



Size of Snake Eyes Correlates With Habitat Types and Diel Activity Patterns

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Eye size influences visual acuity, sensitivity, and temporal resolution and is a result of vertebrate adaptation to the environment. The habitats of snake species are diverse, ranging from fossorial, terrestrial, arboreal, to aquatic. They also demonstrate a variety of behavioral and physiological characteristics, such as activity time, feeding patterns, and prey detection. In this study, we comparatively investigated how the relative eye size (i.e., eye diameter vs. head width) associated with the ecological (i.e., habitat), behavioral (i.e., diel activity pattern, foraging strategy), and physiological traits (i.e., the presence of pits), respectively, across six snake families from Taiwan. Among the traits we examined, we found that terrestrial and/or diurnal snakes tended to exhibit the larger relative eye size, indicating the evolutionary responses of eye size to changes in habitat types and activity patterns, respectively, while no evidence of how foraging strategies and the presence of pits affected snake eye size was found. Our findings not only shed light on the adaptive significance of the visual system in diversifying the behaviors and the environments exploited in snakes, but also underline the interactive effects of multidimensional evolutionary attributes (e.g., behavior, ecology, physiology and phylogeny) on the evolution of optimal visual performance.

Keywords: snake eye size, diel activity patterns, habitat type, allometric growth, phylogenetic regression

INTRODUCTION

Vision is a crucial sensory system connecting organisms to their environments. Eye size, which positively associates with the amount of photoreceptors in eyes (Land and Nilsson, 2002), determines visual acuity, sensitivity, and temporal resolution (Roaf, 1943; Land and Nilsson, 2002). Such a morphological trait can further account for the functional mechanisms of how species adapt to the environmental lights given their physical limitations. For example, organisms with the larger eyes may possess better foraging efficiency due to the improved visual resolution and/or the greater light sensitivity (Land and Nilsson, 2002; Thomas et al., 2006; Ausprey et al., 2021); yet, they may be imposed by higher energy expenditure simultaneously [e.g., the increased body weight (Laughlin, 1995), the development and maintenance of a large number of nerve cells (Laughlin et al., 1998), and/or susceptibility of eye (Harper, 1988)]. Thus, eye size may represent an ideal

indicator of the visual requirements underlying the evolutionary tradeoffs between visual functions and energy expenditure.

In many vertebrates, the absolute eye size often varies allometrically with body size-associated traits [e.g., body length (Burton, 2008), body weight (Howland et al., 2004), head size (Kirk, 2006)], while the relative eye size tightly corresponds to ecological and behavioral attributes of species, such as habitat types (Liu et al., 2012; Thomas et al., 2020), diel activity patterns (Liu et al., 2012; Schmitz and Higham, 2018), and foraging strategies (Thomas et al., 2006; Lisney and Collin, 2007). Currently, the evolution of eye size has been studied thoroughly in many taxa [e.g., fishes (Caves et al., 2017; Vinterstare et al., 2020), frogs (Shrimpton et al., 2021), geckos (Werner and Seifan, 2006), birds (Thomas et al., 2006; Burton, 2008) and mammals (Kirk, 2006; Heard-Booth and Kirk, 2012; Nummela et al., 2013)]. However, it is relatively underexplored how the eye size across different snake species is shaped by the environment, facilitating their demands for behavioral activities and foraging strategies (Katti et al., 2019). For example, it is unclear whether the size of eyes is different in the snakes adopting active and sedentary foraging strategies. Also, do snakes modify the investment in eye size, given the high physiological costs incurred, if they are able to sense environmental cues using the additional sensory system (e.g., pit for infrared perception)?

Snakes have shown the remarkable ability to adapt to diverse environments (Greene, 1997). They heavily rely on visual cues when evaluating the environment (Danaisawadi et al., 2016; Schraft and Clark, 2019) and have been suggested to possess dichromatic vision (Bittencourt et al., 2019). Many of them possess rod and cone opsins (Simões et al., 2015, 2016) and thus are able to perceive different light intensities and colors (Bittencourt et al., 2019). In Colubridae, nocturnal species had larger eyes than diurnal species and species that inhabit arboreal habitats tend to have larger eyes compared with terrestrial or semiaquatic species (Liu et al., 2012). This suggested that the intensity and the propagation of lights provided by different environments can drive the evolution of snake eyes. In the watersnakes that heavily live on frogs, it has been found that the eye size was positively associated with the proportion of frogs in the diet, suggesting that larger eyes benefited the foraging ability of the snakes (Camp et al., 2020). Given the importance of vision in the foraging behavior of snakes, understanding the evolution of snake eyes can thus provide us deeper insights into the diversification of eye morphology and its role in regulating predator-prey interactions across different environmental gradients.

In this study, we examined how the habitat types, behavioral patterns (i.e., foraging strategies, diel activity patterns), and physiological conditions (i.e., the presence of pits) associate with the eye size across multiple snake families, respectively. Based on the potential visual requirements in the given environmental conditions and/or behavioral strategies, we predicted that (1) terrestrial and arboreal snakes should have larger eyes than aquatic snakes; (2) snakes that actively hunt prey have larger eyes than those that ambush; (3) diurnal snakes have larger eyes than nocturnal snakes; and (4) snakes with pits tend to have smaller eyes.

