doi: 10.1111/jeb.13299

Eyes Wide Shut: the impact of dim-light vision on neural investment in marine teleosts

TERESA L. IGLESIAS*† , ALEX DORNBURG‡[a] , DAN L. WARREN†§ , PETER C. WAINWRIGHT¶, LARS SCHMITZ** & EVAN P. ECONOMO††

*Physics and Biology Unit, Okinawa Institute of Science and Technology Graduate University, Okinawa, Japan
†Macquarie University, Sydney, NSW, Australia
‡North Carolina Museum of Natural Sciences, Raleigh, NC, USA
§Senckenberg Biodiversity and Climate Research Center (SBiK-F), Frankfurt am Main, Germany
¶University of California, Davis, CA, USA
**W.M. Keck Science Department Claremont, Claremont McKenna, Scripps and Pitzer Colleges, Claremont, CA, USA
††Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, Okinawa, Japan

Keywords:

brain evolution;
comparative phylogenetics;
diel activity patterns;
fish;
physiological evolution;
vision.

Abstract

Understanding how organismal design evolves in response to environmental challenges is a central goal of evolutionary biology. In particular, assessing the extent to which environmental requirements drive general design features among distantly related groups is a major research question. The visual system is a critical sensory apparatus that evolves in response to changing light regimes. In vertebrates, the optic tectum is the primary visual processing centre of the brain and yet it is unclear how or whether this structure evolves while lineages adapt to changes in photic environment. On one hand, dim-light adaptation is associated with larger eyes and enhanced light-gathering power that could require larger information processing capacity. On the other hand, dim-light vision may evolve to maximize light sensitivity at the cost of acuity and colour sensitivity, which could require less processing power. Here, we use X-ray microtomography and phylogenetic comparative methods to examine the relationships between diel activity pattern, optic morphology, trophic guild and investment in the optic tectum across the largest radiation of vertebrates—teleost fishes. We find that despite driving the evolution of larger eyes, enhancement of the capacity for dim-light vision generally is accompanied by a decrease in investment in the optic tectum. These findings underscore the importance of considering diel activity patterns in comparative studies and demonstrate how vision plays a role in brain evolution, illuminating common design principles of the vertebrate visual system.

Introduction

The past several decades have provided unparalleled insights into the mechanisms that allow animals to adapt to the challenges posed by dim-light environments (Warrant, 1999, 2004; Land & Nilsson, 2012; Narendra *et al.*, 2017). Studies have yielded transformative insights into the anatomical (Palmer *et al.*, 2017) and molecular basis (Viets *et al.*, 2016) of vision, as well as the behavioural (Nørgaard *et al.*, 2008; Narendra *et al.*, 2013), ecological and macroevolutionary dynamics of life in low light (Schmitz & Motani, 2011; Hall *et al.*, 2012; Gerkema *et al.*, 2013; Angielczyk & Schmitz, 2014; Wu *et al.*, 2016, 2017; Maor *et al.*, 2017; Tierney *et al.*, 2017). However, few studies have investigated how evolutionary transitions to lifestyles characterized by low-light environments influence neural investment in the primary visual information processing centre of the vertebrate brain: the optic tectum. Visual performance is an integrated result of the optical and physiological properties of the eyes, combined with neural processing of visual information in the retina

Correspondence: Teresa L. Iglesias, Physics and Biology Unit, Okinawa Institute of Science and Technology Graduate University, 1919-1 Tancha, Onna, Okinawa, 904-0495, Japan.
e-mail: Teresa.L.Iglesias@gmail.com
[a]Co-first author.

itself and further downstream in the optic tectum. In all visually oriented vertebrates, the optic tectum receives substantial amounts of sensory input, and it is expected that the interplay of sensory information and data processing will significantly impact neural investment. Whereas understanding optical and retinal adaptations to dim-light environments is fundamentally important, including the optic tectum in these analyses allows for a more complete understanding of both the evolution of the visual system and expectations of neural investment across the evolutionary history of the vertebrate brain.

