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# Retinal Spectral Sensitivity, Fur Coloration, and Urine Reflectance in the Genus *Octodon* (Rodentia): Implications for Visual Ecology

Andrés E. Chávez,<sup>1</sup> Francisco Bozinovic,<sup>2</sup> Leo Peichl,<sup>3</sup> and Adrián G. Palacios<sup>1</sup>

**PURPOSE.** To determine the eye's spectral sensitivity in three species of the genus *Octodon* (order Rodentia; infraorder Caviomorpha), *O. degus*, *O. bridgesi*, and *O. lunatus*, as well as the spectral properties of the animals' fur and urine and of objects in their habitat. The genus is endemic in Chile and contains species with different habitats and circadian patterns (diurnal versus nocturnal).

**METHODS.** The electroretinogram (ERG) was used to record scotopic and photopic spectral sensitivity. The reflectance of ventral and dorsal body parts, urine, and other objects from the natural microhabitat were measured with a fiber-optic spectrometer.

**RESULTS.** In scotopic conditions, the maxima of sensitivity ( $\lambda_{\max}$ ) were at  $505.7 \pm 7.7$  nm in *O. degus*,  $501 \pm 7.4$  nm in *O. bridgesi*, and  $510.1 \pm 7.4$  nm in *O. lunatus*, representing the rod mechanism. In photopic conditions, only the diurnal species *O. degus* (common degu) was studied. The degu's photopic sensitivity had a  $\lambda_{\max}$  at  $500.6 \pm 1.2$  nm and contained two cone mechanisms with  $\lambda_{\max}$  at 500 nm (green, medium-wavelength-sensitive [M] cones) and approximately 360 nm (ultraviolet, short-wavelength-sensitive [S] cones). In all three *Octodon* species, dorsal body parts were more cryptically colored than ventral ones, and ventral body parts had a significant UV reflectance. The fresh urine of *O. degus*, used for scent marking in various behavioral patterns, was also high in UV reflectance.

**CONCLUSIONS.** It is suggested that territorial urine marks are visual as well as pheromone cues for UV-sensitive species and hence may have favored the evolution of UV-cones in rodents. (*Invest Ophthalmol Vis Sci.* 2003;44:2290–2296) DOI: 10.1167/iows.02-0670

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A major goal in physiological and sensory ecology is to understand the interplay between animals and their particular environment. Rodents are the most diverse group containing the most species among mammals and hence are suitable models to investigate how the visual system adapts to various habitat conditions. The rodent infraorder Caviomorpha encompasses 16 families (also including guinea pigs) and is endemic in South America. Specifically, the caviomorph family Octodontidae offers much diversity at the species and the ecological level, including physiology, morphology, behavior, life modes, and use of habitat.<sup>1</sup> They are distributed from the coast to approximately 3500 m altitude, with microhabitats in matorral with evergreen sclerophyllous shrubs over a seasonal herbaceous layer.<sup>2</sup> The matorral is a characteristic South American scrub ecosystem with very diverse flora and fauna. The genus *Octodon* has three species *degus* (the common degu), *lunatus*, and *bridgesi*, all endemic in Chile. They all are herbivorous and similar in appearance. The population density of *O. lunatus* and *O. bridgesi* is low, whereas degus are abundant.<sup>1,3–5</sup> The circadian activity pattern of degus has been established from experiments on motor activity under natural or laboratory light conditions. The degu is crepuscular during summer, but mainly diurnal during winter.<sup>6</sup> It is a good model species to test hypotheses on behavioral ecology, because it can be easily observed because of its diurnality and its habitat in the seasonal semiarid and Mediterranean environments of northern and central Chile. *O. bridgesi* and *O. lunatus* are markedly nocturnal.<sup>5,7</sup> *O. lunatus* inhabits dense shrublands as well as small forests, from the coastal range up to a 1200-m altitude in the Andes. *O. bridgesi* inhabits rocky areas, forests, and agroecosystems.<sup>5</sup>

Among mammals, the ratios and the retinal distribution of rod and cone photoreceptors vary considerably, depending on habitat and lifestyle.<sup>8–10</sup> Most rodents are nocturnal, with a retina dominated by rods and containing only a small proportion of cones. Even in these species, the cones comprise two spectral types and thus provide for dichromatic color vision, the most common form of mammalian color vision.<sup>8</sup> The two spectral cone types are termed short-wavelength-sensitive (S) cones and middle-to-long-wavelength-sensitive (M) cones. In most mammalian taxa, the S cones have their sensitivity maxima at 420 to 450 nm (blue), and the M cones at or beyond 500 nm.<sup>8</sup> In contrast, a number of rodents have been shown to possess ultraviolet (UV)-sensitive S cones, whereas their M cones are conventional (rat, gerbil, mouse, hamster, and gopher).<sup>11–13</sup> We were interested to see how species of the South American genus *Octodon* fit into this pattern and whether their spectral sensitivities relate to visual challenges set by their habitat and behavior patterns. For this, we assessed the scotopic and photopic responses of their retinas by electroretinogram (ERG) and measured the spectral reflectance of *Octodon* bodies, urine (used for scent-marking in various sorts of behavior), and objects in their natural habitat. Some preliminary results have been published in abstract form.<sup>14,15</sup>

