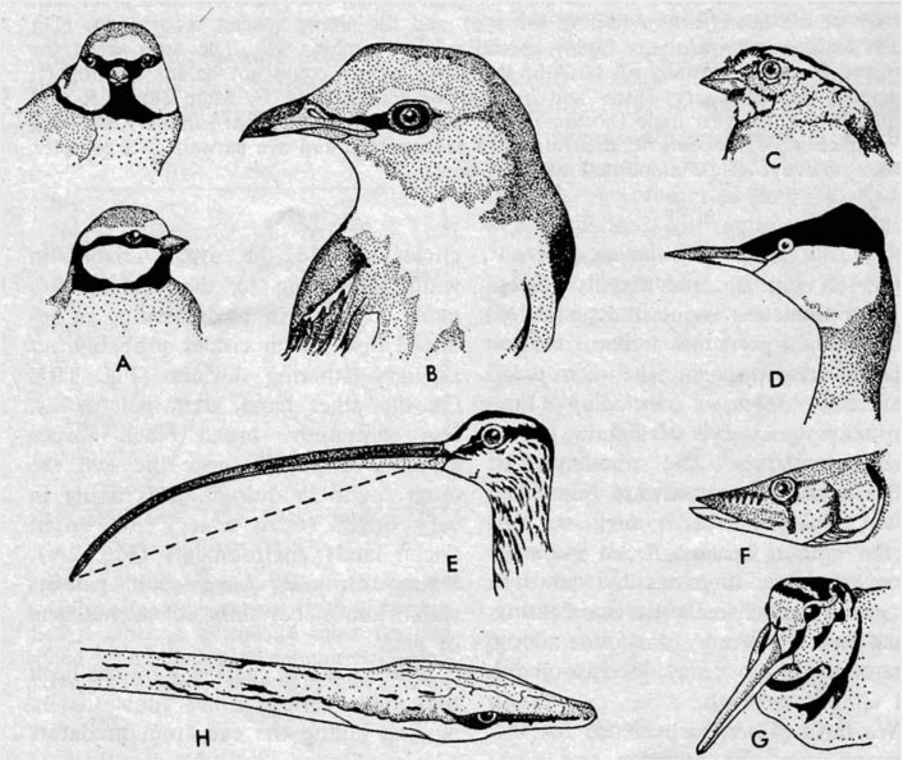

Fig. 1. (A) Simple eye-line of the partially insectivorous blue tit (*Parus caeruleus*). This is the most common type of eye-line in vertebrates. The eye-line in this species is wider than it is in other avian examples, but it was illustrated because it was the only species for which we could find both frontal and lateral photographs. (B) Tracing of close-up photograph showing the combined eye circle and eye-line of the yellow-throated vireo (*Vireo flavifrons*). (C) Raised yellow feathers above the eye-line in a white-throated sparrow (*Zonotrichia albicollis*) which may cast light along the line of sight. (D) Red-necked grebe (*Podiceps griseigena*) showing eye-line slanting downward. Such a line also occurs in some other piscivorous birds. (E) Long-billed curlew (*Numenius americanus*) showing direction of eye-line forward of center of pupil to bill tip. (F) Teardrop mark of the pickerel (*Esox americanus*) associated with downward dashes at prey. (G) Rearward pointed eye-line of the European woodcock (*Scolopax rusticola*), probably used in sighting of predators coming from behind. Associated with 360° vision plus front and back binocularity. (H) Head of the arboreal vine snake (*Oxybelis aeneus*) showing eye-line and groove.

