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A review of color vision in white-tailed deer

Kurt C. VerCauteren and Michael J. Pipas

Abstract A better understanding of the color vision abilities of white-tailed deer (*Odocoileus virginianus*) helps to determine how these animals interpret their environment. We review and summarize the literature related to the color vision abilities of white-tailed deer. Physiological measurements using advanced techniques such as molecular genetics, electroretinography, and electron microscopy have demonstrated conclusively that white-tailed deer possess the anatomical requisites for color vision. Operant conditioning techniques employed in pen studies using trained cervids confirm that deer see color. The eyes of white-tailed deer are characterized by 3 classes of photopigments: a short-wavelength-sensitive cone mechanism, a middle-wavelength-sensitive cone mechanism, and a short-wavelength-sensitive rod pigment. The number and distribution of rods and cones in the retina, augmented by adaptations of the eye, give white-tailed deer high visual sensitivity and visual acuity in light and darkness. During the day deer discriminate colors in the range blue to yellow-green and can also distinguish longer (orange and red) wavelengths. At night deer see color in the blue to blue-green range, although the moderately wide spectral sensitivity of rods permits some discrimination of longer wavelengths. Rods serve a discriminatory role in color vision, especially at low to moderate illumination levels. Benefits of color vision to deer include the ability to discriminate between plant species and parts and enhanced predator-detection capabilities. This information can be used to refine methods of resolving deer-human conflicts and provide insight to deer researchers, photographers, and hunters on how to be more inconspicuous to their subject.

Key words cones, *Odocoileus virginianus*, photopigments, retina, rods, vision, white-tailed deer

Color vision is defined as the ability of an organism to distinguish light of different spectral qualities, irrelevant of light intensity (Ali and Klyne 1985). Color vision in deer is important to our understanding of how deer interpret their environment and how this affects their relationships with humans. Approaches to resolving deer-human conflicts (collisions with vehicles, crop damage, etc.) employ the use of such objects as frightening devices that often target the visual sense (Gilsdorf 2002). A better knowledge of visual acuity in deer could enhance our abilities to design more effective

deterrent devices, and would help answer questions about the evolution of color vision in mammals and assist in elucidating taxonomic relationships. In addition, deer hunters have a strong desire to know whether they are more visible to their quarry while wearing fluorescent orange clothing. Likewise, deer researchers and photographers, wishing to remain unobtrusive so as to avoid influencing the behavior of their subjects, have an interest in the color discrimination capabilities of deer.

We review and summarize the literature related to color vision in white-tailed deer (*Odocoileus*

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virginianus). Topics include physical adaptations, anatomy, and physiology of the deer eye; role of photopigments (rods and cones) and photoreceptors in color vision; and contributions of physiological and behavioral studies to refining our understanding of color vision in deer. We conclude with an evaluation of the importance of color vision to white-tailed deer in their environment.

Electromagnetic spectrum and attributes of color

The electromagnetic spectrum is a band of light energy ranging from short-wavelength cosmic rays to long-wavelength radio waves. A small portion of the spectrum from approximately 300 nanometers (nm) to 800 nm represents the visible light portion of the spectrum. Light is an electromagnetic wave characterized by 2 properties: amplitude and wavelength. These physical properties of light are responsible for the constructs of brightness and color. Brightness is defined as the dimension of color described by a scale of sensations reporting a color's similarity to one of a series of achromatic colors ranging from dark to brilliant. Although both brightness and color are functions of energy and wavelength, brightness is a function of total energy, while color is dependent primarily on wavelength discrimination. Color itself has 2 attributes: hue and saturation (Ali and Klyne 1985). Hue is the perception of a scale of spectral colors, regardless of the predominant wavelength of the light. Saturation is the amount of hue in the spectral distribution. Humans perceive 3 primary colors: blue, green, and red, corresponding to wavelengths of 435 nm, 546 nm, and 700 nm, respectively. Combinations of primary colors produce white or any color in the visible light portion of the electromagnetic spectrum.