## METHODS

### Animals

*O. degus*, *O. bridgesi*, and *O. lunatus* were captured in the wild and kept in a standard animal facility at the University of Valparaíso. Five juvenile degus came from our breeding colony. Animals were maintained at 18°C to 20°C on a 12-hour light–dark cycle, with access to food and water ad libitum. All experiments conformed to the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research. All animal care followed international animal care protocols (NIH Publication No. 80-23). Two 1-year-old adult *O. lunatus* (~220 g), three adult *O. bridgesi* (195–215 g) and nine *O. degus* (five juveniles and four adults) were used for ERG experiments. To assess coloration, the body reflectance of 26 degus, 2 *O. lunatus*, and 2 *O. bridgesi* was measured.

### Electroretinogram

The ERG was recorded under both scotopic and photopic conditions. Before an experiment, the animals were dark or light adapted for 45 minutes with an illuminator (150 W) producing a background illumination of 240  $\mu\text{W}/\text{cm}^2$  per sterad (sr) at the cornea. They were then anesthetized with an intraperitoneal injection of a mixture of ketamine hydrochloride (120 mg/kg) and xylazine (4 mg/kg). A local corneal anesthetic (1% lidocaine) and a few drops of 1% atropine sulfate for pupil dilation were applied to the eye before the contact electrode was placed on the cornea. The body temperature was maintained at 35°C by means of a regulated thermal bed. Most of the experiments were performed in the early afternoon.

The optical system consisted of a stabilized power supply with a quartz lamp (250 W; Oriel, Stratford, CT), a monochromator (1200 lines/mm grating, 20 nm half-bandwidth; Oriel), and long-pass filters (RG540, RG630; Schott Optical Glass, Duryea, PA) to eliminate stray light at short wavelengths from the monochromator. In preliminary experiments a silica optical guide (Oriel) was used to focus the stimulus into the eye. In later experiments, a series of quartz condensers replaced the optical fiber. An electronic shutter (Uniblitz; Vincent Associates, Rochester, NY) set the flash duration and an optical quartz wedge (0–4 optical density) attenuated the incident number of photons. The monochromator, optical wedge and shutter were under computer control and adjusted to deliver 10-ms flashes at wavelengths from 320 to 680 nm in 20-nm steps. During photopic ERG recordings, the eye was kept light adapted by a white background light. To improve the detection of S-cone contributions to the photopic ERG, the M cones were bleached by a bright yellow adaptation background in some of the experiments. The yellow background was obtained by adding a long-pass filter (< 0.00001% transmission below 420 nm; model GG 435; Schott Optical Glass) to the fiber-optic illuminator (150 W), producing a background illumination of 500  $\mu\text{W}/\text{cm}^2$  per sterad at the cornea.

The ERG signals were recorded with a pair of Ag/AgCl electrodes, amplified, and low- and high-pass filtered (100 Hz and 300 Hz) with a high-gain amplifier (model DP-301; Warner Instruments, Hamden, CT). Before each experiment, the photon flux emission from the lamp, between 300 to 800 nm, was measured with a calibrated photocell positioned at the corneal level (Optometry S370; UDT Instruments, Hawthorne, CA).

### Recording and Analysis

The ERG response was evoked by an increasing number of photons per flash (with 1- to 2-second intervals between the flashes) at fixed wavelength(s). The response amplitudes were measured between baseline and peak. The amplitude response was normalized by  $r/r_{\text{max}} = i/i + \sigma$ , where  $i$  is the incident photon number at the cornea,  $r/r_{\text{max}}$  is the normalized response (b-wave), and  $\sigma$  is the half-saturating response. For the spectral sensitivity experiments, the amplitude of the b-wave was measured from the average response ( $n = 10$ –50 trials) to dim flashes, covering the range of 330 to 700 nm. The spectral sensi-

tivity ( $S_\lambda$ ) function was measured as  $S_\lambda = r_{\text{peak}}/I$ , where  $I$  is the flash photon flux, and  $r_{\text{peak}}$  is the b-wave maximum peak response for a dim flash. The wavelength of maximum sensitivity ( $\lambda_{\text{max}}$ ) was calculated by fitting the experimental data for the 440- to 540-nm range to a template (vertically scaled and shifted in the  $\lambda_{\text{max}}$  to the best fit) that describes the action spectrum of mammalian photoreceptors.<sup>16</sup> Because there is not a straightforward relation between a visual pigment absorption and b-wave sensitivity, no further attempt was made to fit regions other than those close to the  $\lambda_{\text{max}}$ . Among the factors contributing to the mismatch are the spectral filtering of the ocular media, self-screening, and relative number and retinal distribution of different cone types and rods.<sup>17</sup>

Statistical differences were evaluated by analysis of variance (ANOVA). Analysis and graphic data presentations were performed on computer (Excel; Microsoft Corp., Redmond, WA; Origin, Microcal, Northampton, MA).