MATERIALS AND METHODS

We examined the specimens of 33 snake species deposited in the National Museum of Natural Sciences (NMNS) in Taiwan. All of the species inhabit mainland Taiwan and the surrounding islands. The systematic classification included the earliest differentiation of the blind snake family (one species; Typhlopidae) and the Xenodermidae (one species), the Viperidae (five species), the Homalopsidae (two species), the Pseudaspidae (one species), the Elapidae (six species), and the latest differentiation of the Colubridae (17 species). The sample size of each species ranged from 3 to 207 individuals, for a total of 1,176 individuals.

We identified the habitat type, the diel activity pattern, the foraging strategy, and the presence of pits of each snake species based on Tu (2004) (Table 1). We measured the diameter of the left eye and head width of the specimens using a vernier scale (accurate to 0.1 mm; electronic vernier calipers; code number 500–138; model: CD-8" BS, [Mitutoyo (Mitutoyo) Corporation, Japan]). We defined the eye diameter as the maximal diameter of the visible spectacle as the horizontal width of the inner edge of the eye contact from the nearest scale of the eye, and the head width as the widest maximal distance between the cheeks when looking down on the head (Supplementary Figure 1). Since the eyes of blind snakes are vestigial (Greene, 1997), we excluded the measurement of blind snakes from the subsequent analyses.

We estimated the effect of the specific ecological/behavioral/physiological factors on the relative eye size (i.e., regressed by the head size) among the six snake families using Bayesian general linear mixed-effect models. The models allowed us to take accounts of the phylogeny and repeated measurements simultaneously. The model was derived as below:

$$\ln(Y_{ij}) = \alpha + (\gamma_p + I_{1i} + I_{2i}) + (\beta + L_{1i} + L_{2i}) \ln(X_{ij}) + c_p \ln(X_{ij}) + \varepsilon_{ij}$$

with the following priors:

$$\alpha, \beta, \gamma, c \sim T(\text{DF} = 3),$$

$$\sigma_I, \sigma_L \sim T_+(\text{DF} = 3),$$

$$\text{Cor}(I), \text{Cor}(L) \sim \text{LkjCholesky}(1),$$

$$\sigma_\varepsilon \sim \text{Scaled } T_+(\text{DF} = 3, \text{scale} = 2.5),$$

where Y and X denote eye diameter and head width; i and j denote species and different samples within species, respectively, α and β denoted the overall intercept and slope, respectively, ε_{ij} denoted the random errors; I and L denoted the random intercept and slope of i th species. The fixed effect, γ_p , including (1) snake family (i.e., Colubridae, Elapidae, Homalopsidae and Viperidae), (2) habitat types (i.e., seawater, freshwater, terrestrial and arboreal), (3) diel activity patterns (i.e., diurnal, cathemeral

TABLE 1 | Summary of the behavioral characteristics, head width and eye diameter of the 33 snake species from Taiwan used in this study.

