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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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Received 7 May 2007; received in revised form 28 December 2007

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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. hammondi*, 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.

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**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 (Djamozy, 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,

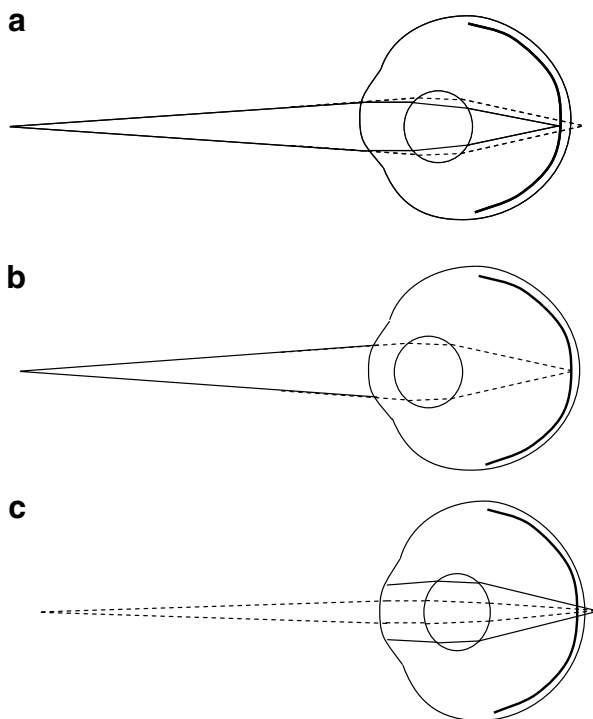


Fig. 1. (a) Effect of water immersion: Solid lines show rays converging on retina (i.e., forming image). Dotted lines show effect of immersion in water—loss of refractive index difference at spectacle results in loss of vergence at spectacle. Rays now converge to a point behind retina (i.e., image distance 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.

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).

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 suggests 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-

bell, & Toure, 1999). The paucity of information is particularly surprising given that snakes occupy such a variety of habitats and niches (e.g., marine, semi-aquatic, terrestrial, fossorial, sand swimming, arboreal) and likely hold some very interesting innovations.

There are, of course, also ecological implications of vision system adaptations. If pupillary constriction provides a substantial amount of acuity enhancement, it may play a role in the differential foraging ability of semi-aquatic snakes. This is of interest in a resource partitioning context, particularly with sympatric congeners like the *Thamnophis* of southern California, where *T. hammondi* is considered an aquatic specialist, *T. sirtalis* a terrestrial generalist, and *T. atratus* an intermediate between the two. Thus, pupillary constriction may be the mechanism behind aquatic foraging ability, and this study takes the opportunity to compare among syntopic congeners.

The purpose of the present study was to determine the role of a variable pupil in *Thamnophis* by comparing among species the pupillary response to (1) submergence underwater and (2) light intensity, and (3) whether pupillary constriction may be responsible for differences in foraging ability.

## 2. Materials and methods

The original research reported herein was performed under guidelines established by the Institution of Animal Care and Use Committee at the University of California, Santa Barbara, and proper state permits were obtained. A total of 21 snakes (6 *T. atratus*, 11 *T. hammondi*, and 4 *T. sirtalis*) was collected from LaBrea Creek, Santa Barbara Co., CA, and maintained on a diet of fish in a temperature (27 °C) and photoperiod (12 light:12 dark) controlled laboratory for 2–10 days for experimental trials, then returned to their sites of capture. To determine the effect of light and medium (air vs. water) on pupillary constriction, each individual was exposed in air to nine different (increasing) light intensities, and the procedure then repeated with the snake underwater.

A square tube 30 cm long and 2.5 cm in diameter was constructed of 2 mm thick clear plexiglass. I chose a square tube to eliminate potential problems with diffractive distortion associated with viewing a subject through the curved surface of a round tube; use of a tube also reduces potential stress. Because the snake's photoreceptors respond to the number of photons (rather than the photon's energy), light intensity (photon flux per unit area) was measured in microEinsteins per square meter per second ( $\mu\text{E}/\text{m}^2/\text{s}$ ) (Ender, 1990) with a LI-COR LI-192S Underwater Quantum Sensor. The tube was placed into a 120 × 35 × 45 cm (height) aquarium with sides covered by white (for high reflectivity) poster board to hide the observers outside. On top of the aquarium was a 35 × 35 cm wooden frame that held eight photographic 50% Filter Gel transparencies, used to control the amount of light entering; the rest of the top was covered by white poster board. Each filter reduced the amount of light entering the aquarium by 50%. A hole was cut into the poster board on the front side of the aquarium, where an eight mm Sony CCD-TR21 Video Camera Recorder was mounted, which pressed the poster board against the glass to insure no light leakage.

