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CONE PIGMENT OF THE GREAT HORNED OWL[1]

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Key words: Cone pigment; vision; Great Horned Owl.

In most diurnal species cone photoreceptors are abundant and, typically, heterogeneously distributed across the retina. These receptors provide the signals that allow for maximum visual acuity and color vision. Cones are also present in the retinas of many nocturnal species where they are usually less prevalent and more homogeneously distributed across the retina (Walls 1942). The function of cones in nocturnal retinas, and the nature of the vision they subserve, have long been topics for debate.

Owls are among the most resolutely nocturnal of the birds, yet they too have cones. Throughout the retina of the Great Horned Owl (*Bubo virginianus*), for instance, about 7 to 8% of all photoreceptors are cones and over the expanse of this retina, thus, there are many thousands of such receptors (Fite 1973). From behavioral measurements of visual acuity in this bird Fite (1973) was led to suggest that the photopigment contained in the cones might be identical to that found in the rods. The photopigment in the latter has been extracted from the eye and measured to have an absorption peak at 503 nm (Crescitelli 1958). If owl cones do contain the same photopigment as owl rods, it would represent an arrangement that has only been infrequently claimed for other species (Jacobs 1981). That possibility prompted the measurement of cone pigment in the Great Horned Owl reported here.

Historically, it has been difficult to measure cone pigments. An in situ, noninvasive technique recently used with success on this problem involves the recording of a gross electrical potential (the electroretinogram—ERG) from a corneal electrode when the eye is stimulated with flickering lights (Neitz and Jacobs 1984, Jacobs et al. 1985). The use of rapid flicker and bright lights make it possible to obviate any contribution from rod photoreceptors and typical short wavelength cones to the recorded signal. This technique has the additional advantages of very high reliability and sensitivity, the latter allowing one to easily detect signals from cones in eyes that contain relatively small numbers of such receptors.

The ERG was recorded from a corneal contact lens electrode placed on the eye of an anesthetized Great Horned Owl. To measure the spectral sensitivity of the cones in that eye a flicker photometric procedure was used in which a 53° circular area in the center of the retina was stimulated with an alternating train of light flashes (flicker rate = 50 Hz) from an achromatic reference light and a monochromatic test light (this procedure is described in detail elsewhere: Neitz and Jacobs 1984, Jacobs et al. 1985). The experimenter then adjusted the radiance of the test light over repeated presentations until the potential produced by that light just nulled the (inverted) response produced by the reference light. Equations of this sort were made for monochromatic lights spanning the spectrum from 460 to 640 nm in steps of 20 nm.

The eye of the Great Horned Owl produced robust ERG responses under these strongly photopic test conditions. The results of the formal measurements are summarized in Figure 1. The data points there are the inverse of the radiance of the test light at the equation, each being expressed in quantal terms. The solid line drawn through each data set is a theoretical function. These functions, wavelength-dependent visual pig-

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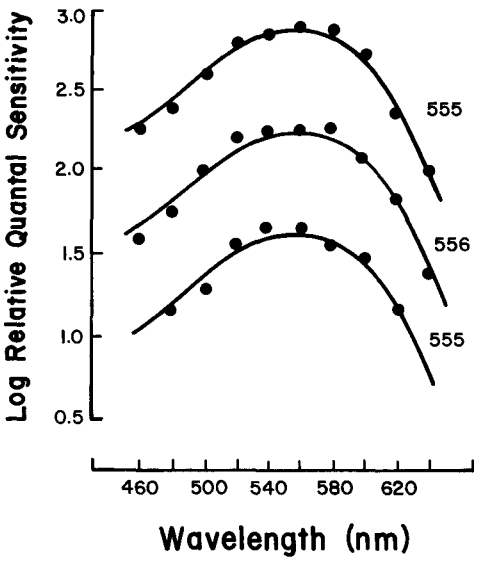

FIGURE 1. Flicker photometric spectral sensitivity functions for the Great Horned Owl. Solid circles are sensitivity values obtained by equating the effectiveness of monochromatic test lights and an achromatic reference light. The lines are best fitting visual pigment nomograms, the spectral peak of which is indicated on each function. The data at the top and middle were obtained using a reference light having a corneal radiance of 0.11 mW; the results plotted at the bottom were obtained with a 0.22 mW reference light. The three data sets are arbitrarily positioned on the sensitivity axis.

ment nomograms, have been shown to accurately describe the absorption spectra for a wide variety of photopigments (Ebrey and Honig 1977). Because the spectral shapes of these curves vary lawfully as they are slid along the wavelength axis, it is possible to specify them by a single number, their peak wavelengths (λ_{max}). A computer routine was used to determine which of these theoretical functions best fit the data array. The λ_{max} value of the best fitting function (determined to the nearest nm) is indicated on the functions. The two functions at the top of Figure 1 were independent measurements obtained under identical stimulus conditions. It may be noted that (a) these pigment curves provide close fits to the sensitivity measurements, and (b) the repeatability of the measurement is high. These close fits strongly suggest that under these conditions of examination only a single cone pigment (λ_{max} = 555–556 nm) contributes to the retinal response of the Great Horned Owl. The bottom function of Figure 1 was obtained using a reference light of considerably higher radiance, but the spectral peak value so obtained is the same as that for less intense lights.

