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Electrophysiological measurements of spectral mechanisms in the retinas of two cervids: white-tailed deer (*Odocoileus virginianus*) and fallow deer (*Dama dama*)

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Abstract. Electroretinogram (ERG) flicker photometry was used to study the spectral mechanisms in the retinas of white-tailed deer (*Odocoileus virginianus*) and fallow deer (*Dama dama*). In addition to having a rod pigment with maximum sensitivity (λ_{max}) of about 497 nm, both species appear to have two classes of photopic receptors. They share in common a short-wavelength-sensitive cone mechanism having λ_{max} in the region of 450–460 nm. Each also has a cone having peak sensitivity in the middle wavelengths, but these differ slightly for the two species. In white-tailed deer the λ_{max} of this cone is about 537 nm; for the fallow deer the average λ_{max} value for this mechanism was 542 nm. Deer resemble other ungulates and many other types of mammal in having two classes of cone pigment and, thus, the requisite retinal basis for dichromatic color vision.

Key words: Cone photopigments – Ungulate – Deer – Electroretinogram – Dichromacy – *Odocoileus virginianus* – *Dama dama*

Introduction

Many large mammals, including most ungulates, show arrhythmic patterns of daily activity, i. e., they may be equally active by day or by night (Nowak 1991). Fifty years ago, Walls (1942) identified several features of the eyes of these animals that he argued were appropriate to support behavior of this kind. He noted, for instance, that such eyes typically contain abundant populations of rods. These are often found in conjunction with a retinal tapetum and the presence of both of these suggest an eye that is adapted to allow high retinal sensitivity. At the same time, the large eyes of these mammals provide an expanded retinal image. This would be expected to allow reasonable visual resolution under conditions of bright illumination, even if the retina contains only a relatively sparse array of cones. From this combination of adaptations he concluded that "The vision of these mammals by night and by day is good enough so that they depend on it" (Walls 1942, p. 145).

Despite their ubiquity, and their importance to our own species, there has been surprisingly little study of either the eyes or the vision of ungulates (Jacobs 1993). Members of the family Cervidae, the deer, are typical in this regard. Like other ungulates deer show arrhythmic patterns of activity (Marchinton and Hirth 1984; Putnam 1988). There is certainly no dearth of opinion about the role of vision in deer. Perhaps not surprisingly, those opinions are often quite contradictory. For example, with respect to the role that vision plays in the behavior of deer, it has been claimed both that "Quality of light is of no import to the deer themselves, since they are not essentially visual animals" (Putnam 1988, p. 58), and that "Eyesight plays an important sensory role" (Sauer 1984, p.78). Similarly, it has been alternatively suggested that the deer "is not entirely colour blind" (Putnam 1988, p. 5) and that, "These animals are completely color blind" (Dalrymple 1975, p. 63). Although opinion is abundant, facts are harder to come by. Early spectrophotometric measurements of photopigments in the timor deer (*Cervus timorensis*) suggested the peak of a presumed rod photopigment to be about 498 nm (Knowles and Dartnall 1977). Witzel et al. (1978) reported anatomical results that demonstrate the presence of both rods and cones in the retina of the white-tailed deer. At the level of examination by light microscopy, the cones appear similar in structure to those of other mammals. Although no systematic counts were made, it was noted that in the central regions of the retina, the density of cones reached about 10,000/mm^2. [From a comparative point of view this number seems possibly too low. For instance, a common carnivore – the domestic cat – has a cone density of about 25,000/mm^2 in the area centralis (Steinberg et al. 1973); another ungulate, the domestic pig, is reported as having an "average cone density" of about 19,000/mm^2 (Hao et

Abbreviations: ERG, electroretinogram; LWS, long wavelength sensitive; MWS, middle wavelength sensitive; SWS, short wavelength sensitive

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al. 1992).] Witzel and colleagues (1978) also recorded the electroretinogram (ERG) in response to single flashes of light. They reported the appearance of two, temporally-separated components in the b-wave of the ERG that was recorded from a light-adapted eye. These components varied in relative prominence as a function of the wavelength of the stimulus light suggesting that they represented the separate contributions of rod and cone signals.