Trials were conducted in Santa Barbara, CA from 23 June to 1 December 1994, between 1000 and 1400 h (primary field activity times for the study species) in ambient direct sunlight, on clear days. With videotape recording the snake's pupillary response, the light intensity was recorded for 20 s, then one light filter removed and light intensity recorded for 20 s, another filter removed, etc. When all eight light filters had been removed, the last (ninth) measurement from the tube was of full sunlight. Because each filter reduced the incoming light by 50%, as each filter was

removed from the stack, the light intensity doubled, resulting in a geometric distribution of light intensity values. The tube was then filled with water, light filters replaced, and the procedure repeated for the same snake. Because other factors such as fear can cause pupillary constriction, and a light to dark order of light intensity presentation might be perceived by the snake as a predator passing overhead, a sequence of dark to light was chosen.

The eyes were photographed along the optic axis so that iris and pupil diameters were from circular profiles as opposed to ellipses. Measurements of the snake's iris and pupil were taken from a 48 cm video monitor; the pupillary responses in the video were also inspected to ensure that they were sustained and not transitory. To determine whether the surface of the eye magnified the pupil to produce an "entrance" (vs. the real) pupil, the refractive power of the spectacle was calculated. In snakes, the cornea is covered by the transparent spectacle, which is the evolutionarily derived from the fusion of the upper and lower eyelids. The spectacle has a very high refractive index of approximately 1.5 and replaces the cornea as a refractive element, as the refractive indices of the subspectacle fluid, cornea, and aqueous humor are each approximately 1.3 (Sivak, 1977). The refractive indices given by Sivak (1977) were from three other colubrid snakes but were very similar between species, and those numbers were used in the calculations for the *Thamnophis* species here. The radius of curvature is more a function of body size than species, at least in *Thamnophis*, and was estimated for snakes in this study to be 1.7 mm, based on Schaeffel and de Queiroz (1990, Fig. 6). Thus, the magnification power of the spectacle was calculated to be 1.12 in air, and 0.92 in water. The raw "entrance" pupil measurements were then multiplied by the magnification power accordingly to determine the actual pupil diameters, which were then used in data analyses. For comparison of the effect, data analyses were run both with and without the magnification adjustment, and found to make no statistical difference. However, only the magnification-adjusted data are reported.

Pupillary constriction was represented as the relative aperture, to account for individual and species differences in body size, and will be used to refer to the pupil aperture as a "structure". This was calculated as: Relative Aperture = Pupil Area/Iris Area. Pupillary constriction refers to the process of reduction rather than the absolute aperture. Because the relative aperture is a ratio, data were log transformed for use in statistical analyses. Also, because eyes respond to the log of the light intensity, light values were also log transformed.

To evaluate whether the light intensities presented in experimental trials were representative of what snakes would be exposed to in the field, a sample of light measurements was taken at LaBrea Creek between 1000 and 1400 h, on 1 May, 1 June, and 1 July. These were done on clear days in full sunlight, with times during the summer representative of when snakes are typically foraging in the creek for tadpoles and fish. Measurements in air were taken at the ground surface where most *Thamnophis* would be, one meter from the creek to avoid reflection from the water surface. Water measurements were taken at 10 cm below the water surface in a 30 cm deep pool with a gravel bottom, an area typical of where most snakes would be foraging for fish or tadpoles.

