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Raptors Lack Lower-field Myopia

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The presence of lower-field myopia (described in chickens, pigeons, quail and amphibians) allows these animals to keep the ground in focus while performing other visual tasks. A relationship has also been reported between the eye height and the degree of myopia observed. All of the animals reported in the literature to date are ground-foraging species. Using infrared neutralizing video retinoscopy and static photoretinoscopy we found a lower-field myopia to be absent in the barn owl (*Tyto alba*), Swainson's hawk (*Buteo swainsonii*), Cooper's hawk (*Accipiter cooperi*) and American kestrel (*Falco sparverius*). These findings suggest that the presence or absence of a lower-field myopia is a function of the visual ecology of the animal.

Bird Raptor Eye Myopia Optics

The presence of a lower-field myopia has been reported in pigeons (Catania, 1964; Millodot & Blough, 1971; Nye, 1973; Fitzke, Hayes, Hodos, Holden & Low, 1985), chickens (Hodos & Erichsen, 1990; Schaeffel, Farkas & Howland, 1987), quail, sand hill cranes (Hodos & Erichsen, 1990), as well as frogs, toads, and salamanders (Schaeffel *et al.*, 1994). An inverse correlation has been documented between the height of the eye above the ground (between species as well as in the growing chick) and the magnitude of the myopia observed. All of the animals reported to date have been ground-foraging species.

The presence of a lower-field myopia would allow ground-foraging species to keep the ground in focus while performing other visual tasks such as scanning the horizon for possible predators. Raptors have a very different visual ecology than any of the species reported, and the presence of a lower-field myopia may not be as advantageous. The study reported here was undertaken to determine the presence or absence of a lower-field myopia in raptors that differ in size and occupy different ecological niches.

Four barn owls (*Tyto alba*, three juveniles of undetermined sex and one 10-yr-old male), two adult Swainson's hawks (*Buteo swainsonii* of undetermined sex), two female adult American kestrels (*Falco sparverius*), and one Cooper's hawk (*Accipiter cooperii* of undetermined sex) were examined. All animals were treated in accordance with the ARVO resolution on the use of animals in eye research. Animals were gently restrained by their feet for brief periods of time. All measurements were made in a single session which took place in a darkened tool shed of the University of California—Davis Raptor Center.

Refractive state was determined using infrared neutralizing videoretinoscopy (Schaeffel, Farkas & Howland, 1987; Mutti, Zadnik, Johnson, Howland & Murphy, 1992) and static photoretinoscopy (Howland, 1985). The entire session was recorded on videotape. Neutralizing videoretinoscopy employs an infrared light source in close proximity to the camera lens and provides a continuous record of refractive state along one (here vertical) meridian. The superior aspect of the pupil becomes illuminated when the eye is hyperopically focused relative to the camera plane, while the inferior aspect of the pupil becomes illuminated when the eye is myopically focused relative to the camera. When focused at the camera plane the entire pupil becomes evenly illuminated. After determining the sign of defocus, corrective lenses of increasing power (convex or concave) are placed in front of the subject's eye until the eye is clearly focused on the camera plane.

The resting refractive state of all animals was determined along the visual axis using this technique with the camera placed at a distance of 1 m from the animal. We made noises and waved fingers and small objects to attract the attention of the birds to the camera. Most of our resting refractions on hawks were along their lateral visual axes (central fovea) as indicated by the relative centration of the Purkinje reflex in the pupil. In the owl refractions the Purkinje images were generally symmetrically disposed in the two eyes.

In addition to neutralizing retinoscopy, an analysis of resting refraction by static retinoscopy on stopped frames of the video tape was also performed. In this technique the refraction is determined from the formula:

$$\text{defocus} = E/(p \cdot a \cdot d)$$

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TABLE 1. Body lengths, resting refractions, estimated eye heights, myopia required to focus ground at 45 deg in front of bird, and refractions at edge of lower visual field

Bird	Body length (cm)*	Resting refraction relative to ∞ (D)	n†	SE (D)	Estimated eye height (cm)	Required myopia at 45 deg (D)	Lower visual field (D)	n†	SE (D)
American kestrel	23–30	−0.1	3 (2)	0.1	13	5.5	0.7	5 (2)	0.1
Barn owl	46	−0.3	5 (4)	0.2	23	3.1	−0.3	9 (4)	0.1
Swainson's hawk	45–56	−0.2	5 (2)	0.1	25	2.8	−0.6	4 (2)	0.1
Cooper's hawk	35–51	0.3	6 (1)	0.4	22	3.2	−0.3	9 (1)	0.1

*All body lengths from Bull and Farrand (1977).

†Number of measurements (No. of animals in parentheses). Data from individual animals did not differ significantly and were lumped together to compute refractions.

where E is the eccentricity of the light source relative to the camera aperture, p is the pupil diameter, a is the camera to cornea distance and d is the fraction of the pupil that is dark (Howland, 1985). While the two techniques give good agreement in near emmetropic eyes, neutralizing photoretinoscopy is to be preferred for the measurement of large refractive errors due to the non-linear sensitivity of static photoretinoscopy.