There have been at least 3 behavioral investigations of basic visual capacities of white-tailed deer. Using an operant discrimination paradigm to assess spectral sensitivity, Zacks (1985) concluded that the peak of the photopic spectral sensitivity function for the deer is at about 545 nm. Two other experiments involved similar attempts to show that deer could be trained to discriminate between stimuli having different spectral energy characteristics under conditions believed to define the presence of color vision (Zacks and Budde 1983; Smith et al. 1989). Both yielded positive results. Further discussion of these studies is offered below.

Because all features of vision are limited by photon absorption, one first step toward better understanding vision in any species is to determine the photopigment complement. Over the past several years we have developed an electrophysiological technique involving the ERG that is useful for determining the spectral mechanisms present in any retina (Neitz and Jacobs 1984; Jacobs and Neitz 1987). The ERG technique has been used to study the spectral mechanisms in the retinas of two of the most common species of deer, white-tailed deer (*Odocoileus virginianus*) and fallow deer (*Dama dama*). Although the systematics of Cervidae have not been completely agreed on, there are in excess of 3 dozen species of deer distributed among some 4 or 5 subfamilies (Baker 1984; Corbet and Hall 1991; Putnam 1988). White-tailed and fallow deer are representatives of two of these subfamilies.

Methods

Subjects. The subjects were adult animals drawn from two captive herds; the white-tailed deer were from the University of Georgia School of Forest Resources, Athens, Georgia and the fallow deer were from Hackett Farms Inc., Rome, Georgia. Recordings were obtained from 8 white-tailed deer (6 females, 2 males) and from 6 female fallow deer.

Apparatus. Details of the apparatus and general procedures have been previously reported (Neitz and Jacobs 1984; Jacobs and Neitz 1987). We recorded the fast-flicker ERG using an adaptation of a flicker photometry paradigm in which ERG signals are substituted for psychophysical responses. The ERGs were differentially recorded from the eyes of deer with a bipolar contact-lens electrode of the Burian-Allen design. The stimuli were square-wave modulated lights delivered as a train that originated from a three-beam optical system. These stimuli were presented to the eye in Maxwellian view (57° retinal subtense). In the train, light derived from a Bausch and Lomb high-intensity monochromator (tungsten-halide lamp, half-energy passband of 10 nm) was used as the test light. Interleaved in the train were lights derived from a second tungsten-halide lamp. These served as the reference light and were thus fixed in intensity and spectral content for each set of measurements by inserting appropriate neutral-density step filters and/or interference filters into the reference beam. The duty cycle of the stimulus train was 25% with successive stimuli from the test and reference lights separated by equal-duration intervals that contained neither test nor reference light. Control of stimulus presentation was accomplished through the use of high-speed electromagnetic shutters (Uniblitz, Vincent Associates) that were located in the optical pathways of each of the light sources. A third beam, also from a tungsten-halide lamp, was used to provide additional adaptation of the eye as required for particular experiments. All three lamps were underrun at 11 V from a regulated DC power supply. The intensity of the test light was varied by adjusting the position of a circular neutral-density wedge. This adjustment was done iteratively over stimulus presentations until the response elicited by the test light matched that produced by the reference stimulus. The dependent measure was the radiance of the test light required to accomplish this equation. The ERGs generated by the test and reference light were electronically compared such that the signals generated by the two lights cancel at the point where the two stimuli are equally effective.

Procedure. Deer were sedated using an IM injected mixture of xylazine hydrochloride and ketamine hydrochloride as described by Mech et al. (1985). The pupil of one eye was dilated by topical application of atropine sulfate (0.04%) and phenylephredine HCl and the cornea was anesthetized by topical application of proparacaine hydrochloride (0.5%). The animal was positioned for recording such that the head was firmly supported in an upright position. The contact-lens electrode was placed on the eye and a ground electrode was placed against the inside of the cheek. Except for one experiment involving conditions of dark adaptation, all measurements were made in a room illuminated by overhead fluorescent lights. The recording sessions themselves lasted for 45 to 75 min. Anesthesia was reversed using Yohimbine hydrochloride (Mech et al. 1985). Subsequent recovery of each animal was uneventful.