### Spectral Reflectance Measurements

To see what behavioral significance the retinal UV sensitivity may have, we measured the spectral reflectance of various body regions, of objects in the natural habitat, and of the animals' scent marks (urine). The reflectance was measured with a fiber-optic spectrometer (model S2000; Ocean Optics, Dunedin, FL) between 250 and 750 nm through a data-acquisition input/output (I/O) card (12-bit 100 ks; DAQCard-700; National Instruments, Austin, TX) fitted into a laptop computer. A white reflectance standard (Spectralon, 99%; Labsphere, North Sutton, NH) was used for calibration. Sample patches were illuminated by a flash xenon lamp (Ocean Optics) through a silica-fused fiber optic (400  $\mu\text{m}$  diameter) with six external concentric fibers. The reflected light was collected with a single central internal fiber. Because reflectance measurements are very sensitive to the incidence and measurement angle of the light, a silica fiber positioned perpendicular to the surface of the patch with a reading acceptance angle of 20° was used in all measurements. The light radiance sensor at a distance of 1 to 2 cm from the sample allowed measurement of a surface area of 0.1 to 0.4  $\text{cm}^2$ . Each recording was integrated over a period of 100 ms and smoothed with a 15-point running average and averages from five discrete recordings. For body reflectance, sample measurements were obtained from dorsal (head, neck, thorax, extremities, tail) and ventral (throat, thorax, tail) body regions. All measurements were performed under controlled laboratory conditions.

Scent marks were collected from adult male degus that had been captured in the wild 2 months previously and kept in our animal facility. The protocol followed that for measuring vole urine reflectance.<sup>18</sup> The animals were placed in a 34 × 24 × 22-cm white box with a sheet of brown cardboard on the floor. Cardboards with fresh urine deposits were collected and analyzed while still moist and also after they had dried. The urine reflectance was determined as spectral contrast  $(A - B)/(A + B)$  between the reflectance spectra of moist or dry urine deposits ( $A$ ) and those of water-moistened or dry blank samples ( $B$ ). To control for optical and chemical interactions between the urine and substrate, reflectance measurements were also performed with samples collected on black cardboard and on rock. The results were similar with all three substrates. To the human eye, fresh degu urine appears mixed with a significant but individually varying amount of salts that form a white deposit when dry. Hence, we also collected a few samples of fresh urine from the cardboards, centrifuged it, and separately measured the spectral profiles of the liquid and solid urine components.

## RESULTS

### Course of Dark Adaptation

The time course of dark adaptation was studied in degus ( $n = 2$ ) and *O. bridgesi* ( $n = 2$ ). After an animal was light adapted for 30 minutes, the lamp was turned off, and the ERG sensitivity was monitored over time with 10-ms flashes ( $\lambda = 500$  nm).

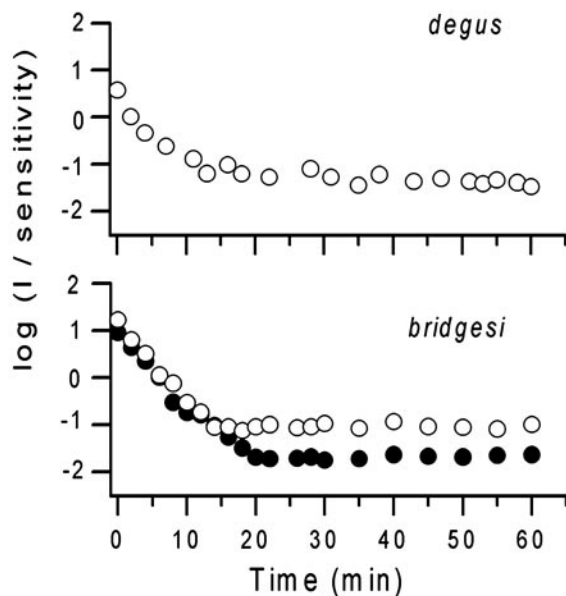


FIGURE 1. Course of dark adaptation of the ERG in one *O. degus* and two *O. bridgesi*. The preadaptation light was turned off at time 0. The stimuli were 10-ms dim flashes of  $\lambda = 500$  nm. After 15 minutes, the ERG sensitivity reached a dark adaptation plateau. The degu and *O. bridgesi* showed a similar slope.

Figure 1 shows that the b-wave sensitivity reaches a fully dark-adapted condition after 15 minutes. This time course is much faster than in the pigmented rat (range of hours<sup>19</sup>). However, the rat data were obtained after a preadaptation to a strong light, which may explain the difference.