To determine the refractive state of the superior retina (the lower visual field), the infrared photoretinoscope was progressively moved below the visual axis until the retinoscopic reflex was no longer evident, and the

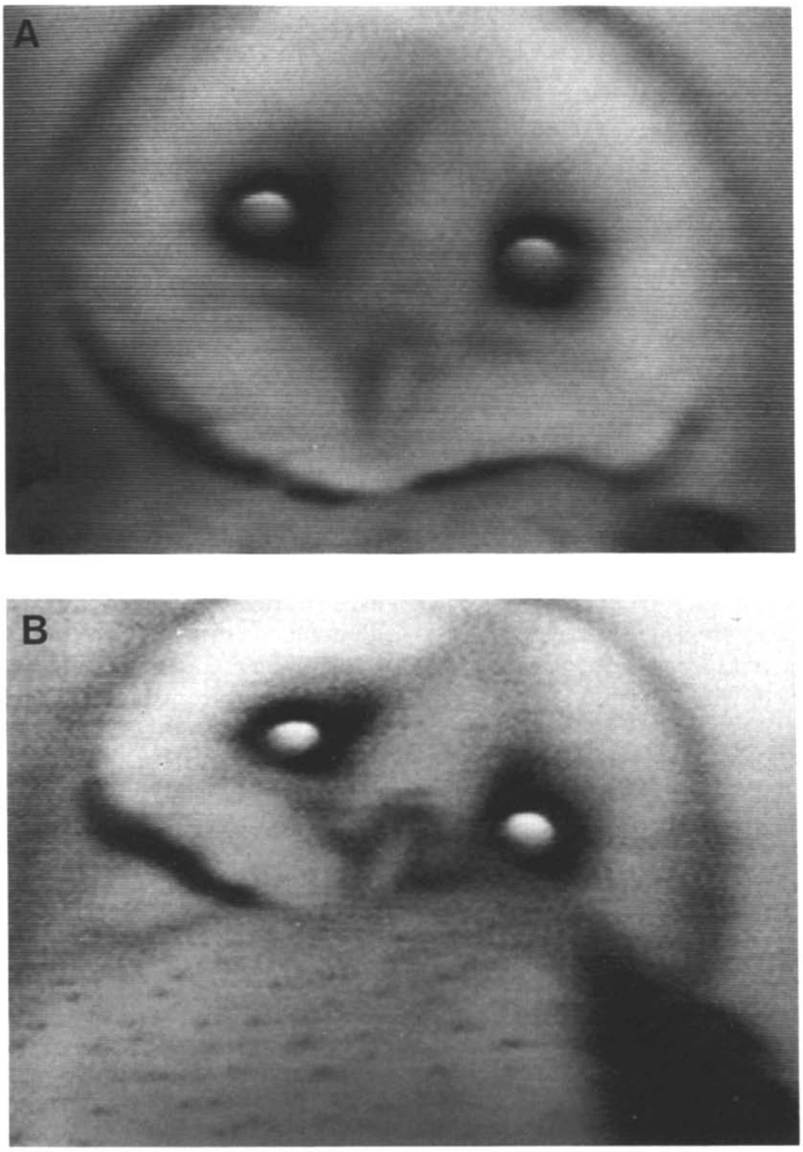

FIGURE 1. Refractive state of the axial region (A) and lower visual field (B) of the barn owl eye as determined by infrared videoretinoscopy. In both images the retinoscopic reflex fills the superior portion of the pupil, indicating a hyperopic focus relative to the camera plane (placed 1 m from the bird). All raptors examined had similar refractions, lacking a lower-field myopia.

measurement made at the margin of the superior retina representing the lowest extent of the visual field.

The amount of lower-field myopia needed for each bird to focus the ground 45 deg in front of itself, were it standing on the ground, is calculated in Table 1 under the assumption that the height of the eyes off of the ground is approximately one-half of the beak to tail distance. This assumption was tested on several stuffed hawks and found to be approximately correct. The exact extent of the visual fields of the birds in the vertical dimension is unknown, but in all cases probably exceeds 45 deg below the horizontal. Thus the values represented in Table 1 probably represent minimal estimates of the required lower-field myopia.

All animals examined were found to have a resting refractive state that was hyperopic and within 1 D of emmetropia. Data from static photoretinoscopy are given in Table 1. Accommodative excursions were noted ranging from 5–6 D for the barn owls to exceeding 12 D for the American kestrels. In these situations a myopic reflex could be observed through a -5 D, or -14 D lens respectively, indicating that the animal's accommodation exceeded the magnitude of the effective power of the lens. (The effective power of a -14 D lens 1 cm from the cornea is approx. 12 D.) A lower-field myopia was not observed in any of the animals examined (Fig. 1), all of the birds exhibited a hyperopic crescent at the extremities of their lower visual fields indicating that they were hyperopically focused relative to the camera, and thus either hyperopic or within 1 D of emmetropia. Refractive estimates by static retinoscopy of the relative hyperopia seen at the field margins is given in Table 1. From a comparison of the measurements made on the visual axes and field margins it may be seen that the kestrel is slightly but significantly ($P < 0.01$, paired, two-tailed t-test) hyperopic in the lower visual field, there is no significance between axes and field margins in the barn owls and Cooper's hawk, and the field margin is slightly but significantly ($P < 0.004$) more myopic in Swainson's hawk. The amount of the difference in refraction between axis and field edge in the Swainson's hawk is approximately one-fifth of that required by the lower-field myopia hypothesis.

The presence of a lower-field myopia is thought to be advantageous for ground-foraging, animals allowing them to keep the ground in focus while occupied with other visual tasks. Such an adaptation is clearly beneficial for prey species that can scan the sky for predators while maintaining the ground in focus during foraging. Our findings suggest that selective pressures for the development of a lower myopic field does not exist in predator species that must pursue and capture highly mobile prey.

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