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Variation in pupil diameter in North American Gartersnakes (*Thamnophis*) is regulated by immersion in water, not by light intensity

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Abstract

A variable pupil generally regulates the amount of incoming light available for image formation on the retina. However, some of the semi-aquatic snakes (North American Gartersnakes, *Thamnophis*) that forage in relatively low light conditions reduce the pupil aperture in response to submergence underwater at the expense incoming light. Given that these snakes have all-cone retinas, reduction of incoming light because of pupillary constriction upon immersion seems counterintuitive. To test the effect of light and water on pupil aperture, three species of North American Gartersnakes (*T. atratus*, *T. hammondii*, and *T. sirtalis)* were exposed to nine light intensities in air and water. There was no effect of light on relative pupil aperture for any species. However, all three species showed a significant reduction in pupil aperture upon submergence underwater. The lack of a light response is surprising, and may be related to the method of accommodation in snakes. Snakes lack a ciliary muscle, and move the lens by constricting the pupil, which increases pressure in the posterior chamber and pushes the lens forward. Upon submergence, the snakes may be attempting to overcome the change in refractive index and defocus imposed by the water, by constricting the pupil. Thus, having the iris muscle involved in accommodation may preclude it from much of a light regulating function.

Keywords: Snake; *Thamnophis*; Pupil; Aperture; Vision; Accommodation; Light; Water; Aquatic

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1. Introduction

A variable pupil generally regulates the amount of light entering the eye (Erichsen, Hodos, & Evinger, 2000). Reducing the pupil aperture presumably serves to optimize the amount of incoming light for image formation (Djamgoz, Vallerga, & Wagner, 1999). Other effects of decreased aperture of a round pupil include reduction of the Stiles–Crawford effect (Bossomaier, Wong, & Snyder, 1989; Snyder & Love, 1983), reduction of aberrant rays striking the periphery of the lens (Land, 1981), and increased depth of field (Malmström & Kröger, 2006; Martin, 1999; Murphy & Howland, 1991; Ott, 2005).

Because a round pupil generally allows for less variability in aperture area than a vertical pupil, snakes that have a round pupil are typically diurnal or nocturnal, and snakes that have significant overlap in these light-related activity times typically have a vertical pupil (Walls, 1942). However, the round pupil of the colubrid snake *Spalerosophis diadema* from Israel showed an extreme pupillary response to light (Werner, 1970), which he attributed to a unique shift in seasonal activity from diurnal in winter to crepuscular/nocturnal in summer.

Although light regulation is presumed to be the primary function of a variable pupil, studies of North American Gartersnakes (*Thamnophis*) eyes have produced somewhat counterintuitive results in a light-regulating context. Schaeffel and de Queiroz (1990) showed that *T. sirtalis*, *T. elegans*, *T. couchii* (two individuals of which were actually *T. atratus*, following current taxonomy; A. de Queiroz,

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pers. comm.), and *T. melanogaster* reduced their relative pupil aperture underwater, thereby increasing depth of field, and overcoming defocus imposed by the change in refractive index upon submergence (Fig. 1). The pupillary constriction observed by Schaeffel and de Queiroz (1990) was not in response to an increase in ambient light, as snakes experienced slightly lower light conditions simply by being underwater. Unfortunately, they did not test for effects of light. The severe reduction in light input from pupillary constriction should be particularly important for an animal with an all-cone retina, as is the case for at least *T. sirtalis* (Sillman, Govardovskii, Röhlich, Southard, & Loew, 1997; Wong, 1989) and *T. marcianus* (Jacobs, Fenwick, Crognale, & Deegan, 1992). The only information available regarding pupillary response to light in *Thamnophis* suggests that *T. sirtalis* has a relatively large pupil (1.1 mm in photopic, 1.9 mm in scotopic conditions) for its eye size (3.8 mm axial length) and showed little response to light compared to other vertebrates (Land & Snyder, 1985).