### Scotopic Spectral Sensitivity

Figure 2 (top) shows a family of ERG responses to flashes of different intensity in the degu. The recovery kinetics of the flash response was fast and lasted for close to 100 ms. The two graphs show response-intensity functions for the b-wave in the degu (Fig. 2, middle,  $n = 9$ ) and *O. bridgesi* (Fig. 2, bottom,  $n = 3$ ). Individual data were fitted and then normalized using  $V/V_{\max} = I/I + \sigma$ , where  $I$  is the flux intensity and  $\sigma$  is the intensity flux for half-maximum saturating response.<sup>20</sup> The mean maximum b-wave amplitude obtained in the degu was  $86 \pm 10$   $\mu$ V, compared with  $67 \pm 23$  and  $45.0 \pm 12.5$   $\mu$ V for *O. bridgesi* and *O. lunatus* ( $n = 2$ ), respectively.

Figure 3 shows the scotopic spectral sensitivity functions obtained in *Octodon*. The  $\lambda_{\max}$  was  $505.7 \pm 7.7$  nm in the degu ( $n = 4$ ),  $501 \pm 7.4$  nm in *O. bridgesi* ( $n = 3$ ), and  $510.1 \pm 7.4$  nm in *O. lunatus* ( $n = 2$ ). The bandwidths of the spectral sensitivity functions seem, particularly in *O. bridgesi*, narrower than those in a standard visual pigment template.<sup>16</sup> Although special care was taken to use dim flashes, we cannot exclude that a fraction of the b-wave response amplitude may contain cone contributions, which would induce small changes in the final shape of the spectral function. No attempt was made to correct spectral sensitivity data for self-screening, light scattering, or possible spectral filtering by the ocular media. Nevertheless, we believe that the calculated  $\lambda_{\max}$  is reliable and corresponds to the  $\lambda_{\max}$  of the rods.

### Photopic Spectral Sensitivity

Figure 4 (top) shows an intensity-response function for degus ( $n = 7$ ), obtained with a white light background of photopic intensity (see the Methods section). The spectral sensitivity data (Fig. 4, bottom) were best fitted by a visual pigment

template (continuous line) with  $\lambda_{\max}$  at 500 nm.<sup>16,21</sup> The individual  $\lambda_{\max}$  average was  $500.6 \pm 1.2$  nm. To check for the presence of a second, short-wave sensitive cone pigment in degu retina, ERG spectral sensitivity functions were also measured with a bright yellow adapting background (see the Methods section). The yellow background predominantly bleaches the M-cone pigment and hence favors the detection of an S-cone contribution. Figure 5 shows such experiments in three degus. In each case, with yellow adaptation the long-wave sensitivity decreased more than the short-wave sensitivity ( $<400$  nm). This strongly suggests the presence of a second, UV-sensitive cone mechanism. The sensitivity function can be modeled by two templates with  $\lambda_{\max}$  at 500 nm (Fig. 5, bottom; dotted line) and 360 nm (continuous fine line). This indicates two spectral cone types, an M cone (near 500 nm; green-sensitive) and a UV-sensitive S cone (near 360 nm). Both templates were vertically adjusted by eye to best fit the data, and the continuous bold line results from adding the two templates. The fit was less satisfactory for the other two animals, possibly reflecting the spectral properties of ocular media or other aspects mentioned before. For the UV cones, such ocular properties are expected to shift the sensitivity to longer wavelengths—that is, the isolated visual pigment's sensitivity maximum may actually be below 360 nm. In the guinea pig, behavioral and ERG measurements of the S-cone mechanism

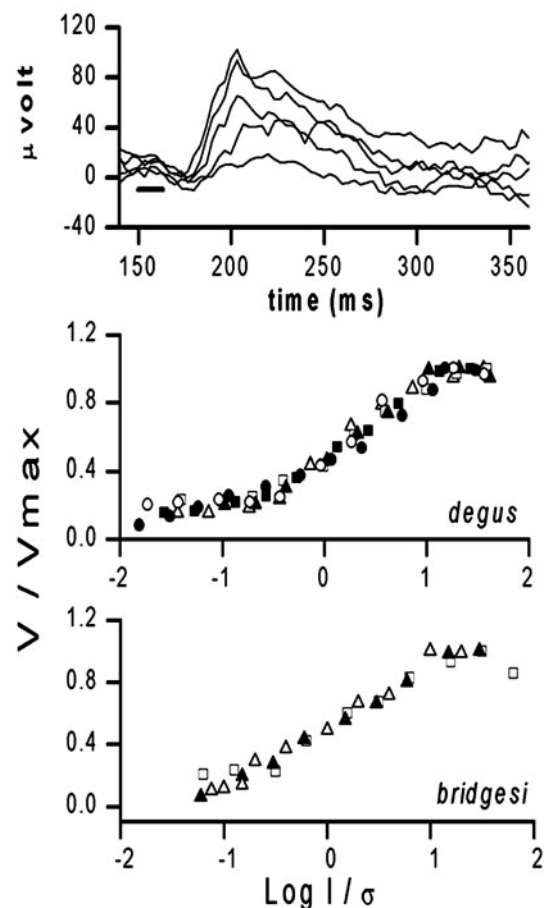


FIGURE 2. Top: representative family of scotopic ERG responses to different flash intensities, obtained in one degu. The dimmest flash ( $\lambda = 500$  nm, 10 ms) was 12 photons/ $\mu\text{m}^2$  incident at the cornea, and successive flashes were 46 (twice), 116, and 233 photons/ $\mu\text{m}^2$ . Each trace indicates the average of results in 50 trials. Middle and bottom: normalized b-wave intensity-response functions for degu ( $n = 6$ ) and *O. bridgesi* ( $n = 3$ ), also obtained with 500-nm flashes of 10 ms.