For each combination of test light, adaptation light, and pulse rate, flicker photometric equations were determined by averaging the responses to the last 50 cycles of a total of 70 stimulus cycles. The equations were made iteratively with the neutral-density wedge being adjusted repeatedly until the best cancellation of the two signals was achieved. The wedge values required for cancellation were recorded to the nearest 0.01 log unit. For each stimulus condition the equations were made at least twice and these separate values were averaged together. Several different experiments were attempted; the details of these are described below as they become appropriate.

Results

Scotopic spectral sensitivity

Recordings were obtained from two female white-tailed deer under test conditions appropriate for eliciting scotopic signals. The measurements were made in a darkened room. The stimulus rate was 8 Hz and a dim, achromatic reference light was used (color temperature $=2250$ K; corneal radiance $= 0.48\ \mu W/cm^2$). For one animal measurements were made at successive 10 nm steps from 430 to 590 nm. The second animal was tested at 7 separate wavelengths lying between 440 and 590 nm.

The spectral sensitivity values obtained from the two subjects are shown in Fig. 1. Those values are quantally-based and express spectral sensitivity at the level of the cornea. The array of results from the two animals were shifted vertically so that the two had the same average sensitivity. That accomplished, the relative sensitivity functions for the two are virtually identical. The solid

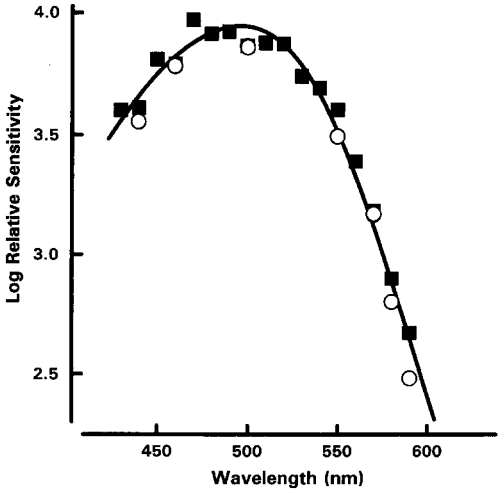

Fig. 1. Scotopic spectral sensitivity of the white-tailed deer. Each individual symbol shows sensitivity as determined by ERG flicker photometry for the dark-adapted eye. The *circles* and *squares* represent data obtained from two separate animals. The data sets for the two were slid on the ordinate so as to have equal average sensitivity. The *continuous line* is that for a visual pigment absorption curve determined as described in the text. The λ_{max} value for the curve is 497 nm; the goodness of fit (the least mean difference squared between the theoretical absorption curve and the data points) is 2.81×10^{-3} log unit

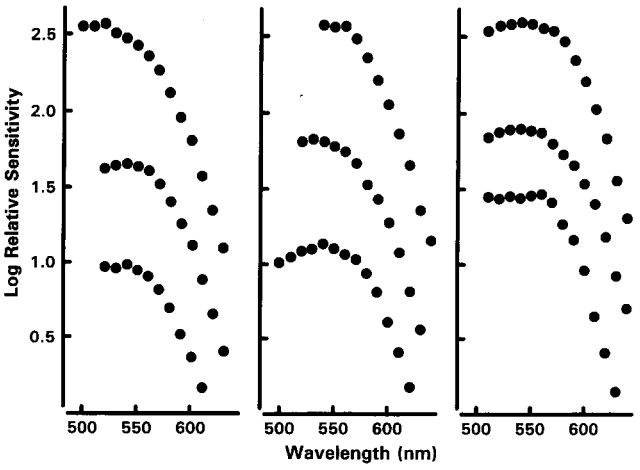

Fig. 2. ERG flicker (50 Hz) photometric spectral sensitivity functions obtained from the light-adapted eyes of 6 white-tailed deer (*left and middle panel*) and 3 fallow deer (*right panel*). Each point is a quantally-based sensitivity value. The data for individual animals are arbitrarily spaced along the ordinate

curve in Fig. 1 is a best-fit photopigment absorption curve. To generate this fit, a standard photopigment absorption curve (Ebrey and Honig 1977) was shifted in successive steps of 1 nm along a log wavenumber axis (Baylor et al. 1987) until the best least-squares fit between the data array and the pigment absorption curve was obtained. As can be seen, the fit is good for a peak value (λ_{max}) of 497 nm.