The experimental light values in air were similar to those collected in the field, barely exceeding the field range (experimental = 30–900  $\mu\text{E}/\text{m}^2/\text{s}$ , field = 3–840  $\mu\text{E}/\text{m}^2/\text{s}$ ). However, the experimental light values in water far exceeded the range of water light values collected in the field, presumably because the water depth for the light sensor in the experimental trials was only about 1 cm (experimental = 2–480  $\mu\text{E}/\text{m}^2/\text{s}$ , field = 0.25–12  $\mu\text{E}/\text{m}^2/\text{s}$ ). In either case, the ranges of field light intensities are largely included within the experimental light intensity ranges, so the relative aperture responses seen here should be a reasonable representation of what happens in the field. In addition, having the experimental range of light values similar between air and water is fortuitous because any difference in pupil aperture is then attributable to the medium, rather than being confounded by uneven comparison of light values.

To determine the effect of light intensity, species, medium, and individual variation on pupillary constriction, ANCOVA (Analysis of Covariance) was used with log relative aperture as the dependent variable, light as the covariate, and species, medium, and "individuals" as independent



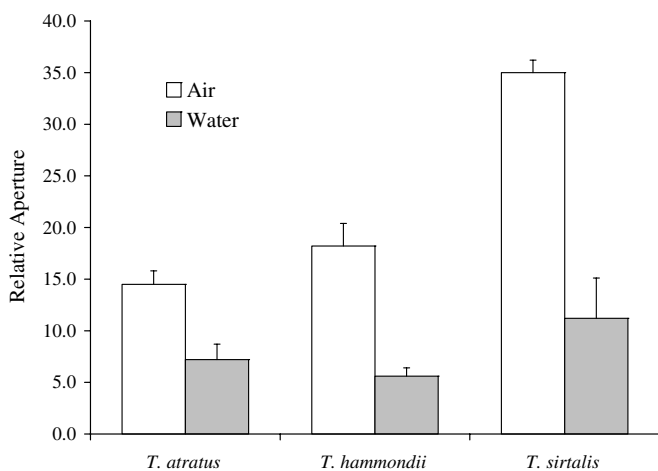


Fig. 2. Comparison of mean relative aperture in three species of *Thamnophis* in air and water. The mean relative apertures were in full sunlight with light means in microEinsteins for air and water, respectively, of 385, 207 (*T. atratus*,  $n = 6$ ), 521, 348 (*T. hammondii*,  $n = 11$ ), and 556, 358 (*T. sirtalis*,  $n = 4$ ).

categorical variables. To refine the model and produce the most robust test, non-significant variables were removed and the model retested. To avoid dependence among data points (an assumption of ANCOVA), individuals were coded as such for use as a variable because the data points were “pseudo-replicates” in that there were nine light (and respective pupil) values for each snake (Hair, Anderson, Tatham, & Black, 1998). The “individuals” variable was then nested within species, and the “individuals” mean-square used as the denominator in  $F$ -tests for each effect in the model, which accounts for the replicate-inflated sample size (Neter, Wasserman, & Kutner, 1990). Because each of the  $F$ -values was calculated by hand, statistical probabilities are reported relative to critical values, rather than the actual probabilities.

To produce a clear understanding of the effect of light (independent variable) on relative aperture (dependent variable), Regression Analyses were performed for each species (air and water data separately). Separate ANOVAs were used to determine the effect of medium (air vs. water) for each species. Because reduction in relative aperture underwater was presumed to be a method of adjusting for underwater defocus (Schaeffel & de Queiroz, 1990), which may be responsible for species differences in aquatic prey specialization, species pairs were tested separately (three tests) by ANOVA for differences in relative aperture underwater. In addition, data for *T. atratus* and *T. hammondii* were combined as an “aquatic” group and compared to *T. sirtalis* (a terrestrial generalist). Examination of scatterplots confirmed that assumptions for parametric statistics (normality, homoscedacity, linearity) were met. Statistical significance was  $P < 0.05$  unless otherwise indicated.

### 3. Results

#### 3.1. Effect of light

Preliminary ANCOVA showed no difference in slopes among individuals (individual  $\times$  light interaction) ( $df = 21, 19, F = 0.03, P > 0.1$ ), nor was there a species  $\times$  medium interaction ( $df = 2, 19, F = 0.50, P > 0.1$ ), and these variables were dropped from subsequent analyses. In a general model with light as the covariate, species (all three), medium, and individual (nested within species) as categorical independent variables, and log relative aperture as the dependent variable, ANCOVA indicated no sig-

nificant effect of light ( $df = 1, 19, F = 1.10, P > 0.1$ ). None of the six separate Regression Analyses (by species for air and water) showed a significant relative aperture response to light intensity, and light was also dropped from subsequent analyses. That light had no effect on relative aperture was rather startling, as a positive relationship is generally the case for most vertebrates (Erichsen et al., 2000). Fig. 3 shows for *T. atratus*, *T. hammondii*, and *T. sirtalis* separately, the lack of relationship between light intensity and relative aperture, and the effect of air and water. These show data for only two arbitrarily chosen but representa-