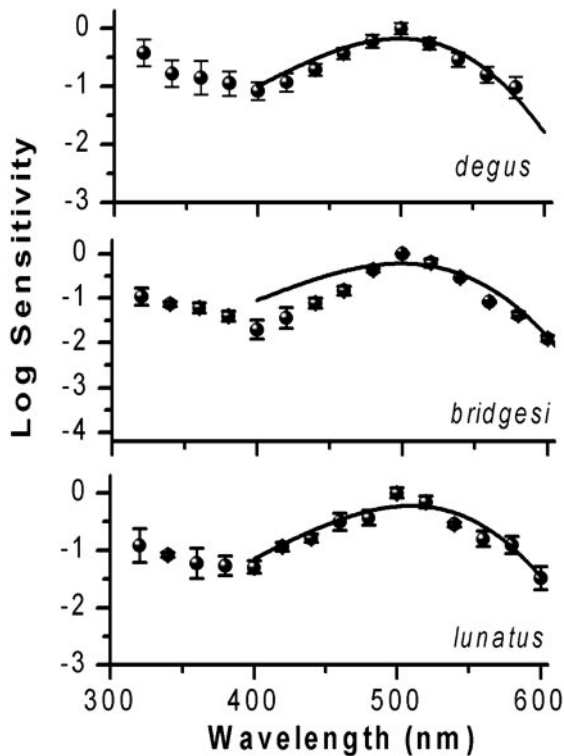


FIGURE 3. Scotopic spectral sensitivity of degu ( $n = 9$ ), *O. bridgesi* ( $n = 3$ ), and *O. lunatus* ( $n = 2$ ), with  $\lambda_{\max}$  at  $505.7 \pm 7.7$ ,  $501 \pm 7.4$ , and  $510.1 \pm 7.4$  nm, respectively. The continuous lines represent Lamb templates with  $\lambda_{\max} = 500$  nm for degu,  $\lambda_{\max} = 500$  nm for *O. bridgesi*, and  $\lambda_{\max} = 510$  nm for *O. lunatus*.

have shown a  $\lambda_{\max}$  near 430 nm,<sup>22</sup> whereas microspectrophotometric measurements of the isolated S cones have shown a  $\lambda_{\max}$  near 400 nm.<sup>23</sup>

In the case of the two *O. bridgesi* subjects, all attempts to obtain photopic responses were, after many trials, unsuccessful. For *O. lunatus*, no photopic ERG experiments were conducted, because the setup for this test was not yet ready when the animals (collected from the wild) were available.

### Reflectance Properties

A series of body reflectance measurements were performed in degu ( $n = 26$ ), *O. bridgesi* ( $n = 2$ ), and *O. lunatus* ( $n = 2$ ). Figure 6 shows the average reflectances for dorsal and ventral body parts, in the wavelength range from 300 to 750 nm. All three species showed a similar reflectance pattern, with higher reflectance in ventral than dorsal body parts. The ventral part of the body in the degu and *O. bridgesi* reflects more UV than in *O. lunatus*.

The reflectances of several essential objects belonging to the natural habitat of degus are plotted at the top of Figure 6. The samples measured were foliage and crop from *Acacia cavens*, ground vegetation (*Muehlenbeckia hastulata*,  $n = 3$ ; *Litbraea caustica*,  $n = 3$ ; *Colliguaja odorifera*,  $n = 3$ ), grassland (*Nassella chilensis*,  $n = 3$ ), as well as soil ( $n = 3$ ), rocks, ( $n = 2$ ) and feces ( $n = 3$ ). This object reflectance was rather similar to the dorsal body reflectance in the three species, suggesting some camouflage effect.

In a search for further behaviorally relevant signals in the UV part of the spectrum, we measured the reflectance of degu urine, which these social animals use to for scent-marking of their foraging trails and meeting areas.<sup>24,25</sup> The spectral reflectance contrast of fresh degu urine monotonically increased

with decreasing wavelength, reaching a maximum at approximately 310 to 360 nm (Fig. 7, continuous curve). Hence, fresh urine marks represent a strong visual UV signal.

The reflectance of older, dried-up urine marks was shifted to longer wavelengths with a peak reflectance contrast of approximately 450 nm. Separate measurements of the liquid and salt components of fresh degu urine (see the Methods section) showed that high-UV reflectance resided in the liquid part, whereas the freshly centrifuged salts had the same spectral properties as dry urine (Fig. 7, dotted curve).