Photopic spectral sensitivity: signals from MWS/LWS cones

Robust electrical signals were recorded from both white-tailed and fallow deer under test conditions that favor the contribution of cone signals to the ERG (i. e., higher stimulus rates, bright reference lights, presence of additional adaptation lights). The impression thus gained was that these ungulates have the retinal basis for significant photopic visual capacities. Spectral sensitivity measurements were made under conditions intended to characterize the properties of any cones selectively sensitive to middle and long test wavelengths (MWS/LWS cones). In all cases the stimulus rate was 50 Hz. The nature of the reference light and the presence of additional adaptation varied somewhat across subjects. For the fallow deer the reference light was achromatic (color temperature = 2600 K; corneal radiance = 37.5 $\mu W/cm^2$) and measurements were made in the presence of a steady, additional adaptation light. This light was produced by placing an interference filter (Optical Thin Films; peak wavelength = 460 nm with half-energy bandpass of 10 nm; corneal radiance = 181.5 $\mu W/cm^2$) in the third channel of the optical system. For the white-tailed deer, measurements also were made using the supplemental 460 nm adaptation. For these subjects we used a long-wavelength reference light that was produced by placing a high-pass filter in the reference beam (50% transmission at 580 nm; corneal radiance = 226 $\mu W/cm^2$). Both short-wavelength adaptation and long-wavelength reference lights were employed to try to achieve the same end – to minimize any residual contribution of signals from mechanisms maximally sensitive in the short wavelengths, i. e., either short-wavelength (SWS) cones or rods.

The spectral sensitivity values obtained from 6 white-tailed deer and 3 fallow deer are given in Fig. 2. Because the recording time on these animals was limited, and because the long side of these spectral sensitivity functions are generally most crucial for accurately specifying the spectral positioning of the underlying mechanisms, measurements were made from long wavelengths (650–640 nm) down only to wavelengths where sensitivity appeared to decline again (500–530 nm). With that restriction, the photopic spectral sensitivity functions of all these deer appear generally similar with sensitivity rising rapidly from the long wavelengths to achieve a peak in the vicinity of 530–550 nm.

Photopic spectral sensitivity: signals from SWS cones

We also searched for an indication of the presence of SWS cones in the retinas of deer. The stimulus conditions were those found previously useful for accessing SWS cone signals (Neitz and Jacobs 1989; Jacobs et al. 1993). These included a slower pulse rate (25 Hz), a short-wavelength reference light (460 nm, corneal radiance = 7.9 $\mu W/cm^2$) and intense, long-wavelength adaptation (produced through the use of a high-pass filter having 50% transmission at 580 nm that yielded a corneal radi-

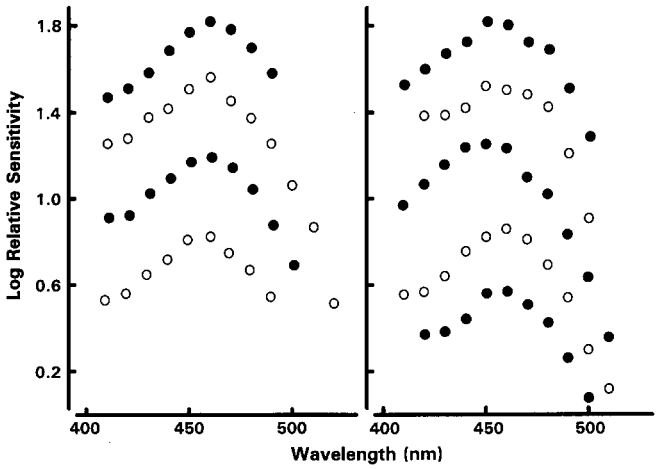

Fig. 3. Spectral sensitivity of a short-wavelength sensitive mechanism in 4 white-tailed deer (*left panel*) and 5 fallow deer (*right*). These sensitivity values were obtained under stimulus conditions intended to advantage contributions to the ERG of any SWS mechanism (see text). Data for individual animals are arbitrarily spaced along the sensitivity axis and the symbols for the data points have been varied for ease of viewing