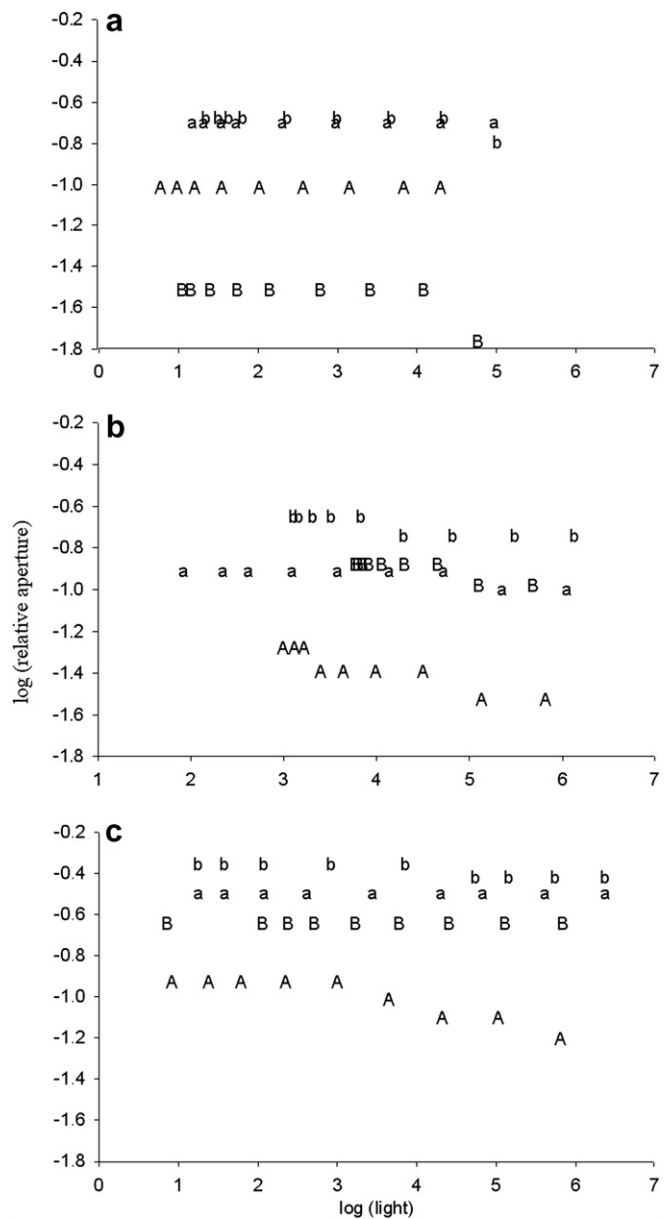


Fig. 3. Representative scatterplots showing the relationship between light intensity and relative pupil aperture, and the effect of air vs. water for (a) *T. atratus*, (b) *T. hammondii*, and (c) *T. sirtalis*. Each individual's data points are represented by a letter, with data for air in lower case and water in upper case. For clarity, only data for two arbitrarily chosen individuals per species are shown.

tive individuals per species. There were, however, significant differences in relative aperture among species ( $df = 2, 18, F = 6.76, P < 0.05$ ), media ( $df = 1, 18, F = 47.37, P < 0.001$ ), and individuals ( $df = 18, 355, F = 32.44, P < 0.0001$ ).

### 3.2. Air vs. water

All three species reduced their relative aperture underwater (Fig. 2), and ANOVA performed on each species separately supported this observation: *T. atratus* ( $df = 1, 5, F = 18.82, P < 0.01$ ), *T. hammondi* ( $df = 1, 10, F = 21.85, P < 0.001$ ), and *T. sirtalis* ( $df = 1, 4, F = 15.93, P < 0.05$ ). Differences in relative aperture between air and water in Fig. 2 suggest that *T. sirtalis* has a greater range of mobility than either *T. atratus* or *T. hammondi*. This may reflect differences in ability to control light input or differences in the mechanics of the vision system.