### DISCUSSION

The adaptive design of the visual system in mammals has recently been reviewed in terms of ecological relevance and evolutionary constraints.<sup>9</sup> The rodent radiation represents the largest diversification among mammals, and the morphologic and functional study of their retinas provides an excellent instrument to appraise ecological adaptation. In this study we examined spectral sensitivity and animal and habitat reflectances in the genus *Octodon* as a contribution toward understanding the ecological and behavioral significance of color vision.<sup>26</sup>

The present ERG experiments demonstrate a rod mechanism in all three *Octodon* species and cone mechanisms in the degu. The presence of rods and cones in all three *Octodon* species has been confirmed by histology (Ref. 27 and Peichl et al., manuscript in preparation). The high scotopic sensitivity and the relatively fast time course of dark adaptation indicate good low-light vision in the three species. Previous studies of motor activity have shown a dominant nocturnal activity pattern for *O. lunatus* and *O. bridgesi* (Ref. 7 and F. Bozinovic, unpublished observation, 2000). In contrast, the degu is a

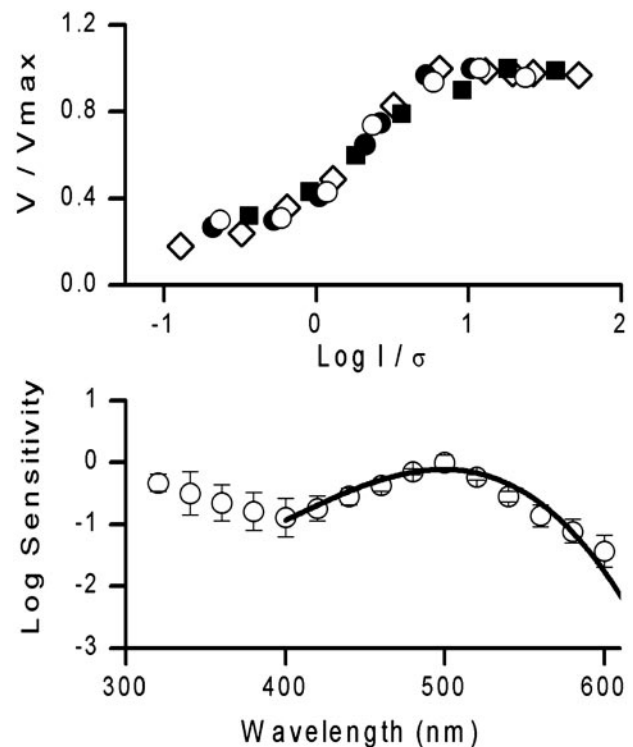


FIGURE 4. Photopic spectral sensitivity of *O. degus*. Top: normalized b-wave intensity-response function ( $\lambda = 500$  nm, 10 ms;  $n = 4$ ). Bottom: photopic spectral sensitivity function ( $n = 7$ ) shows a  $\lambda_{\max}$  at  $500.6 \pm 1.2$  nm. The continuous line represents a Lamb template with  $\lambda_{\max} = 500$  nm.

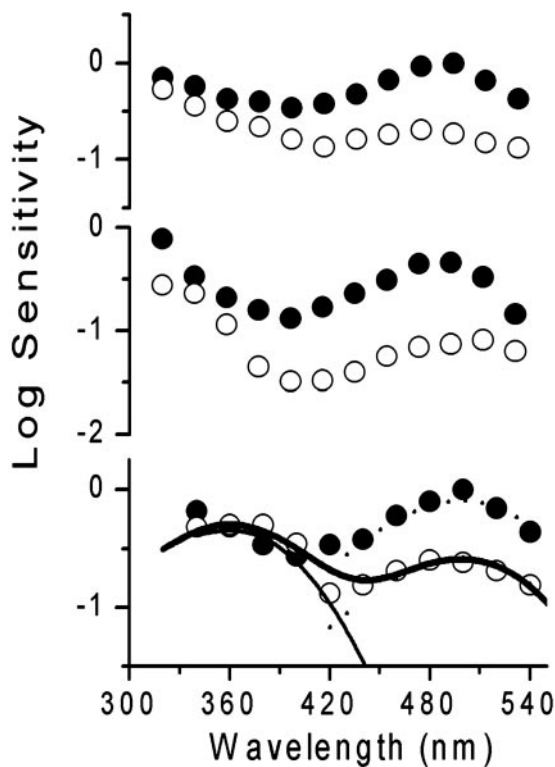


FIGURE 5. Photopic spectral sensitivity with white light adaptation (●) and with yellow light adaptation (○) for three degu subjects. In all three cases, yellow adaptation resulted in a larger decrease of sensitivity in the middle-wavelength range than in the UV range (<400 nm). Solid and dotted lines, bottom: lamb visual pigment templates with  $\lambda_{\max}$  at 360 and 500 nm, respectively (vertically adjusted to obtain the best fit by eye). Bold line: sum of the templates. The fit is quite good and strongly suggests the presence of a UV- and an M-cone mechanism in degus.

crepuscular-to-diurnal animal. In all three species, the scotopic  $\lambda_{\max}$  is approximately 500 nm, which corresponds to the absorption of a typical mammalian rod pigment. A 496-nm rod mechanism in degu has also been reported in an abstract (Calderone JB, Fenwick JA, Jacobs GH, ARVO Abstract 956, 2001).