We have previously shown that the intersubject variability in measurement of cone pigments with the ERG flicker photometric technique is quite small; the standard deviations of λ_{max} values across multiple subjects amounting to no more than about 1.5 nm (Jacobs et al. 1985). Thus although the present results were obtained from only a single bird, they can be expected to fairly represent this species. As Figure 1 makes clear, there is a cone pigment in the Great Horned Owl that absorbs maximally at about 555 nm and so the early conjecture that rods and all of the cones contain the same photopigment in this species is not correct. Using microspectrophotometry Bowmaker and Martin (1976) have detected the presence of three cone pigments in the Tawny Owl, *Strix aluco*. Most cones contained a pigment having λ_{max} at about 555 nm, but very small numbers of cones were found to have peak values at 463 nm and 503 nm. The former pigment appears identical to that we have found. If either of the 463 or 503 nm cone pigments are present in the eye of the Great Horned Owl, or indeed any other cone pigments, they appear to make no discernable contribution to retinal signals recorded under photopic test conditions. In *S. aluco* most of the cones contain a pale yellow oil droplet (Bowmaker and Martin 1976). The absorption spectrum of this droplet is such that its presence shifts the measured peak of the 555 nm photopigment by only 1 nm. Whether the Great Horned Owl has a similar oil droplet is not known.

We conclude that the retina of the Great Horned Owl is similar to that of other nocturnal species in having a small population of cones that contain a photopigment the peak of which is shifted toward the long wavelengths relative to that of the more prevalent rod pigment. The utility of such an arrangement in this species can only be guessed. The 555 nm cone might provide, either in conjunction with the rods or other cone types whose signals are not seen in the present measurements, the basis for a weak color vision capacity of the sort claimed for the Tawny Owl (Martin 1974). Whether that occurs or not, this pigment broadens the spectral window through which visual information may be gained; this might be particularly useful during the occasional daylight hunting forays of this species (Austing and Holt 1966).

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AMINO ACID COMPOSITION OF THE CALAMUS, RACHIS, AND BARBS OF WHITE-CROWNED SPARROW FEATHERS[1]

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Key words: Feathers; plumage; amino acids; cystine; molt; White-crowned Sparrow; Zonotrichia leucophrys gambelii.

The amino acid composition of the plumage of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) in general resembles that of plumage, feathers, or feather parts of the handful of other species for which data are available (Schroeder and Kay 1955, Harrap and Woods 1967, Fisher et al. 1981, Nitsan et al. 1981), but includes substantially more cystine (Murphy and King 1982). Cystine concentration (μmoles/g dry mass) in White-crowned Sparrow plumage averaged 894, compared with averages of 756 in feather parts of domestic chickens, geese, ducks, and turkeys, 753 in the Silver Gull (*Larus novaehollandiae*), and 480 in the Emu (*Dromaius novaehollandiae*). The samples, however, consisted of the homogenized entire plumage in the case of the sparrow, but of feather parts (calamus, rachis, barbs) in the case of the other species. To provide a more reliable basis for the comparison of the amino acid composition of feather parts between White-crowned Sparrows and other species we undertook the analysis reported herein.

MATERIALS AND METHODS

We washed (Harrap and Woods 1967) separate samples of primary remiges obtained from each of five *Z. l. gambelii* that had recently completed the postnuptial molt. We cut the calamus from the rachis at the superior umbilicus and trimmed the vanes (barbs) from the rachis. We were not able to remove the medulla from the calamus and rachis, although other investigators using larger feathers have sometimes done so (e.g., Schroeder and Kay 1955, Harrap and Woods 1964).

We measured the nitrogen content of duplicate desiccator-dried samples of pooled feather parts by the micro-Kjeldahl method (Horwitz 1980). To prepare subsamples for amino acid analysis we hydrolyzed ca. 10-mg portions of each feather part from each bird in 6 *N* HCl for 24 hr, vacuum-dried the hydrolysates, redissolved them in sodium citrate buffer (pH 2.2), and analyzed the solutions (Beckman model 121 MB) in the Bioanalytical Laboratory, Washington State University. The concentration of cyst(e)ine was measured in parallel as cysteic acid after oxidation with performic acid (Schram et al. 1954), and is reported in this paper as cystine/2.

Finally, we weighed samples of calami, rachises, and vanes (barbs) from White-crowned Sparrow remiges and rectrices (ca. 100 mg, 10 to 12 feathers each), and dorsal and ventral contour feathers (ca. 20 to 30 mg, 20 to 30 feathers each). Combined with estimates of the proportions of remiges, rectrices, and body feathers in the total plumage (Murphy and King 1984), these data enabled us to estimate the amino acid composition of the entire plumage from that of feather parts and to assess the differentiation of feather parts with respect to amino acid composition.

TABLE 1. Percentages of calamus, rachis, and barbs in feather classes and weighted percentages for the entire plumage of White-crowned Sparrows.

Class of feathers	% of plumage[a]	% of feather in		
		Calamus	Rachis	Barbs
Body	77	2.5	17.8	79.7
Rectrices	8	11.3	43.4	45.3
Remiges	15	18.3	50.9	30.8
Weighted % parts[b]:		5.57	24.82	69.61
Proportionate parts:		1.00	4.46	12.50

[a] Murphy and King (1984).
[b] For each part (calamus, rachis, barbs), weighted % part = $\sum$[% part × (% plumage/100)].

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