Anatomy and physiology of deer vision

The deer's retina consists of an outer nuclear layer underlying the pigment epithelium and composed of rod and cone photoreceptors. The photoreceptors are supported by a complex underlying network of horizontal, amacrine, bipolar, and ganglion cells. Each of these cell types has a specialized function (Ali and Klyne 1985). Horizontal cells contact the photoreceptors in the outer plexiform layer and serve in the lateral transmission of the visual sig-

nal between photoreceptors. Amacrine cells serve a similar function within the inner plexiform layer with the ganglion cells as horizontal cells do in the outer layer with the photoreceptors. Bipolar cells serve as the channels through which visual impulses must travel on their way to ganglion cells before leaving the retina to be conveyed to the brain. Ganglion cells are the final cell type through which visual impulses travel before leaving the retina.

Each photopigment of the retina is composed of an opsin transmembrane protein and the chromophore 11-cis retinal (Yokoyama and Radlwimmer 1998). When the chromophore absorbs light energy, it changes shape and activates the opsin, which serves as a catalyst for subsequent reactions; the retinal then combines with the opsin and becomes a photopigment that absorbs light in the visible range of the spectrum (McIlwain 1996). When light is absorbed by a photopigment in a rod or cone, the photoreceptor cell membrane hyperpolarizes, generating an electrical charge. The charge is transmitted electronically to synapses on both bipolar and horizontal cells. Bipolar cells pass electrical signals to amacrine and ganglion cells. Ganglion cells generate action potentials, which travel along the optic nerve to the lateral geniculate nucleus and the visual cortex, where the signals are converted into visual images (Ali and Klyne 1985).

Photopigments and photoreceptors of the visual system

Color vision typically requires the presence in the retina of at least 2 photopigments with different spectral sensitivities (McIlwain 1996). Each photopigment is sensitive to a specific range of wavelengths and produces a maximum response to a specific wavelength, its peak sensitivity. Physiological and genetic studies have shown that the eyes of white-tailed deer are characterized by 3 classes of photopigments. One of these, associated with a cone mechanism, is a short-wavelength (blue)-sensitive pigment with a peak sensitivity between 450 nm and 460 nm; a middle-wavelength (yellow-green)-sensitive photopigment with a peak sensitivity of 537 nm is also associated with a cone mechanism. The third class of photopigment has a peak sensitivity of 497 nm and is associated with a rod mechanism (Jacobs et al. 1994). In the retina of white-tailed deer, cones approach a density of 10,000/mm² (Witzel et al. 1978). By comparison, the human retina has a cone density of 20,000/mm² (Müller-Schwarze 1994).

Visual capabilities of mammals are determined by the proportion of rods and cones in their retinas (Müller-Schwarze 1994) and the number of cone mechanisms. Hence, mammals can be classified as monochromats, dichromats, or trichromats (Ali and Klyne 1985). Monochromats, typified by the elephant (*Elephas maximus* and *Loxodonta africana*) possess a single type of cone mechanism, no cone mechanisms at all, or cone mechanisms that are not functional due to various factors (Smythe 1975, Jacobs 1981). Dichromats, which possess 2 types of cones with different spectral sensitivity curves, can distinguish colors in a band of the spectrum defined by the range of sensitivity of their cone mechanisms. White-tailed deer are dichromatic (Jacobs et al. 1994, Jacobs et al. 1998). Trichromats, exemplified by humans and Old World monkeys (infraorder Catarrhini), are characterized by 3 cone mechanisms with differing peak sensitivities and spectral sensitivity curves (McIlwain 1996).

The spectral composition of light absorbed by the photoreceptors depends on the object's reflectance characteristics, spectral content of the incident light, and differential absorption of certain wavelengths in ocular fluids before light reaches the retinal photoreceptors (McIlwain 1996). Cone photoreceptors dissect the incoming light into its chromatic components. Each hue is associated with a unique ratio of cone responses because the nature of the stimulus is encoded in the pattern of activity of a number of cells, rather than in the isolated activity of a single cell; slight changes in wavelength result in slight shifts in the ratio of activation of the cones (McIlwain 1996).