Although the energy of our optical system was high enough to evoke a reliable photopic response across the spectrum in albino rats (data not shown), we were unable to evoke any photopic response in *O. bridgesi*. We did not have the opportunity to perform photopic ERG measurements in *O. lunatus*. Our histologic data with antisera against the cone opsins show the presence of a sparse population of M and S cones in both these species (Peichl et al., manuscript in preparation). At present, we have no convincing explanation for the failure to detect these cones by ERG in *O. bridgesi*. Because further studies on the behavior and the visual system of *O. bridgesi* and *O. lunatus* are not available, we will limit our discussion on photopic vision to the degu.

*O. degus* showed a photopic  $\lambda_{\max}$  around 500 nm, with additional significant UV sensitivity. This  $\lambda_{\max}$  is in the range of an M-cone mechanism present in a number of rodents, such as gerbil, rat, and hamster (Refs. 11-13; Calderone JB, Fenwick JA, Jacobs GH, ARVO Abstract 956, 2001). To check whether UV sensitivity originates from an independent cone mechanism or represents the secondary maximum ( $\beta$ -band) of the M-cone visual pigment,<sup>21</sup> we undertook a series of experiments using yellow light adaptation to bleach the M-cone pigment. The results argue for a second independent UV cone pigment.

Hence, our data reveal two cone mechanisms in the degu, with maximum sensitivity near 500 nm (M cone) and near 360 nm (UV sensitive S cone). This is in line with an abstract reporting two cone types in degu, with peak sensitivities near 508 and 360 nm (Calderone JB, Fenwick JA, Jacobs GH, ARVO Abstract 956, 2001). With antibodies against opsins, these S and M cones have also been identified histologically (Ref. 9; Calderone JB, Fenwick JA, Jacobs GH, ARVO Abstract 956, 2001; Peichl et al. manuscript in preparation). Hence, all available evidence supports the conclusion that degus have the potential for dichromatic color vision on the basis of green-sensitive M cones and UV-sensitive S cones. Cone dichromacy is the basic and most common type of mammalian color vision.<sup>8</sup>

In many mammalian species the S-cone sensitivity is in the range of 420 to 450 nm (blue),<sup>8</sup> but in degu it is in the near UV. Are there any features in the environment or behavior that correlate with this spectral shift? Our spectral reflectance measurements of the body surface, of objects in the natural habitat and of the urine used for scent marking give some indications for the relevance of UV vision. In degu and *O. bridgesi*, the ventral body parts (throat and thorax), but not the dorsal ones, showed modest (10%–20%) but significant UV reflectance. Behavioral studies in degus show that they are highly social.<sup>24,25</sup> For example, during alert call behavior degus raise upright on their hind paws and expose their thorax to the view of conspecifics.<sup>4,28</sup> In those circumstances, UV sensitivity may be relevant. In contrast, the low dorsal UV reflectance, which matches the low UV reflectance of objects in the habitat, could contribute to making the animal inconspicuous to predators,

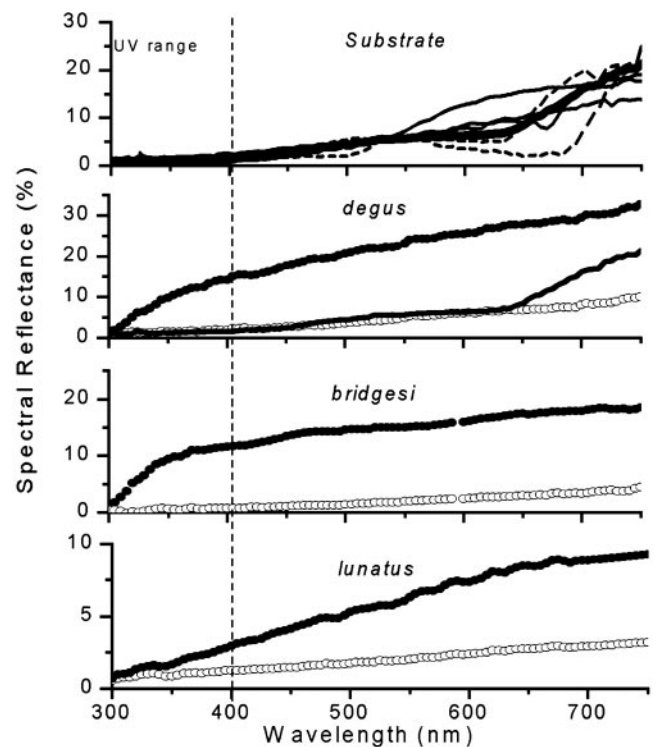


FIGURE 6. Spectral reflectance of body parts in *Octodon* and of objects in their habitat. Top: spectral reflectance of various types of vegetation (see text for species; broken lines) and of ground components (soil, rock, feces; fine solid lines). Bold line: the average substrate reflectance. Bottom: (●) average reflectance of ventral body parts; (○) average reflectance of dorsal body parts in degus ( $n = 26$ ), *O. bridgesi* ( $n = 2$ ), and *O. lunatus* ( $n = 2$ ). In the degu panel, the average substrate reflectance is given again for comparison. Left of the vertical dotted line is the UV part of the spectrum.