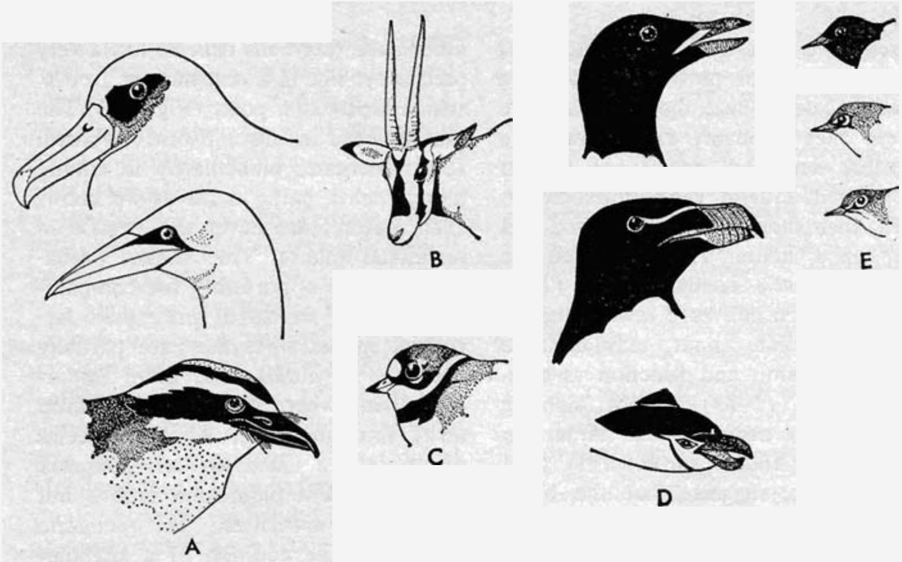

Fig. 2. (A) Facial patches and stripes associated with reduction of glare in very bright habitats. Laysan albatross (*Diomedia immutabilis*) (top), northern gannet (*Morus bassanus*) (middle), and great kiskadee (*Pitangus sulphuratus*) (bottom). (B) In the beisa oryx (*Oryx beisa*) eye-lines may hide eyes and further decrease visibility to potential predators by interrupting the beast's outline; also, the pattern may decrease glare on the line of sight toward clumps of grass in the animal's usually bright open habitat, and the pattern may be important as a social signal. (C) The semipalmated plover (*Charadrius semipalmatus*) has no sighting line; stripes are probably mainly for disruption of the head pattern (hiding the eye) and for aiding species recognition. (D) Alcids and penguins are very highly specialized for catching fish. The lines about the eyes and heads of virtually all birds of these two groups could not be for sighting on prey; they probably serve intra- and interspecific recognition. (E) Male (top), female (middle), and first-year male (bottom) American redstart (*Setophaga ruticilla*), showing an interaction of selection for recognition of sex, species, and age as well as a complex eye-line and eye circle associated with feeding.

Old World bittern (*Botaurus stellaris*) points its bill up and fixedly stares down a subocular stripe in reaction to mammalian predators. The stripes pointing rearward in the European woodcock (*Scolopax rusticola*) (Fig. 1G) may also serve as sighting lines toward predators. The woodcock is well known for its rearward binocular vision. Duke-Elder (*15*) suggests that in the goliath heron (*Ardea goliath*) the eye groove increases binocularity; his photograph reveals the eye sighting along this groove. A dark line along part of this groove may decrease glare, aid aiming, or both.

We have presented evidence for the association of the presence and position of eye-lines as aids in feeding. A line drawn through the center of the eye to the farthest extent of the eye-line usually bisects the eye-line. Further, the eye-line is directed toward the point where prey would be expected. No other function that we know of would require such precise positioning (Fig. 1, A to H), although there may be secondary functions.

Now we consider some facial marking other than eye-lines. Light-colored circles around the eye, variable in width according to the species, are more common in birds feeding in reduced light. Such circles probably act as light-gathering devices (Fig. 1B). On the other hand, dark patches or, less commonly, broad black stripes around, across, or near the eye are often found in diurnal birds living in very bright (open water) and bright (open land) environments (Fig. 2A). Some mammals have such patches which almost certainly act as reducers of glare.

Other types of markings on the head may have various other functions including hiding the eye from predators (*2*) or disrupting the head pattern as camouflage (*1*). In the beisa oryx (*Oryx beisa*) (Fig. 2B) eye-lines may hide eyes and further decrease visibility to potential predators by interrupting the animal's outline; also, glare may be decreased along the black line of sight when the animal feeds in its bright open habitat. Another suggested function of facial markings in this species is mimicry of the antlers, which probably enhances their effect as social signals (*16*). This is a good example of the multiple functions of such eye markings. The head pattern of the short-billed semipalmated plover (*Charadrius semipalmatus*) is probably mainly disruptive (Fig. 2C). Facial marks in the alcids and penguins are probably used only as social signals (Fig. 2D). Eye-lines are absent. Smith (*17*) found that eye circles of certain Arctic gulls, which vary in color in sympatric species, were part of a pattern of contrast of eye and head that forms the basis for species recognition. Certain facial markings in other species have similar functions.

Mutually exclusive demands for facial adaptations may override selective pressures for eye circles and eye-lines, or a compromise may be reached. Figure 2E shows the faces of three plumages of the American redstart (*Setophaga ruticilla*). These birds live in the understory of deciduous forest where there is subdued light. The first-year male and the adult female have complete or nearly complete eye circles which may increase light entering the eye. The black-headed male has no eye marks, very likely because of the demands of age, species, and sexual recognition.

ROBERT W. FICKEN

Department of Zoology, University of Wisconsin–Milwaukee, Milwaukee 53201

PAUL E. MATTHIAE

Field Station, University of Wisconsin–Milwaukee, Route 1, Box 216, Saukville 53080

ROBERT HORWICH

Chicago Zoological Society, Brookfield, Illinois 60513

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