The 2 cone pigments of white-tailed deer retinas provide the requisite basis for dichromatic color vision. However, rods may serve a discriminatory role in color vision, especially in low-light conditions (Jacobs et al. 1994). Rod-assisted color vision is especially likely in species such as the white-tailed deer, whose retinas lack rod-free areas. Thus, visual sensitivity at lower light levels could involve the participation of a rod-based mechanism (Jacobs et al. 1994). Evidence suggests that rods can input signals into channels carrying color signals (Jacobs 1981). Rods are triggered by lower light levels than cones and become saturated at moderate illumination levels, beyond which the central visual system receives only cone-generated signals. However, there still exists a reasonably extended luminance range over which stimuli will produce both rod and

cone signals (Jacobs 1981). In summary, under low light intensities, rods, with a peak sensitivity in the blue portion of the spectrum, dominate, and deer are therefore most sensitive to colors in what humans describe as the blue to blue-green portion of the spectrum.

Adaptations of the deer eye

Adaptive radiation of the vertebrate eye has resulted in an array of specialized visual systems. Visual capabilities are reflections of the specialized niches animals occupy (Smythe 1975). On a molecular scale, changes in single amino-acid groups at critical points in the complex rod or cone photopigment molecules can significantly alter spectral sensitivity of these molecules. As the amino-acid sequences of the molecules are determined genetically, mutations over time have produced a wide range of photopigments with spectral sensitivities frequently matched to the ecological niches of animals possessing them (McIlwain 1996). The cumulative effects of these amino-acid changes explain the color vision capabilities of white-tailed deer (Yokoyama and Radlwimmer 1999).

The type of retina and its shape are important determinants of the function of the visual system in deer (Smythe 1975). In deer and a great number of other ungulates, the cornea is horizontally oval, corresponding to the configuration of the pupil (Duke-Elder 1958). The linear concentration of ganglion receptor cells on a portion of the retina (the visual streak) enhances visual acuity by focusing light on this horizontal band (Müller-Schwarze 1994). In combination with the deer's wide field of vision (310°), the visual streak accounts for the deer's ability to discern distant objects across a wide field of view without turning its head (Müller-Schwarze 1994).

Another adaptive feature of deer eyes is the tapetum lucidum, a feature possessed by some nocturnal animals to improve vision in dim illumination. More specifically referred to as a tapetum fibrosum in deer because of its structure of dense fibrous tissue of closely woven fibers of the vessels of the choroid, it "glistens like a piece of fresh tendon" (Duke-Elder 1958). The tapetum acts as a mirror, reflecting incident light back through the retina so that it passes the rods and cones twice, thereby increasing differences in apparent brightness (Duke-Elder 1958). The tapetum lucidum enhances vision under low-light conditions and is responsible

for the eye glare that deer exhibit when viewed in vehicle headlights at night (Müller-Schwarze 1994). Deer also possess an adaptive feature for enhancing eyesight during daylight, a ring of pigment that surrounds and penetrates into the deep interstitial tissue of the cornea. This pigmentation is hypothesized to be an antiglare device because it is absent in crepuscular and nocturnal animals (Duke-Elder 1958).

Methods of elucidating color vision

Physiological methods

Possession of a retinal mechanism for analyzing wavelength differences does not necessarily indicate that a given species possesses color vision (Ali and Klyne 1985). Many techniques have been developed or employed to demonstrate color vision in various mammalian species. Among these are DNA cloning, electroretinography, scanning electron microscopy, and transmission electron microscopy.

On a molecular level, Yokoyama and Radlwimmer (1998, 1999) cloned and sequenced the opsin complementary DNAs of red and green visual pigments from 8 mammalian species (including white-tailed deer) representing 5 taxonomic orders. They determined that in many cases, evolution of red-green color vision in mammals was achieved by nonrandom substitutions of 5 amino acids at a few sites in the photopigments. In white-tailed deer, such amino-acid substitutions shift the absorption peaks (relative to that of the ancestral form) of the green (medium-wavelength-sensitive) pigment 15 nm toward blue (a shorter wavelength). In general, the additive effects of these amino-acid changes explain color vision in a range of mammalian species, including white-tailed deer. The inferred amino-acid sequences of mammalian progenitors suggest that the contemporary red and green pigments in mammals appear to have evolved from a single ancestral green-red hybrid pigment by structured (e.g., nonrandom) amino-acid substitutions. From an evolutionary standpoint, natural selection and adaptive radiation have favored various forms of color vision in mammals, including white-tailed deer.