| Species | Hab. | Act. | For. | FP | N | HW mean ± SD (mm) | ED mean ± SD (mm) |
|--------------------------------------|------|------|------|-----|-----|-------------------------|-------------------------|
| Colubridae | | | | | | | |
| <i>Ptyas dhumnades</i> | T | D | Ac | W/o | 13 | 11.44 ± 3.566 | 6.53 ± 1.357 |
| <i>Ptyas major</i> | A | D | Ac | W/o | 9 | 12.26 ± 2.691 | 3.34 ± 0.609 |
| <i>Ptyas mucosa</i> | T | D | Ac | W/o | 5 | 18.86 ± 3.591 | 6.18 ± 0.783 |
| <i>Ptyas korros</i> | T | C | Ac | W/o | 57 | 17.76 ± 3.171 | 7.13 ± 0.867 |
| <i>Elaphe carinata</i> | T | C | Ac | W/o | 83 | 15.05 ± 5.063 | 4.09 ± 1.405 |
| <i>Elaphe taeniura</i> | T | C | Ac | W/o | 6 | 24.04 ± 8.545 | 6.33 ± 0.991 |
| <i>Oreocryptophis porphyraceus</i> | T | N | Ac | W/o | 4 | 11.79 ± 2.997 | 3.18 ± 0.408 |
| <i>Boiga kraepelini</i> | A | C | Ac | W/o | 6 | 13.68 ± 3.394 | 4.29 ± 0.626 |
| <i>Lycodon ruhstrati</i> | T | N | Ac | W/o | 7 | 9.35 ± 3.139 | 2.34 ± 0.548 |
| <i>Lycodon rufozonatus</i> | T | N | Ac | W/o | 22 | 13.51 ± 3.581 | 3.17 ± 0.460 |
| <i>Oligodon ornatus</i> | T | D | Ac | W/o | 4 | 7.70 ± 2.123 | 2.46 ± 0.661 |
| <i>Oligodon formosanus</i> | T | C | Ac | W/o | 9 | 11.11 ± 1.993 | 2.89 ± 0.203 |
| <i>Trimerodytes annularis</i> | F | N | Ac | W/o | 80 | 18.56 ± 6.552 | 3.26 ± 0.929 |
| <i>Rhabdophis tigrinus</i> | T | D | Ac | W/o | 3 | 12.42 ± 2.567 | 4.03 ± 1.455 |
| <i>Fowlea piscator</i> | T | D | Ac | W/o | 79 | 14.49 ± 4.242 | 3.64 ± 0.677 |
| <i>Amphiesma stolatum</i> | T | D | Ac | W/o | 3 | 5.72 ± 1.065 | 2.80 ± 1.047 |
| <i>Pseudagkistrodon rudis</i> | T | C | Ac | W/o | 3 | 16.39 ± 8.702 | 4.25 ± 1.553 |
| Elapidae | | | | | | | |
| <i>Hydrophis melanocephalus</i> | S | D | Ac | W/o | 28 | 12.90 ± 3.171 | 2.02 ± 0.395 |
| <i>Emydocephalus ijimae</i> | S | D | Ac | W/o | 7 | 14.65 ± 1.852 | 2.70 ± 0.428 |
| <i>Laticauda semifasciata</i> | S | C | Ac | W/o | 53 | 21.04 ± 6.687 | 3.15 ± 0.772 |
| <i>Laticauda colubrina</i> | S | C | Ac | W/o | 144 | 19.35 ± 4.000 | 3.30 ± 0.524 |
| <i>Bungarus multicinctus</i> | T | N | Ac | W/o | 207 | 15.55 ± 2.536 | 2.29 ± 0.335 |
| <i>Naja atra</i> | T | D | Ac | W/o | 98 | 24.43 ± 4.609 | 4.30 ± 0.530 |
| Pseudaspidae | | | | | | | |
| <i>Psammodynastes pulverulentus</i> | T | C | Ac | W/o | 13 | 9.00 ± 1.986 | 3.23 ± 0.426 |
| Homalopsidae | | | | | | | |
| <i>Myrrophis chinensis</i> | F | N | Ac | W/o | 65 | 13.37 ± 5.466 | 1.89 ± 0.473 |
| <i>Hypsicopus plumbea</i> | F | C | Ac | W/o | 3 | 9.59 ± 4.812 | 1.93 ± 0.558 |
| Viperidae | | | | | | | |
| <i>Protobothrops mucroscquamatus</i> | T | N | Am | W/ | 19 | 16.34 ± 1.433 | 3.07 ± 0.354 |
| <i>Trimeresurus stejnegeri</i> | T | N | Am | W/ | 37 | 16.67 ± 3.399 | 3.38 ± 0.399 |
| <i>Deinagkistrodon acutus</i> | T | N | Am | W/ | 36 | 28.46 ± 3.399 | 3.99 ± 0.619 |
| <i>Daboia siamensis</i> | T | C | Am | W/o | 36 | 22.38 ± 4.359 | 3.82 ± 0.493 |
| <i>Pareas formosensis</i> | T | N | Ac | W/o | 9 | 7.36 ± 0.834 | 3.04 ± 0.471 |
| Xenodermidae | | | | | | | |
| <i>Achalinus formosanus</i> | T | N | Ac | W/o | 9 | 6.32 ± 1.867 | 1.25 ± 0.189 |

(Continued)

TABLE 1 | (Continued)

| Species | Hab. | Act. | For. | FP | N | HW mean ± SD (mm) | ED mean ± SD (mm) |
|------------------------------|------|------|------|-----|----|-------------------------|-------------------------|
| Typhlopidae | | | | | | | |
| <i>Indotyphlops braminus</i> | T | N | Ac | W/o | 19 | 4.24 ± 0.654 | 0 ± 0 |

Hab, Habitat; T, terrestrial; A, arboreal; S, seawater; F, freshwater. Act, daily activity pattern: D, diurnal; C, cathemeral; N, nocturnal. For, foraging type: Ac, active; Am, ambush; FP, facial pit; HW, head width; ED, eye diameter. The species are listed in the same order as in Figure 1. The information of habitat types, diel activity patterns, and foraging strategies were based on Tu (2004).

and nocturnal), (4) foraging strategies (i.e., active and ambush), or (5) the presence of pits (present and absent), were examined, respectively, in the models. We also included the interaction term between the fixed factor examined and the head width, $c_p \ln(X_{ij})$, where c_p denoted the interaction effect.

Including the two parameters, I_1 and L_1 , allowed us to take account of the intraspecific variation caused by repeatedly measuring multiple snake individuals within the same species. The other two parameters, I_2 and L_2 , allowed us to adjust the proportionality coefficients and allometric growth indices of each species, eliminating the problem of false duplication of relatives. The covariance matrix adopted in this study was based on the most approximate affinity tree published in Figueroa et al. (2016) (see **Supplementary Figure 2**; Hadfield and Nakagawa, 2010). Given that four species from our study were not included in Figueroa et al. (2016), we substituted them by the most phylogenetically closest species (**Supplementary Figure 2**). We yielded the final results using the averaged models, where we were able to integrate the information of the posterior probabilities produced by the models including and excluding the interactive effects [i.e., $c_p \ln(X_{ij})$].

To better illustrate the effect of each of the fixed factors on the eye size of snakes, we introduced the term, expected eye diameter, to allow us to directly compare the eye size. The magnitude of expected eye diameter was extracted, based on the linear regression of the allometry of eye size vs. head width, at the point where the head width equaled 14.84 mm (i.e., the mean head width among all the snake species). We excluded the blind snake, *Indotyphlops braminus*, from all of the analyses (except for morphological description) because the eye size was very close to zero. We also excluded the other two species, *Achalinus formosanus* and *Psammodynastes pulverulentus*, from the analysis of the history of eye size evolution due to the small species number within the respective family.