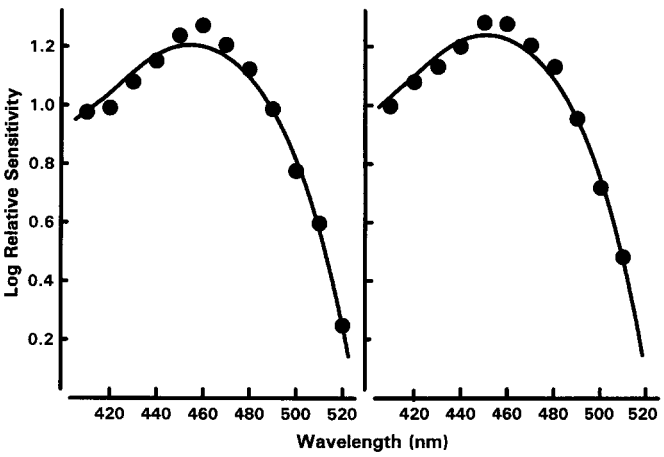

Fig. 4. Average spectral sensitivity functions for the SWS cone mechanisms in 4 white-tailed deer (*left panel*) and 5 fallow deer (*right panel*). Prior to averaging the curves for functions for individual animals were shifted vertically so that all had the same average sensitivity. The *continuous lines* are the visual pigment absorption curves determined to provide the best fit to each data array. For the white-tailed deer the λ_{max} of the best-fitting curve is 457 nm (goodness of fit – 1.18×10^{-3} log unit); for the fallow deer the corresponding peak is 453 nm (goodness of fit – 1.03×10^{-3} log unit)

ance of 7400 $\mu W/cm^2$). With these test conditions a spectral mechanism having maximum sensitivity in the short wavelengths was readily apparent. Spectral sensitivity determinations were made at 10 nm steps; depending on the sensitivity of the individual subject the range tested extended from 410 or 420 nm to about 500 nm. Beyond that point, sensitivity dropped below the level at which it was possible to make measurements. Results from 4 white-tailed deer and 5 fallow deer are shown in Fig. 3. For all of these animals the peak sensitivity of a photopic SWS mechanism is at about 450 to 460 nm.

Finally, because it has recently been reported that some mammalian eyes have receptors with maximum sensitivity to ultraviolet (UV) lights (Jacobs et al. 1991), we also tested two deer to see if a recordable electrical signal could be generated in response to 25 Hz stimulation with UV test light (produced by placing a Rolyn Optics UG-11 3-nm filter that has peak transmission at 325 nm with a half-energy bandpass of 80 nm) having a corneal radiance of 30.2 $\mu W/cm^2$. No substantial response to UV stimulation was detected. We note that under this exact set of stimulus conditions large responses can be recorded from those rodents whose retinas do contain UV receptors (Jacobs et al. 1991).

Discussion

Spectral sensitivity of deer photoreceptors

There are two potential limitations inherent in attempts to derive estimates of the spectral sensitivity of the photoreceptors of these deer from the spectral sensitivity measurements reported above. First, we have no direct measurements of absorption by the ocular media nor any measurements of tapetal reflectivity in the eyes of deer. To the extent that either or both of these features are spectrally selective, they can alter the relationship between the ERG spectral sensitivity functions and the spectral absorption characteristics of the underlying photopigments. Measurements of the scotopic spectral sensitivity function (Fig. 1) suggest that neither of these factors greatly distort this relationship. The photopigment absorption curve closely fits the scotopic spectral sensitivity function over the entire spectral range of the measurements (430–590 nm), and the peak value (497 nm) of this absorption curve is not far from the peak value for the rhodopsin of the timor deer (498 nm) as measured spectrophotometrically in pigment extracts by Knowles and Dartnall (1977).

A second potential limitation is that more than one photopigment class might contribute to the recorded spectral sensitivity functions. By the nature of the stimulus and adaptation lights, and as seen from the consequent complete loss of long wavelength sensitivity, it seems unlikely that this would be true for the attempt to measure an SWS cone mechanism (Fig. 3). It is less easy to be sure that only one pigment class contributed to the measurement of MWS/LWS spectral sensitivity. In past efforts at measuring such pigments we have employed a comparison of two conditions of intense, long-wavelength adaptation to test for spectral univariance (e. g., Jacobs and Neitz 1987). It was not possible to employ that procedure in the present experiments. However, we did measure partial MWS/LWS spectral sensitivity functions for several deer under two conditions where the only change was that the long-wavelength reference light was 0.6 log unit more intense in one case than in the other. If there were more than one spectral mechanism sensitive over the tested wavelengths (in the range from 540 to 640 nm) we expected to see a differential adaptation effect in these two cases. To the contrary, the two functions never showed any systematic differences in

their spectral shapes. Although this is not the most stringent test possible, it does suggest that the MWS/LWS measurements made over this part of the spectrum represent contributions from only a single class of photoreceptor.