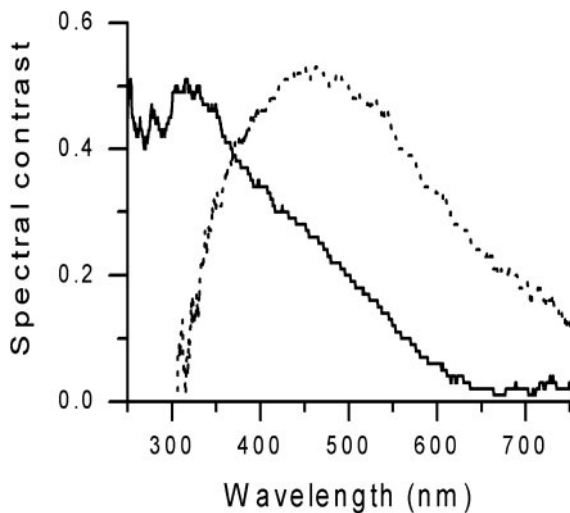


FIGURE 7. Spectral reflectance contrast of degu urine. *Solid curve*: moist, fresh urine scent marks. *Dotted curve*: dry salt deposits obtained by centrifugation. Measurements were obtained at wavelengths from 250 to 750 nm, in 0.3-nm steps. Each trace is the average of two experiments. Spectral contrast was highest in the UV (<400 nm) in moist urine and maximum near 450 nm in dry urine.

particularly diurnal birds of prey that hunt by vision. Birds have UV-sensitive cones and good vision in the UV.<sup>29</sup>

Among the social behavior patterns of degus is the use of common paths when moving around in their territory and the use of common wallowing places; these “public” trails and places are scent marked with urine and feces.<sup>24,25</sup> Our measurements show that fresh degu urine has a strong UV reflectance, whereas old dry urine does not. Hence these scent marks represent visual as well as olfactory cues to a UV-sensitive animal—a potential advantage for longer-range orientation. The possession of M cones and UV cones provides a visual detector system that could reliably distinguish between fresh and old urine deposits.

There is one interesting drawback in the urine-marking of community trails and wallowing places. In open habitats, these UV marks can also be seen over long distances by avian predators with UV vision and thus betray worthwhile hunting grounds. Like *Octodon*, voles have UV-reflecting urine and scent mark their trails (for summaries, see Refs. 18,30). It has been shown that kestrels can see and use these UV scent marks to discriminate between active vole trails and abandoned or sparsely used trails, thereby increasing their hunting success.<sup>30</sup>

UV sensitivity is widespread in vertebrates, including fishes, birds, and reptiles.<sup>29–33</sup> In eutherian mammals, however, UV sensitivity has been found so far only among the rodents (rat, gerbil, mouse, hamster, gopher<sup>11–13</sup>). The S cones of these rodents have a  $\lambda_{\max}$  of approximately 360 nm, equal to that of degus. The S cones of the guinea pig (a caviomorph like *Octodon*) are sensitive to longer wavelengths ( $\lambda_{\max}$  approximately 400 nm<sup>23</sup> or approximately 430 nm<sup>22</sup>). The ancestral mammalian S cone sensitivity was UV, but has been shifted to blue in most mammals.<sup>29</sup> The evolutionary reasons for maintaining UV-sensitive S cones in rodents are still unclear. To date, no convincing correlations between rodent UV sensitivity and taxon-specific adaptive pressures by habitat or behavior have been identified.<sup>34</sup> We propose that the important communicative role of scent-marking with UV reflecting urine in many rodents may have been one of perhaps several driving forces in maintaining the UV sensitivity of the S cone pigment. Urinary marking as a component of ranking and other social behavior is well documented in rodents, and rodent urine generally

seems to have UV reflectance (mouse,<sup>35</sup> voles<sup>18,30</sup>). A link between UV sensitivity and strongly UV-absorbing pheromone deposits has been suggested for desert iguanas,<sup>36</sup> but this suggestion has not made its way into the mammalian vision literature.

As UV sensitivity is mediated by a cone type, it should be advantageous only in photopic conditions—that is, for diurnal species such as the degu and the gerbil. In scotopic conditions, rodents have to rely on rod vision with a  $\lambda_{\max}$  near 500 nm and low UV sensitivity, as do all other mammals. Nevertheless, UV-sensitive S cones are also present in nocturnal rodents (rats, mice), and we assume that the nocturnal *O. bridgesi* and *O. lunatus* similarly have UV-sensitive S cones. Hence, it is very likely that additional adaptive pressures are involved. This is an intriguing topic for further research. For example, the higher UV content of skylight during morning and evening twilight has been discussed as a possible factor.<sup>34</sup>

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