The models were estimated using the Bayesian Markov chain Monte Carlo method with the R-based brms suite (Bürkner, 2018). Each linear model was tuned with 10,000 warm-up Markov chains. Thereafter, we ran 10,000 Markov chains and used the results as the posterior probability distribution of each parameter. To conduct the significance tests, we compared the posterior distribution of each parameter among the categorical levels of the targeted fixed factor, and calculated the median (hereafter, M), 95% highest density interval (HDI),

and two-tailed P_{MCMC} . The significant statistical difference between the two categories was recognized if the corresponding $P_{MCMC} < 0.05$, and vice versa.

RESULTS

Phylogeny

There was a significant negative allometric growth of eye diameter vs. head width in snakes (**Figures 1A,D**), since the overall median ($M = 0.469$) and 95% HDI [i.e., (0.361, 0.562)] were significantly smaller than 1 ($P_{MCMC} < 0.001$). The allometric growth (i.e., the slope) was the maximum in the Colubridae and the weakest in the Elapidae (**Table 2A**). Multiple comparisons indicated that the scaling coefficients were significantly higher in the Colubridae than in the Elapidae, but no significant differences existed between the other families (**Table 2A**). In the comparison of scaling coefficients, both Viperidae and Colubridae were significantly higher than the family Homalopsidae (**Table 2B** and **Figure 1B**). In comparing the expected eye diameters, significant differences were observed among the four groups (**Table 2C** and **Figures 1C,D**). The Colubridae have the largest eyes relative to head width, followed by the Viperidae, followed by the Elapidae, and the family Homalopsidae was the smallest (**Table 2C**). Taken together, the higher allometric growth index and proportionality coefficient of the later-emerging Colubridae resulted in a significantly larger increase in eye diameter with head width than the other three taxa, and a significantly larger expected eye diameter than the other three taxa (**Figure 1D**).

Habitat Types

In terms of the correlation between eye diameter and head width and habitat type, the median of the allometric growth index was very similar and not statistically significant for the four habitat types ($P_{MCMC} > 0.997$; **Figure 2A**). In terms of the proportionality coefficients, the magnitude of the terrestrial type was significantly higher compared with the freshwater type ($P_{MCMC} = 0.013$; **Figure 2B**) and marginally higher compared with the seawater type, respectively ($P_{MCMC} = 0.055$; **Figure 2B**). There was no significant difference in the proportional coefficients when comparing marine and freshwater types ($P_{MCMC} = 0.518$; **Figure 2B**) or the arboreal type with the other three types ($P_{MCMC} = 0.624$; **Figure 2B**). Similarly, in terms of the expected eye diameter, the magnitude of the terrestrial type was significantly higher compared with the freshwater type ($P_{MCMC} = 0.013$; **Figure 2C**) and marginally higher compared with the seawater type, respectively ($P_{MCMC} = 0.055$; **Figure 2C**). There was no significant difference in the expected eye diameter when comparing marine and freshwater types ($P_{MCMC} = 0.518$; **Figure 2C**) or the arboreal type with the other three types ($P_{MCMC} = 0.624$; **Figure 2C**). In summary, the relative eye diameter of aquatic snakes was significantly smaller than that of terrestrial snakes, and this phenomenon was mainly due to the difference in the ratio coefficients rather than the allometric growth index (**Figure 2D**).

Diel Activity Pattern

With regard to the correlation between eye diameter and head width and diel activity pattern, the median allometric growth index was higher for the diurnal type, but there was no statistically significant difference among the three types (**Figure 3A**). In terms of the proportionality coefficient, the coefficient for the diurnal type was the highest and significantly higher than that for the nocturnal type ($P_{MCMC} = 0.043$; **Figure 3B**), while the cathemeral type was at the intermediate level and did not differ significantly from the other two types (**Figure 3B**). In comparing the expected eye diameter, the median coefficient was the lowest for the nocturnal type ($P_{MCMC} = 0.038$; **Figure 3C**) and intermediate for the diurnal type ($P_{MCMC} = 0.038$; **Figure 3C**), which was not significantly different from the other two types (**Figure 3C**). In summary, the relative eye diameters of nocturnal snakes were significantly smaller than those of diurnal snakes, and this was mainly due to the difference in the scaling coefficients (**Figure 3D**).

Foraging Strategy and the Presence of Pits

We found no significant difference in the regression coefficients of the eye diameter when comparing the two foraging types (allometric growth index, $P_{MCMC} = 0.391$; proportionality coefficient, $P_{MCMC} = 0.469$; expected eye diameter, $P_{MCMC} = 0.581$; **Figure 4**). Also, we found no significant difference in the regression coefficients of the eye diameter when comparing the snakes with and without pit (allometric growth index, $P_{MCMC} = 0.350$; proportionality coefficient, $P_{MCMC} = 0.496$; expected eye diameter, $P_{MCMC} = 0.610$; **Figure 5**).