Given these possible limitations, photopigment absorption curves were fit to both SWS and MWS spectral sensitivity functions. The average functions for the SWS measurements are shown for white-tailed and fallow deer in Fig. 4. In each case the best-fit curve reasonably accounts for the data sets with λ_{max} of 455 nm (white-tailed deer) and 453 nm (fallow deer) respectively. Photopigment absorption curves were individually fit for each subject. The best peak estimates were not systematically different for the two species (white-tailed deer: mean = 456 nm, SD = 2.6 nm; fallow deer: mean = 453.6 nm, SD = 2.6 nm).

It is perhaps noteworthy that the photopigment absorption curves fit the measured sensitivity of the SWS mechanism reasonably down to 410 nm[1]. Most species that have any substantial lens density do show significant absorption at this point, e. g., at this wavelength the human ocular lens has an average optical density of about 0.8 (Wyszecki and Stiles 1982). The fact that without lens corrections the SWS spectral sensitivity curves follow photopigment absorption curves suggests that the lens of the deer eye does not have much spectrally-selective absorption, at least for those wavelengths 410 nm and longer.

Since the long-wavelength slope of the MWS spectral sensitivity functions could be used to most accurately characterize the spectral position of the underlying photopigment (see above), those sensitivity values lying in the range from 580 to 650 nm were fit individually to photopigment absorption curves. These functions are shown for 6 white-tailed deer and 6 fallow deer in Fig. 5. In each case the λ_{max} of the best-fit function is indicated. The λ_{max} values vary modestly for each species (a total range of 5 and 6 nm). However, the peak value of the MWS photopigment is significantly longer ($t = 5.55$; $df = 10$; $P < 0.001$) in fallow deer than in white-tailed deer (mean values of 542.2 nm versus 536.8 nm).

Although the difference between the spectral positioning of the MWS photopigment in white-tailed and fallow deer is not large it may be significant, not only statistically, but also from the viewpoint of the nature of the photopigments in the two species. There is evidence that the biological mechanism underlying the spectral tuning of mammalian cone photopigments is quantized in the sense that these pigments are positioned at any one of a restricted number of discrete locations. The λ_{max} values of these permissible locations are separated by an average distance of about 6 nm (Jacobs and Neitz 1985). Note that the estimated values for the peaks of the MWS pigments of white-tailed and fallow deer are separated by approximately this magnitude. Furthermore, these two approximate peak locations (c. 536 and 542 nm) have been identified as characterizing the λ_{max} values of cone pigments found in other species of mammal (Jacobs 1993). Both these coincidences lend credence to the conclusion that the MWS pigments of these two types of deer are in fact discretely different.

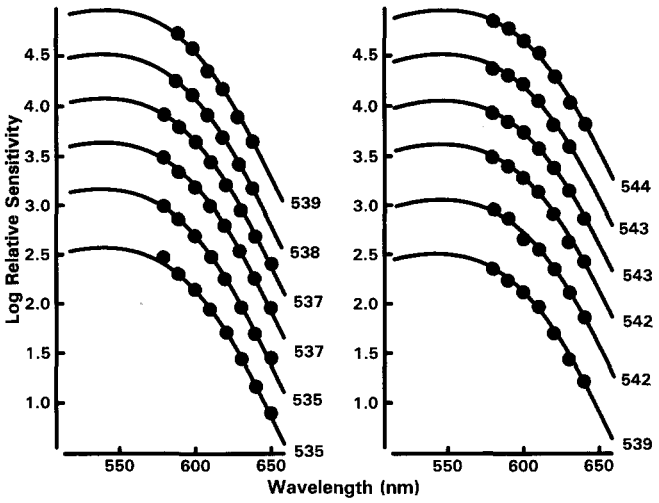

Fig. 5. Spectral sensitivity of MWS cone mechanism in 6 white-tailed deer (*left panel*) and 6 fallow deer (*right panel*). Plotted are the sensitivity values measured at 50 Hz for a range of long wavelength test lights. The data arrays for individual animals are positioned arbitrarily along the ordinate. Each data array was best fit with a photopigment absorption curve (*continuous line*). The λ_{max} value for each such function is shown to the right of the curve. The average λ_{max} value for the white-tailed deer is 536.8 nm; the corresponding value for the fallow deer is 542.2 nm