A curious and potentially related aspect of snake vision is the method of accommodation. Among vertebrates, accommodation is generally accomplished by changing lens shape (reptiles (except some snakes), birds, mammals), or position (moved posterior: most fishes; moved anterior: elasmobranchs, amphibians, snakes) (reviewed by Ott, 2005; Sivak, 1980; Walls, 1942). The method of accommodation in snakes is unique and, according to Walls' (1942), related to their evolution from a fossorial (Holman, 2000; Wiens & Slingluff, 2001) lizard ancestor (but see Caprette, Lee, Shine, Mokany, & Downhower, 2004; Lee & Caldwell, 2000) that had extensively "degenerated" eyes to the extent of having lost most of the primary structures including the scleral cartilage, scleral ossicles, ciliary processes, annular pad, and "iris muscles" (Walls, 1942). The ciliary muscle is incorporated into the iris where its function is in accommodation as well as operating the pupil aperture. The circular fibers are not evenly distributed, and are most concentrated at the root of the iris (Beer, 1898; Michel, 1933). Walls (1942, p. 282) regarded this "powerful aggregation of sphincteral fibers" as the "accommodatory muscle", and the rest of the iris musculature as "sphincter muscle of pupil", based on a modified "vertical section" drawing by Schwarz-Karsten (1933). However, drawings of the surface of the iris do not show such a clear distinction (Michel, 1933). The lens is relatively far forward (toward the cornea) at rest, such that contraction of the "accommodatory muscle" causes an increase in vitreous pressure in the posterior chamber and pushes the lens forward (Beer, 1898; Kahmann, 1932). In addition, the radial fibers serve to stiffen the iris so that contraction of the bundle of fibers around the pupil edge compress and deform the anterior portion of the lens (Michel, 1933).

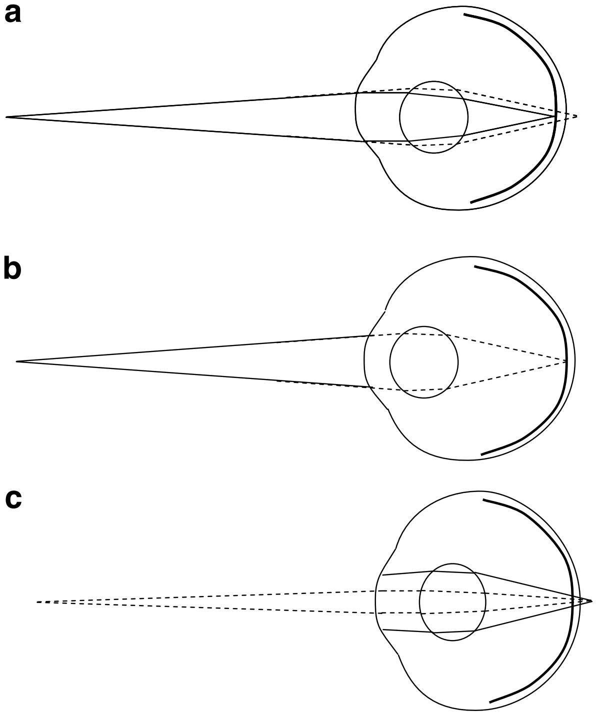

Fig. 1. (a) Effect of water immersion: Solid lines show rays converging on retina (i.e., forming image). Dotted lines show effect of immersion in water—loss of refractive index difference at spectacle results in loss of vergence at spectacle. Rays now converge to a point behind retina (i.e., image distance increases so that image on retina is out of focus). (b) Accommodation: The lens moves forward so that distance between lens and retina is the same as the image distance. In effect, movement of lens "drags" image forward onto retina. (c) Pupillary constriction: The dashed lines show the effect of reducing the pupil aperture. Incoming rays are closer together throughout the optical system and so make a smaller spot on the retina. While still in "out of focus", the image is clearer. The snake has increased the "depth of field" to include the out of focus object.

Walls (1942, p. 282) states that all of the iris musculature, including the concentrations at the root and pupil, as well as radial fibers, contract simultaneously during accommodation. If true under natural conditions, this could be a significant problem for snakes that need to see underwater and in air. Because accommodation to compensate for defocus involves the iris, and particularly the pupillary musculature, accommodation may prohibit active use of the pupil aperture as a light input regulating mechanism. This should be true particularly for snakes experiencing substantial defocus that requires excessive lens movement, although a few snakes are suspected of changing the shape of their lens, e.g., *T. melanogaster* (Schaeffel & de Queiroz, 1990) and *Natrix tessellata* (Beer, 1898).

While the work of Beer (1898), Heine (1907), Fritzberg (1913), Lesser (1914), Kahmann (1932) and Michel (1933) unanimously suggest that the iris musculature is responsible for lens displacement, deformation, or both, there is debate about how contraction of the musculature translates into forward movement and/or deformation of the lens (Ott, 2005). In addition, the studies of snake accommodation referenced above are nearly exhaustive in terms of available literature. That said, most of our knowledge of accommodation (and snake vision in general) is based on less than 25 of over 2700 species (McDiarmid, Camp-