Electroretinography is another method for elucidating various aspects of color vision. This technique involves directing a test light into the subject's eye and varying the wavelength of the light to determine the spectral sensitivity of the cone

mechanisms. The sensitivity values are plotted to generate spectral sensitivity curves that indicate wavelengths to which the photopigments are most sensitive. Witzel et al. (1978) used electroretinography to identify 2 classes of cone pigments in white-tailed deer. They determined that photopic activity dominated the light-adapted eye and was enhanced by long-wavelength stimuli (peak sensitivity = 665 nm), while scotopic activity dominated the dark-adapted eye and was enhanced by short-wavelength (peak sensitivity = 470 nm) stimuli. Jacobs et al. (1994) also demonstrated 2 classes of cone pigment (short-wavelength-sensitive and medium-wavelength-sensitive) in white-tailed deer and fallow deer (*Dama dama*) using a modified electroretinography technique. Under photopic test conditions, these 2 species share a short-wavelength-sensitive cone mechanism with peak absorption in the region of 450–460 nm. Each species also has a cone mechanism peaking in the middle wavelengths and averaging 537 nm for the white-tailed deer, about 5 nm shorter than the corresponding value for fallow deer. Limitations of electroretinography include the possibility that more than one photopigment class contributes to the spectral sensitivity curves and the inability to obtain measurements of absorption of light by ocular media or tapetal reflectivity (Jacobs et al. 1994). Though electroretinography has limitations, it is a valuable tool for refining insights into color vision in deer.

Scanning and transmission electron microscopy also have been used to show the ultrastructure of the retina. Witzel et al. (1978), using both types of microscopy, clearly identified rods and cones in the retinas of white-tailed deer.

Behavioral methods

Behavioral studies using penned, trained animals are structured as discrimination tests, in which choices between visual stimuli are made solely on the basis of color (Birgersson et al. 2001). Challenges to behavioral studies include the difficulty of effectively eliminating all non-color cues such as smell, hearing, touch, or relative position of the test materials and even attributes (such as luminance) of the colors themselves (Neitz and Jacobs 1989).

Discrimination tests evaluate learned responses. Benefits of employing discrimination tests are that learned responses closely approximate behaviors involved in visual perception (sensation) and that

the researcher has control over the learning response because the experimental conditions can be controlled (Jacobs 1981). There are 2 categories of learned responses: classical conditioning and instrumental conditioning (Jacobs 1981). Classical conditioning, exemplified by the famous dog experiment of Pavlov, is the repeated pairing of a conditioned stimulus (the sound of a bell ringing) with an unconditioned stimulus (meat) to ultimately produce a conditioned response (salivating by the dog to the sound of the bell). Although this is an appropriate approach to test innate, physiologically based responses such as color sensation, such experiments are rarely conducted (none with deer have taken this approach).

With instrumental or operant conditioning, an animal is trained to perform some variation of a discrimination task; once this response is learned, the subject is presented with a positive stimulus and ≥ 1 negative stimuli. A response to a positive stimulus is reinforced, and if positive and negative stimuli can be discriminated, the animal will solve the problem. By varying the characteristics of the stimuli, the researcher can test for discrimination between as many stimuli as desired. All color discrimination experiments with deer have utilized this approach. Typically, such studies require intensive training, and the researcher is limited to the use of intelligent and tractable species. Furthermore, the researcher must find ways to eliminate non-color cues. Sample sizes in studies to date have been small, and both sexes of a test species have not always been well represented. Nonetheless, well-designed instrumental conditioning experiments have enhanced our understanding of color vision in deer.

Color discrimination is based on wavelength, but because discrimination also can be made on the basis of brightness, brightness must be controlled for in color discrimination experiments (Smith et al. 1989). Not controlling for brightness was a major limitation of early behavioral studies of color vision in animals (Jacobs 1981, but see Blough 1961). Brightness is a psychological aspect of color and must be established through an ordering or scaling within the confines of a particular stimulus (Jacobs 1981). A similar complicating factor is luminance, a photometric quantity that weights radiance according to a standard spectral sensitivity curve (Jacobs 1981). Equating stimuli to be equiluminant may or may not also make them equally bright (and vice versa). Unfortunately, most color

discrimination studies have not specified whether brightness, luminance, or both were controlled for, if at all (Jacobs 1981). For example, elk (*Cervus elaphus*) in a color discrimination study were considered able to distinguish fluorescent orange from other colors, including white, in a two-choice feeding test in which the colors were painted on feed buckets (Müller-Schwarze 1994). However, the researcher failed to control for brightness or luminance, leaving one to speculate whether non-color cues may have been involved.