Photopigments and vision in deer

The measurements reported here suggest that the eyes of these two species of deer contain three classes of photopigment – a rod pigment and two classes of cone pigment. These are summarized by standard photopigment absorption curves in Fig. 6 and are assumed accurate in spectral positioning subject to the reservations noted above. We conclude from the results that the two species share a SWS cone photopigment and that they have slightly different versions of an MWS cone photopigment. No measurement of rod pigment was made for the fallow deer, but it seems reasonable to assume it to be not greatly different from that measured for the white-tailed deer.

Vision ultimately depends on many of features of the visual nervous system that presently are unknown for deer, but the estimates of photopigments reported here

[1] The data sets of Fig. 4 diverge slightly from the photopigment absorption curves, being a little too high near the peaks of the curves and slightly too low at the shortest wavelengths. One possible interpretation of such a pattern of deviation is that it results from progressive attenuation of short-wavelength lights as might be expected from lens pigmentation. To examine this possibility, we fit a series of absorption curves to data sets from which the shortest test points were progressively removed. If there were some selective short-wavelength filtering, one would expect that the peaks of the fitted curves obtained from this procedure would shift toward the shorter wavelengths. They did not. For example, as the data obtained from the white-tailed deer (Fig. 4, left panel, was narrowed in 10 nm steps from a spectral range of 410–520 nm, the λ_{max} values for the best-fit curves varied nonsystematically over a small range – from 454 to 457 nm. This suggests that the small deviations seen in Fig. 4 likely did not arise from systematic effects of lens filtering.

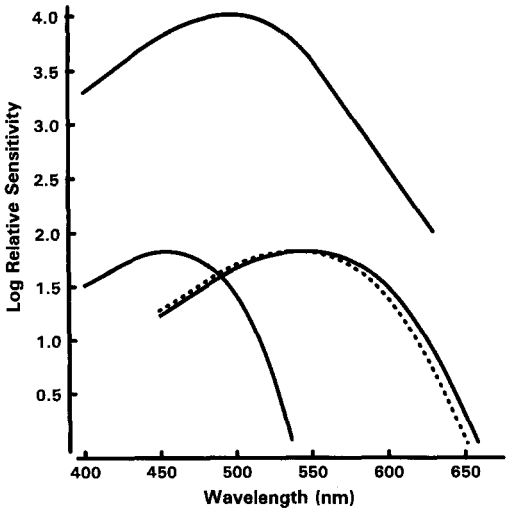

Fig. 6. Sensitivity curves for the 3 spectral mechanisms present in the retinas of white-tailed deer and fallow deer. The curves are derived from standard photopigment absorption curves set to the peak values suggested from the results of the ERG spectral sensitivity measurements. These indicate a rod (*top*) having a peak of about 497 nm and two classes of cone. The SWS cone appears similar for the two types of deer (λ_{max} of ca. 455 nm). The MWS cone is displaced slightly toward the long wavelengths for the fallow deer as compared to the white-tailed deer, as indicated by the separate symbols used for the two species. The functions for rod and cone mechanisms have been arbitrarily positioned on the sensitivity axis

do suggest some observations about their likely visual capacities, both in comparison to other species and relative to the behavioral measurements so far reported for these animals.