### 3.3. Species comparisons

The mean relative apertures showed only small differences between *T. atratus* and *T. hammondi*, which were not significant for air ( $df = 1, 15, F = 0.38, P > 0.1$ ) nor water data ( $df = 1, 15, F = 0.20, P > 0.1$ ). *T. sirtalis* had a significantly greater relative aperture in air than both *T. atratus* ( $df = 1, 8, F = 52.75, P < 0.001$ ) and *T. hammondi* ( $df = 1, 13, F = 12.64, P < 0.01$ ). However, there was no statistical difference in relative aperture underwater between *T. sirtalis* and *T. atratus* ( $df = 1, 9, F = 0.68, P > 0.1$ ) nor between *T. sirtalis* and *T. hammondi* ( $df = 1, 14, F = 1.46, P > 0.1$ ). With data for *T. atratus* and *T. hammondi* combined as an “aquatic” group, there was still no difference vs. *T. sirtalis* ( $df = 1, 14, F = 1.45, P > 0.1$ ).

## 4. Discussion

### 4.1. Light

The only garter snake photoreceptors studied (*T. sirtalis*), showed an all-cone retina (Jacobs et al., 1992). With no photoreceptors that are particularly effective at low light levels, the lack of a pupillary response was especially surprising because these species regularly experience a range of light intensities. In particular, *T. hammondi* forages for fish in rock crevices at depths up to 3 m (pers. obs.).

Little other information is available regarding the effect of light on pupillary constriction in snakes. Although the objectives and methods of Werner (1970) were different from this study, several colubrid species tested (i.e., *Coluber rogersi*, *Psammophis schokari*, *Malpolon monspessulanus*) showed little pupillary response to light, while *S. diadema* showed a very clear pupillary constriction response to light. Anecdotal personal observations during informal preliminary tests of North American terrestrial colubrid snakes (e.g., *Lampropeltis getula*, *Coluber constrictor*, *Pituophis*

*catenifer*, *Pantherophis obsoleta*) showed obvious pupillary constriction in response to sunlight. Thus, differences in pupillary responses (including both measured and anecdotal reports) are not explained purely by activity patterns.

The significant within-species variation in relative aperture among individuals may have been due to differences in stress. Interestingly, Werner (1970) also reported a substantial amount of intra-individual variation in *S. diadema*, which was dramatically true in the present study. Part of the reason for observing the snakes in a tube was that preliminary trials showed a substantial reduction in relative aperture in response to tactile stimuli (touching the snake while holding it under a dissecting microscope). Because the pupil is presumably under sympathetic nervous control, it is also possible that temperature, odor, or some other stimulus could have influenced individual responses. Alternatively, if accommodation is linked to pupillary constriction, individual variation may have resulted from differences in distance to the object on which each individual was focusing. Individual snakes could have been focusing on the tube in which they were contained or any point within the aquarium (including the camera), any of which would have been at different distances.

### 4.2. Air vs. water

While all three species showed a distinct relative aperture reduction in response to submergence underwater, a more relevant aspect is the minimum aperture achieved, rather than the range of aperture sizes possible. This consideration is critical because the potential for a large range of relative apertures is limited by the relative aperture size in air. For example, a snake like *T. atratus* whose relative aperture in air is 0.15 has only a 15% theoretical capacity for further reduction, whereas *T. sirtalis* is beginning in air with 0.27, for a 27% constriction capacity. Thus, range of pupil variability as an index of vision enhancement can be misleading because semi-aquatic snakes relying heavily on aquatic prey may be evolutionarily committed to aquatic vision by having the initial pupil size relatively small in air.

In a foraging context, if the reduced aperture indeed affords an increase in acuity, then at what point do prey items like fish (at a given distance) become visibly distinct enough to detect and pursue? Presumably, at some point in aperture reduction all objects at any distance come into focus, but at what point that occurs for these snakes was not tested. However, the decreasing average aperture size underwater (Fig. 2) for *T. sirtalis*, *T. atratus*, and *T. hammondi*, corresponds to increased aquatic specialization of each species, respectively (Drummond, 1983; Dunn, 2004; Rossman, Ford, & Seigel 1996), as well as the distance at which they can detect prey underwater (pers. obs.). Thus, although differences in underwater relative apertures were not statistically significant among species, the differences were consistent with behavioral ability and may be ecologically important. If a small relative aperture in air facilitates

achieving a smaller minimum relative aperture, and minimum relative aperture is a good indicator of visual acuity, both *T. atratus* and *T. hammondi* seem equally well adapted.