There are different ways to address brightness and luminance in color discrimination experiments. One way is to make brightness an irrelevant cue by randomly varying the relative luminances of the target stimuli over a wide range (Jacobs 1981). The researcher determines the luminance increments and their order of presentation, and ensures that the range of luminance variation is symmetric about the point of equal brightness. Determining these increments requires the researcher to adjust the intensity of the spectral stimuli. Intensity is defined as the energy transferred by a wave per unit time across a unit area perpendicular to the direction of propagation. Another method to address brightness and luminance is to make the stimuli to be discriminated between equal in luminance or brightness by experimentally determining a complete spectral sensitivity function to ascertain the subject's sensitivity to various spectral stimuli (Blough 1961, Jacobs 1981, Ali and Klyne 1985, Reitner et al. 1991).

If a deer was trained to go to a green object (the target stimulus) and to avoid a red one, the researcher would have to adjust the intensities of the green and red stimuli until they appeared equally bright to the deer. To do this, the researcher must have knowledge of the deer's spectral sensitivity curve. If green and red stimuli are of equal intensity, the red one will appear darker to a deer, whose retina is less sensitive to long wavelengths. Because a deer's spectral sensitivity curve is not the same as a human's, the researcher cannot simply equate the intensities so that they look equally bright to the human eye. It is critical therefore to establish the spectral sensitivity curve for deer before proceeding to test hue discrimination. To establish the sensitivity curve, the researcher trains the subject to respond positively to the brighter of 2 targets, after which it is relatively easy to establish which parts of the spectrum look brighter and which darker by exposing different-colored stimuli in pairs. The

researcher can then train the subject to respond positively to a target of a given color and to match this color with various others so that they will appear equally bright to the test animal. By this means it is possible to determine whether there is discrimination on the basis of hue alone and to ascertain the efficiency of hue discrimination throughout the spectrum (Ali and Klyne 1985).

Numerous behavioral studies have attempted to address the issues of brightness, luminance, and other non-color cues in color discrimination experiments with animals (Blough 1961, Smith et al. 1989, Müller-Schwarze 1994, Birgersson et al. 2001). Zacks and Budde (1983) used an operant conditioning approach to demonstrate that white-tailed deer can detect long-wavelength and achromatic stimuli, regardless of intensity. They next determined that deer could discriminate between long-wavelength and achromatic stimuli when the relative intensities were adjusted to eliminate luminance cues. In a forced-choice feeding test, white-tailed deer learned to discriminate between colors (Smith et al. 1989). The deer altered their response rate as the wavelength of a stimulus (a given color) varied from the stimulus to which they were trained. The subjects were able to discriminate short-wavelength (500 nm) stimuli from long-wavelength (580–620 nm) stimuli. Smith et al. (1989) concluded that white-tailed deer can make discriminations based on different wavelengths. Jacobs et al. (1994) argued that though Smith et al. (1989) presented the chromatic stimuli at fixed intensities, they did not account for the potential variation in brightness, which could have been used as a discrimination cue. This was particularly relevant in the longer-wavelength tests because it is precisely in this part of the spectrum where the pigment measurements demonstrated by Jacobs et al. (1994) show that sensitivity of the deer's eye changes rapidly with wavelength. For example, white-tailed deer would be expected to be about 4 times as sensitive to a 600-nm light as to a 620-nm light of equal intensity (Jacobs et al. 1994). In contrast to the results of Smith et al. (1989), the findings of Murphy et al. (in Müller-Schwarze 1994), who measured the electrical activity of the photoreceptors in the retinas of white-tailed deer, suggested that deer are less sensitive to light of long wavelengths (orange and red) and actually rely upon the sensation of only 2 primary colors: yellow and blue.

Birgersson et al. (2001) addressed the brightness issue by designing a sound study to control bright-

ness. Noting that animals can generalize over similar perceptual stimuli (e.g., wavelengths), they developed a two-choice discrimination test in fallow deer using different chromatic and achromatic stimuli. The stimuli (colored plates affixed to the doors of feeding boxes) varied in brightness (dark green versus light gray and dark gray versus light green). The deer chose the green (positive) stimulus independently of whether it was lighter or darker than the corresponding gray stimulus. They concluded that fallow deer use color to discriminate between visual stimuli.