Although information is still restricted, it appears that the retinas of the majority of mammals may have two classes of cone pigment (Jacobs 1993). Outside of rodents, which have interesting variations of their own, the most usual mammalian arrangement is that one of these photopigments has peak absorption in the short wavelengths, from perhaps 420 to 450 nm, and a second pigment whose peak falls in the range of 530 to 565 nm. Deer appear typical in this regard. There are only a few other measurements of cone pigments in other ungulates. Four domestic species, the pig (Neitz and Jacobs 1989) and 3 species from the family Bovidae – sheep, goats and cows (unpublished) – all have two classes of cone pigment. In each of these species the longer of the two pigments has peak sensitivity in the range of 550 to 555, a value significantly longer than that found for the deer. From a comparative point of view, likely the most unique feature of the deer pigment complement is the relatively short λ_{max} value of the MWS/LWS pigment. If one wishes to identify an analogue to the deer cone-pigment complement, and thus gain some notion of the prospects for spectral sensitivity and color vision, then perhaps the most convenient is to that offered by individuals who make up a class of human color vision defectives, the protanopes. In such individuals, spectral sensitivity and dichromacy is based on an SWS cone and a cone having peak sensitivity at about 530 nm (Pokorny et al. 1979). The photopigment complement of these deer is also similar to that found for some platyrrhine monkeys (Jacobs 1993).

The presence of two cone pigments predicts dichromatic color vision, and in those mammals that have been properly tested this prediction appears to be true. In the absence of any other facts, one would thus assume deer to have dichromatic color vision. As noted above, there have been two examinations of the possibility of deer color vision. Zacks and Budde (1983) first measured the ability of a white-tailed deer to detect a broad-band and a long-wavelength stimulus as a function of stimulus intensity. They then showed that the deer was able to discriminate between these two stimuli when the relative intensities of the two were so adjusted as to obviate luminance cues. A successful discrimination of this sort (long wavelength light versus an achromatic light) is consistent with the dichromatic color vision predicted for the deer by the present pigment estimates. Smith et al. (1989) employed a less conventional approach. In their experiment deer were exposed to pairs of chromatic stimuli (e. g., 620 and 500 nm) and were reinforced for operant responding in the presence of one stimulus and not reinforced for responses made in the presence of the other stimulus. After the animals had learned the discrimination, they were given a series of generalization tests in which response rate was recorded for spectral lights that systematically varied in wavelength away from the location of the formerly reinforced stimulus. The fact that response rate varied systematically as a function of the spectral distance from the reinforced light was taken to indicate that these deer could "discriminate green from yellow and orange." Whereas the discrimination seems clear, its biological basis is not. In the experiment of Smith et al. (1989) the spectral stimuli were presented at fixed intensities with no apparent attempt to insure that their consequent potential variation in brightness might not provide a potent cue for behavioral control. This would be particularly important to do for those longer test wavelengths, because it is precisely in this part of the spectrum where the pigment measurements (Fig. 6) show that deer sensitivity is changing rapidly with wavelength, e.g., on the basis of their photopigments white-tailed deer would be expected to be about four times as sensitive to a 600 nm light as to a 620 nm light if the two were presented at equal quantal intensity. The results of Smith et al. (1989) do not appear necessarily inconsistent with the photopigments proposed here for the deer.

Although the presence of two types of cone pigment predicts spectral discriminations consistent with dichromatic color vision in the deer, there may be a potential role for rod signals as well. There is evidence from recent studies on a number of species to suggest that rod signals may frequently contribute to discrimination in manifest tests of color vision conducted under a range of viewing conditions, and this may be particularly the case for those species whose retinas both contain many rods and lack rod-free areas (Jacobs 1993). Deer certainly fall in this latter category, opening the possibility that visual discriminations made at moderate to high light levels in this species could involve the participation of more than two independent spectral mechanisms.

Zacks (1985) measured spectral sensitivity for a female white-tailed deer using an increment-threshold paradigm in which various monochromatic test stimuli were added to a steady, dim achromatic light. The derived curve shows peak sensitivity for this animal that is characterized as being at "about 545 nm" (Zacks 1985). That value is slightly longer than the peak estimated for the MWS pigment of the white-tailed deer in this investigation. However, we have recently best-fit the spectral sensitivity data obtained by Zacks to photopigment absorption curves using the same techniques as have been employed throughout this paper. For test wavelengths from 495 nm to 598 nm the λ_{max} value for the best-fitting curve to these behavioral data is 534 nm, a value remarkably close to that we derived for white-tailed deer with the ERG. Unfortunately, it was not possible in these behavioral experiments to make any detailed measurements of spectral sensitivity in the short wavelengths, so comparisons between the measured SWS photopigment and behavioral sensitivity remain to be accomplished.

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