DISCUSSION

In this study, we demonstrated the important role of environmental pressures in driving the evolution of the eye size in snakes. Among the four families we examined, Colubridae exhibited the most apparent trend of evolutionary allometry of eyes. In addition, we showed that terrestrial and/or diurnal snakes have larger eyes, based on our comparative analyses, whereas foraging strategies and the presence of pits did not correlate with the relative eye size of the snakes we examined.

Phylogeny

Colubridae, the latest differentiated family examined in this study, have the larger relative eye size. This suggests that they may have developed better vision and/or relied more on the visual cues in engaging in the daily activities compared with the rest of more ancestral snake families. Such implications comply with the conventional thought regarding the evolutionary direction of snake vision. Snakes have improved the visual ability along with the evolutionary history. There might be up to five visual opsins present in the ancestral vertebrate (i.e., RH1, RH2, SWS1, SWS2, and LWS; Simões et al., 2015). While the snakes that belong to the basal lineage, scolecophidians, only express RH1 genes likely as an adaptation of fossorial habits, most of the stem snakes

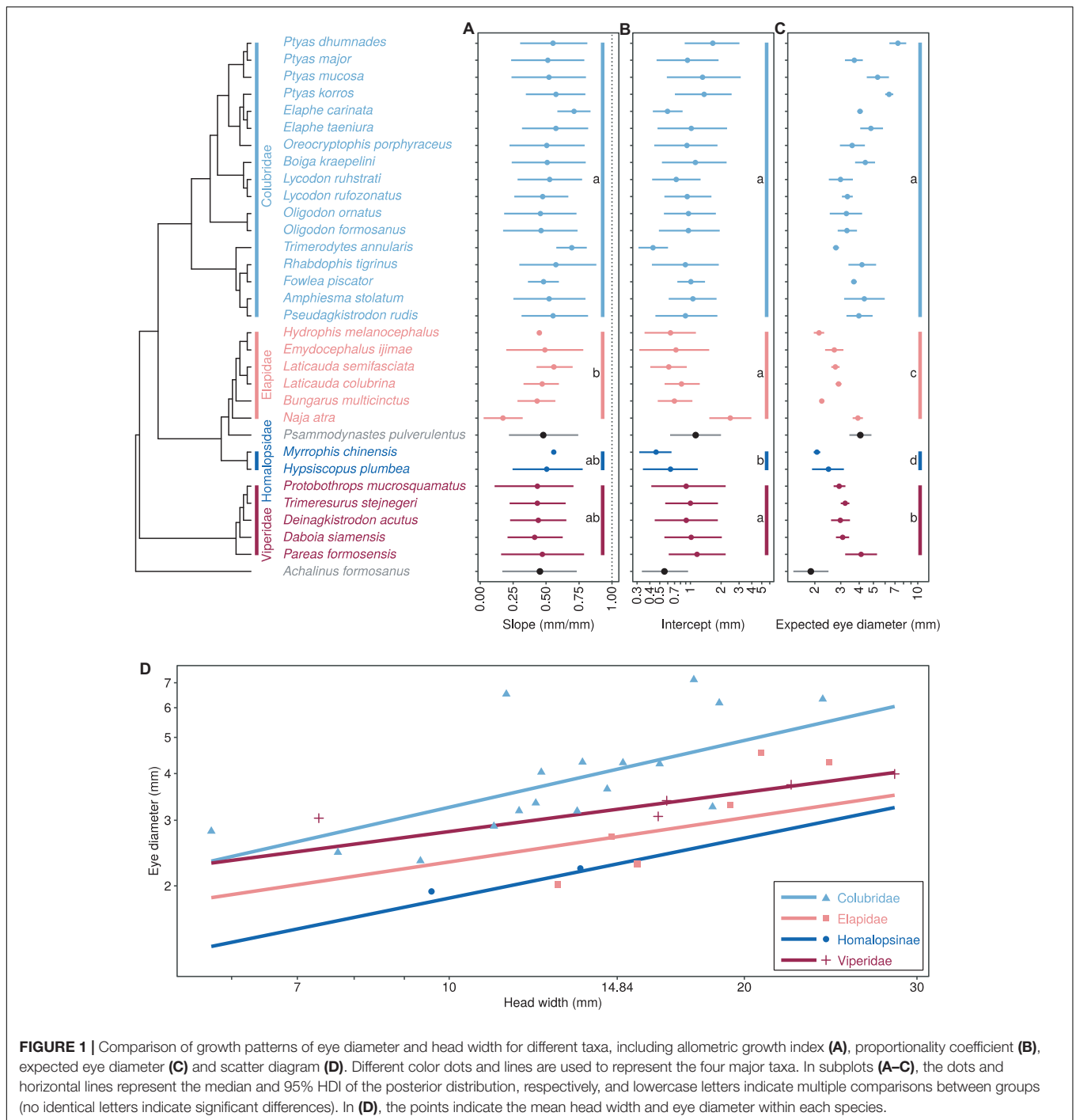


FIGURE 1 | Comparison of growth patterns of eye diameter and head width for different taxa, including allometric growth index (A), proportionality coefficient (B), expected eye diameter (C) and scatter diagram (D). Different color dots and lines are used to represent the four major taxa. In subplots (A–C), the dots and horizontal lines represent the median and 95% HDI of the posterior distribution, respectively, and lowercase letters indicate multiple comparisons between groups (no identical letters indicate significant differences). In (D), the points indicate the mean head width and eye diameter within each species.

express the additional two opsin genes that enable dichromatic color vision (i.e., SWS1 and LWS) (Tu, 2004; Davies et al., 2009; Simões et al., 2015; Katti et al., 2019). The better visual ability, as the result of the development of larger eyes (Corral-López et al., 2017), could have further advanced the performance of how they explore and utilize resources in the environment. Snakes have generally been considered to evolve from slow, passive cavity-dwelling predators to agile, aggressive predators (Underwood, 1967). The larger eye size associated with the extremely high

proportion of the active hunting strategy, at least among the Colubridae species examined here, may thus provides a hint on how the visual system could have facilitated the evolution of foraging strategies in this organism.