The conclusions of these conditioning experiments must be viewed with caution because motivated animal subjects will solve discrimination problems any way they can. Furthermore, interpreting results of such experiments with many complicating variables is the researcher's responsibility (Jacobs 1981). Such complicating issues can be adequately addressed with well-designed experiments using tractable animal subjects and appropriate equipment to evaluate hue, brightness, luminance, and other variables that influence color vision systems in deer and other mammals.

Ramifications of color vision in deer

Although deer rely primarily on hearing and olfaction to monitor changes in their environment (Müller-Schwarze 1994), their vision is an essential complement. They utilize vision to confirm what the other senses detect and to move through their environment. From this standpoint alone, vision may be an underrated sense.

The ramifications of color vision in white-tailed deer are great. Birgersson et al. (2001) proposed that color vision gives deer additional cues for discriminating between plant species or parts that vary in nutrient or toxin levels. Another benefit of color vision Birgersson et al. (2001) proposed was increased predator-detection capabilities. This is enhanced by the wide field of view of the deer's eyes (310° combined, without moving the head) (Müller-Schwarze 1994). However, movement detection and brightness contrast are probably more reliable predator-detection strategies to deer than the perception of color alone. Smith et al. (1989) surmised that color might not be a dominant cue in a deer's natural environment, although the deer in their study were able to make discriminations based on different wavelengths. Their stance was based on the observation that color

discrimination training among their study deer took quite a long time. In any event, white-tailed deer possess the requisite attributes of color vision (Neitz and Jacobs 1989, Jacobs et al. 1998), giving them the ability to make interpretations of chromatic visual cues.

Conclusions

White-tailed deer possess 2 types of cone mechanisms with sensitivity in the short (450–460-nm range) to middle wavelengths (537 nm) and a short-wavelength-sensitive rod mechanism (maximum sensitivity of about 497 nm). The relative abundance and distribution of rods and cones in the retina, augmented by the physical adaptations of their eyes, give deer excellent vision during both daylight hours and at night. During the day deer see colors in the range that humans would define as blue to yellow-green. They can also discriminate longer wavelengths (red and orange) from medium wavelengths (green). At night deer perceive color primarily in the human-defined blue to blue-green portion of the electromagnetic spectrum, although the moderately wide spectral sensitivity of rods does not preclude detection of longer-wavelength stimuli.

Visual frightening devices should de-emphasize lights or colors at the longer wavelengths, to which deer are less sensitive (VerCauteren et al. 2003). Amino-acid sequencing of visual pigments of a wide range of mammals has enabled researchers to construct phylogenetic tree topologies of red and green color pigments, thereby adding insight into the evolution of mammalian color vision (Yokoyama and Radlwimmer 1998). Although deer can visually detect the color orange, it is the brightness of the fluorescent clothing worn by hunters and not the color *per se* that most likely draws a deer's attention. Those who must approach and work close to deer without being detected should not wear bright or contrasting clothing, and must respect the deer's other senses (hearing, smell) at least equally. More operant conditioning studies are needed to determine the sensitivity of deer to colors of various wavelengths. In addition, subsequent research should address the value deer place on interpreting color in their natural environment.

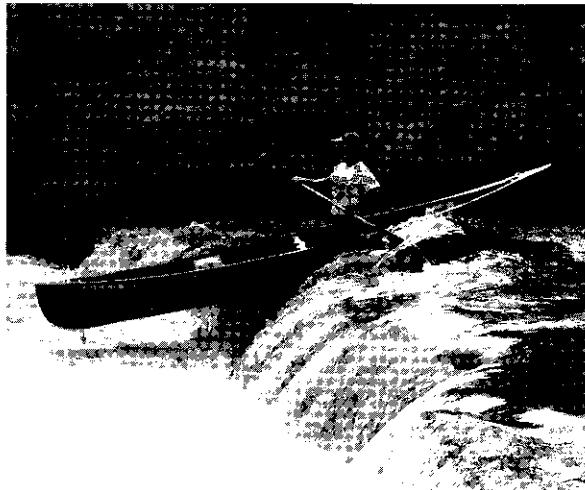
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