#### 4.3. Snake vision

As introduced in the beginning of this paper, the concept of aperture reduction in low light conditions seems counterintuitive. However, consideration of the evolution of snake eyes is instructive. The spherical lens of snakes is an inherently difficult shape because light rays striking the periphery of the lens are increasingly aberrant and detract from the clarity of the image. The reduced aperture has two related effects. (1) Incoming light rays experience the least refraction possible because they are restricted to the center of the lens surface and enter at a more perpendicular angle. Similarly, (2) the reduced aperture excludes rays that would strike the periphery of the spherical lens and become aberrant. The reduced aperture may be more important for acuity than accommodation via lens movement, particularly underwater, but it also functions to reduce the Stiles–Crawford effect (Snyder & Love, 1983). The resulting increase in depth of field at such a reduced relative aperture may even preclude the need for much lens movement.

If these factors increasing visual acuity are intimately linked to pupillary constriction, we would expect to see extensive constriction when an aquatic snake enters the water because of the effect of the change in refractive index. Consequently, these snakes may not have much ability to regulate light input because the pupil is committed to a function of accommodation, which seems a plausible explanation for the lack of a pupillary response to light in the present study.

All studies of *Thamnophis* species thus far (i.e., *T. atratus*, *T. couchii*, *T. hammondi*, and *T. sirtalis*) show a significant reduction in relative aperture upon submergence underwater (Schaeffel & de Queiroz, 1990; this study). Interestingly, a study of closely related water snakes (*Natrix*) showed little pupillary response to water but substantial defocus in *N. natrix*; only moderate pupillary constriction with no defocus occurred in *N. tessellata* and *N. maura* (Schaeffel & Mathis, 1991). This led Schaeffel and Mathis (1991) to suggest that the mechanism of pupillary constriction would not be sufficient to overcome the amount of defocus calculated for those species, and that some other mechanism must be involved such as lens deformation, but this has not been tested yet for any snake species.

Taken together, there is a lot of variation in how different species are compensating for defocus, most of it based on semi-aquatic species. For example, *T. couchii* and *T. atratus* showed substantial pupillary constriction underwater, but were hypermetropic (Schaeffel & de Queiroz, 1990); despite their hypermetropia, both are successful piscivores (Rossman et al., 1996; pers. obs.). On the other

hand, *T. melanogaster* and *T. rufipunctatus* (both piscivorous) showed only modest pupillary constriction underwater, but were emmetropic (Schaeffel & de Queiroz, 1990). A table from Walls (1942, p.273) indicates that the pupil of sea snakes is stenopaic when out of water. While no species name or reference is given, all sea snakes are fully aquatic and spend most of their lives in water, but many mate, bask, and lay eggs or give birth on land (Greene, 1997). In this case, myopic sea snakes out of water may also benefit from increased depth of field afforded by pupillary constriction.

Personal anecdotal observations of terrestrial colubrids, combined with the *S. diadema* light response observed by Werner (1970) brings into question the hypothesis that the light-regulating role of the pupil may be restricted by the connection between pupillary constriction and accommodation in snakes. While the hypothesis may be plausible, it may only occur in semi-aquatic taxa. Again, however, our knowledge of accommodation in snakes is based on just a few of more than 2700 species, and most studies of accommodation have produced conflicting conclusions (Kahmann, 1932; Michel, 1933; Ott, 2005). Thus, any interpretation based on ophidian accommodation must be considered with caution, pending comparative studies among snake taxa.

#### Acknowledgments

Brett Wilson was instrumental to data collection in the lab trials; this study would not have been possible without his help. Gary Shaffer provided statistical advice, and David Norwood assisted with the production of Fig. 1. Volker Stiller provided translation of the German references. Samuel Sweet, John Endler, and Alan de Queiroz, provided helpful comments on earlier versions of this manuscript. For all of these contributions, I am deeply grateful.

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