Habitat Type

Terrestrial snakes have a larger relative eye size than that inhabit the freshwater environments, while there was no difference in the relative eye size among the comparisons across other habitat

TABLE 2 | Summary of posterior distributions and multiple comparisons of scaling coefficients (A), proportionality coefficients (B) and relative eye diameters (C) among four clades.

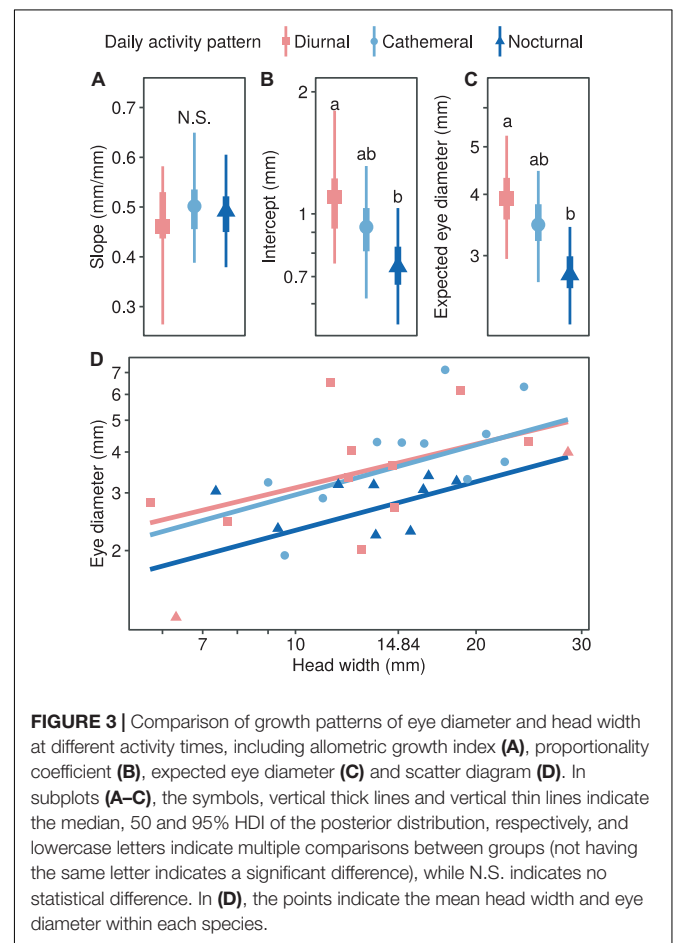
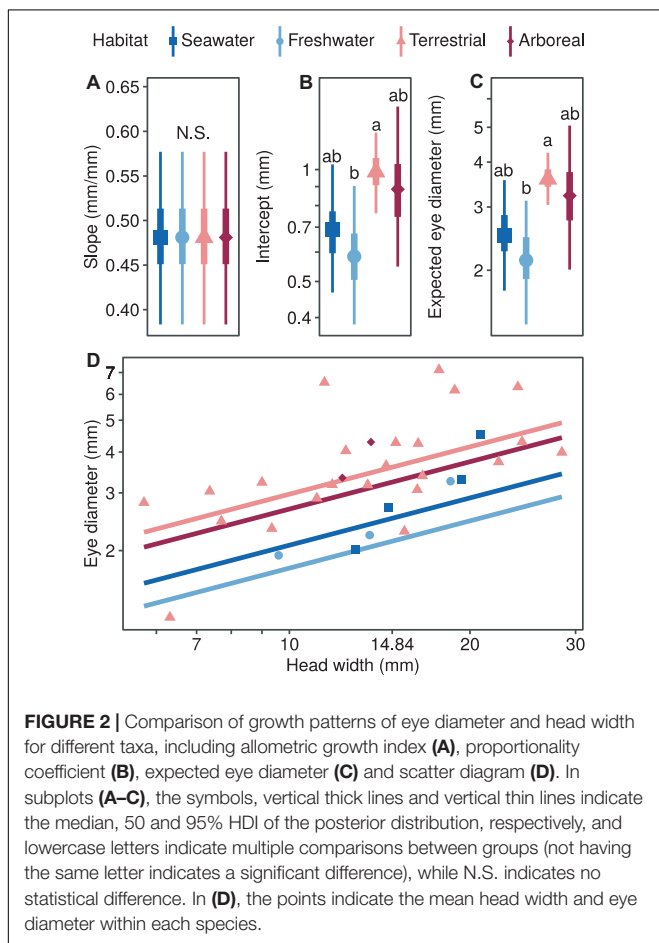
| | Family | Estimate | P _{MCMC} of multiple comparisons | | | |
|-----|--------------|----------------------|---|----------|--------------|-----------|
| | | | Colubridae | Elapidae | Homalopsidae | Viperidae |
| (A) | Colubridae | 0.541 (0.456, 0.627) | — | — | — | — |
| | Elapidae | 0.430 (0.340, 0.512) | 0.049 | — | — | — |
| | Homalopsidae | 0.531 (0.372, 0.696) | 0.916 | 0.237 | — | — |
| | Viperidae | 0.438 (0.305, 0.559) | 0.110 | 0.896 | 0.343 | — |
| (B) | Colubridae | 0.948 (0.754, 1.169) | — | — | — | — |
| | Elapidae | 0.856 (0.661, 1.071) | 0.504 | — | — | — |
| | Homalopsidae | 0.543 (0.349, 0.768) | 0.009 | 0.031 | — | — |
| | Viperidae | 0.996 (0.682, 1.388) | 0.783 | 0.415 | 0.012 | — |
| (C) | Colubridae | 4.066 (3.892, 4.248) | — | — | — | — |
| | Elapidae | 2.719 (2.628, 2.812) | <0.001 | — | — | — |
| | Homalopsidae | 2.263 (0.198, 2.553) | <0.001 | <0.001 | — | — |
| | Viperidae | 3.240 (3.041, 3.460) | <0.001 | <0.001 | <0.001 | — |

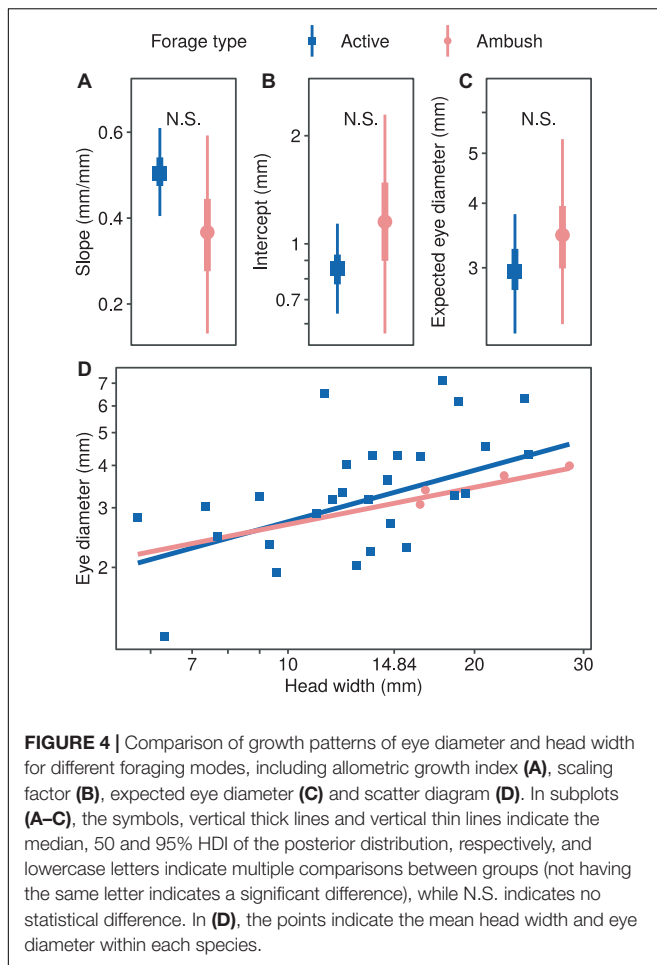
Posterior medians and 95% highest density intervals are listed.

types. Our findings are inconsistent with the previous study that concluded that arboreal snakes had larger eyes than the terrestrial and semiaquatic snakes (Liu et al., 2012). This inconsistency may

have occurred because the phylogenetic effects were not included in the analyses of the previous study.

Notably, the difference in the eye size between terrestrial and freshwater snakes were not generated by the allometry of eye size

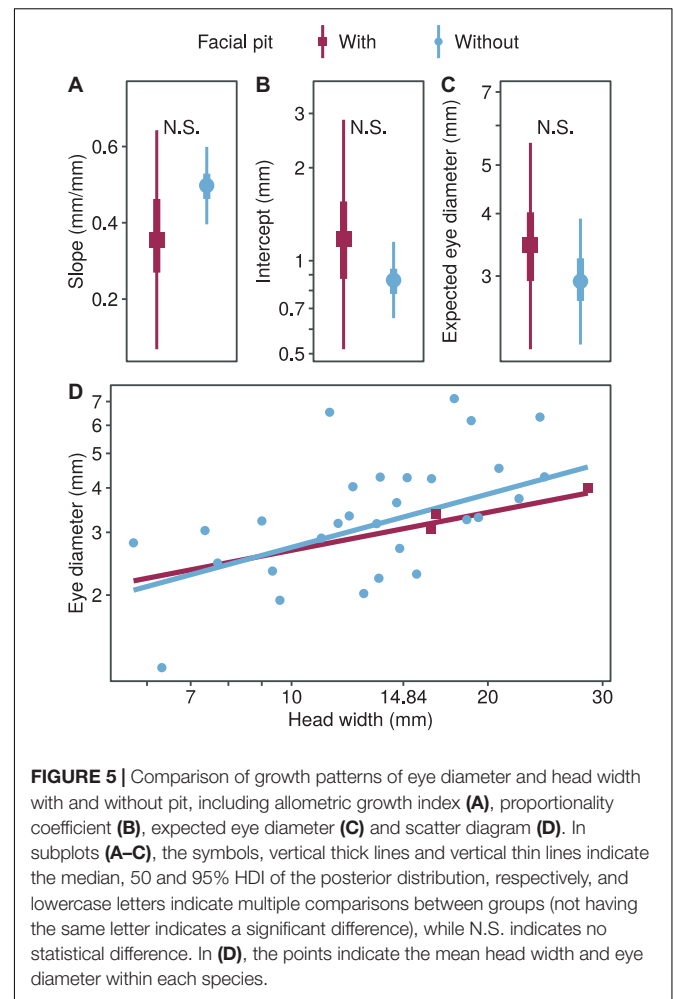




vs. head width (i.e., the slope), but primarily by the absolute eye size (i.e., the intercept; **Figure 2**). Given that it is the absolute eye size that directly determines the visual functions and optical limits (Heesy and Hall, 2010; Veilleux and Kirk, 2014), the results suggests that it would require the freshwater snakes to either expand the body size dramatically or suppress the development of other vital organs in skulls in order to employ vision in the same level as terrestrial species. Such evolutionary strategies may not be as beneficial for the freshwater snakes, considering the high energetic costs potentially incurred and that information may be delivered more efficiently by other sensory systems (e.g., olfactory) than the visual system in aquatic environments due to limited illuminance.

Diel Activity Pattern

Our results showed that the eyes of nocturnal snakes appeared to be smaller than diurnal snakes, indicating that the diel activity pattern acts as the causal, behavioral mechanism, shaping the evolution of snake vision. Such a statement aligns with the conclusion derived by the two previous studies of Colubrid snakes (Liu et al., 2012; Hauzman et al., 2018) and one of them further showed that nocturnal snakes have reduced visual acuity and poorer spatial resolution power (Hauzman et al., 2018).



Despite the difficulty in navigating the environment in the dim-light condition, some nocturnal, highly mobile animals (e.g., geckos; Werner and Seifan, 2006), waterfowls (Thomas et al., 2006), or primates (Kirk, 2006) have shown to overcome the obstacles with the large eyes evolved. Distinctively, in our case, we showed how the less mobile animals (e.g., snakes) could have adopted the other evolutionary trajectory by adapting to the nocturnal activity pattern with other sensory systems complemented (Chen and Wiens, 2020). The majority of Viperidae are classified as nocturnal species in this study; this family has demonstrated the remarkable ability of exploiting the vomeronasal and the infrared sensing systems for discriminating prey species (Yang and Mori, 2021) and thermoregulatory (Krochmal et al., 2004). Our findings, regarding the eye size reduction in nocturnal snakes, thus yield a new hypothesis in terms of the evolutionary origin of multiple sensory modalities associated with the diel activity in snakes. Meanwhile, such a bipolar adaptive response of eye size across a broader taxonomic scale to the nocturnal environments also stresses the complexity of optimal sensory performance as the product of multidimensional evolutionary attributes (e.g., behavior, ecology, physiology, and phylogeny).

Foraging Strategy and the Presence of Pits

Both foraging strategies and the presence of pits showed no effect on the eye size based on the analyses, suggesting that snakes may have similar visual demands when exploiting either active hunting or ambush strategy. It also implies that the information perceived through the visual system is as important as that through the infrared system and, therefore, the presence of pits does not necessarily relax the selection intensity in the evolution of snake eyes. Despite that we did not detect the significant effect of the two respective traits on the eye size, the results indeed generate some research directions worthwhile to examine subsequently. For example, considering the strong association between foraging strategies and the spatial structure of feeding habitats (Gilmour et al., 2018), as well as the evolutionary directions of the foraging strategy and optical ability cohered in snakes (Underwood, 1967; Tu, 2004; Simões et al., 2015; Katti et al., 2019), one may test whether the arboreal snakes tend to possess smaller eyes and adopt the ambush strategy disproportionately. By exploring how the behavioral, physiological, and ecological traits contribute to the evolution of eye size interactively, we are able to foster our ability to account for the evolution of innovative sensory systems and their role in promoting species adaptation across a broader geographical landscape.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by NMNSH002.

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AUTHOR CONTRIBUTIONS

MC-WH and W-SH conceived the study. MC-WH measured all of the specimens. C-PL performed the statistical analyses. C-PL, C-CC, and W-SH led the writing. J-WL revised several sections with critical inputs in research discussions. All authors gave final approval for the publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.821965/full#supplementary-material>

Supplementary Figure 1 | The measurement of snake eye diameter (A) and head width (B).

Supplementary Figure 2 | The most approximate relatives of 31 snake species from Taiwan used in this study. The phylogenetic tree is adapted from Figueroa et al. (2016) based on the most approximate phylogenetic tree. The numbers to the right of the nodes indicate the support of the bootstrap method. Red texts indicate that species in this study could not be matched with Figueroa et al. (2016) and should be synonyms. Blue texts indicate species were not included in Figueroa et al. (2016), so they are represented by similar species.

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