In the continuum of light environments, bright, spatially and chromatically complex habitats are a richer source of sensory information than dark, plain and monochromatic environments (Warrant & Johnsen, 2013). To effectively gather photic information across these environment types, vertebrates utilize two types of photoreceptors: (i) cones, which detect various energy wavelengths, some including UV; and (ii) rods, which do not detect the same energy wavelengths as cones but are sensitive to movement and contrast in low-light conditions (Fishelson *et al.*, 2004). Photon abundance in bright (photopic) environments facilitates the use of cone photoreceptors with colour discrimination and high visual acuity, allowing organisms to distinguish fine detail (Land & Nilsson, 2012). In contrast, the photon-limited environment of dim (scotopic) habitats allows vertebrates to make use of the rod photoreceptor system, which is characterized by much higher sensitivity modifications to improve image brightness (Land & Nilsson, 2012). This photopic–scotopic dichotomy of photon availability is a major axis of morphological and functional evolution of vertebrate eyes (Warrant, 2004); however, the impact of diversification along this axis on the optic centre of vertebrate brain remains unclear.

Both rods and cones converge onto retinal ganglion cells, the axons of which form the optic nerves and optic tracts that project to the optic tectum (Northmore, 2011). Light sensitivity is improved through increasing rod convergence to ganglion cells, and as a result, tens or even hundreds of rods may converge onto a single cell (Hughes, 1977; Warrant, 1999, 2004; Joselevitch & Kamermans, 2009). In contrast, acuity is maximized by low convergence; therefore, as little as one cone will interface with a single ganglion cell (Hughes, 1977; Kolb & Dekorver, 1991; Warrant, 1999; Querubin *et al.*, 2009). This difference in visual information flow between the different cell types implies a relationship between visual information and patterns of retinal convergence: for a given eye size, scotopic vertebrates should have a much lower number of retinal ganglion cells than their photopic counterparts. If this is true, the optic tectum of scotopic vertebrates should also be relatively smaller.

Marine teleosts, which comprise 25% of the planet's vertebrate diversity, present an exemplary system for assessing general trends of neural investment following transitions to dim-light environments. Marine fishes such as bigeyes (Priacanthidae) or squirrelfishes (Holocentridae) represent some of the most iconic examples of a temporal niche in vertebrates and are just a few of the dozens of clades that have independently evolved true nocturnality (Schmitz & Wainwright, 2011b; Dornburg *et al.*, 2017a). These nocturnal fish lineages generally have larger eyes than diurnal fishes relative to body size (Goatley & Bellwood, 2009; Goatley *et al.*, 2010; Schmitz & Wainwright, 2011b), as well as a larger lens and pupil, which increases light-gathering capacity and is evidence that vision is still an important modality in nocturnal species. However, whether transitions to nocturnality increase investment in the optic tectum remains unknown.

If nocturnal fishes predominantly use rod-vision with increased retinal convergence as predicted from physiological optics, we would expect that living life in the dark comes with a decreased cost to neural investment. There is evidence that this may be the case. Work on nocturnal cods (Gadidae) with larger eyes has repeatedly revealed a decrease in the size of the optic tecta (Evans, 1940; Kotrschal *et al.*, 1998). In contrast, some lineages of diurnal fishes have vastly expanded their repertoire of cone cells to capture additional portions of the visible light spectrum (Losey *et al.*, 2003), thereby increasing demands on visual processing. However, light availability may not be the only factor affecting teleost investment in the optic tectum; accounts in the literature suggest feeding behaviour, in particular prey detection and predation avoidance, may affect tectal volume (Evans, 1940; Huber & Rylander, 1991, 1992; Huber *et al.*, 1997; Edmunds *et al.*, 2016; Kotrschal *et al.*, 2017). To date, no phylogenetic comparative analyses have attempted to examine the relationship between eye size, neural investment and activity patterns across a broad representation of marine teleosts, leaving us in the dark regarding how evolutionary changes in diel activity affect neural investment.

Here, we use a time-calibrated phylogenetic comparative framework to assess the relationship between diel activity, visual morphology and investment in the optic tectum. Using an information theoretic framework, we first assess the predictive power of activity and visual morphology on neural investment, expanding the candidate pool of predictors to also include the potential effect of trophic guild on neural investment. We next quantify overall patterns of neuro-visual phylomorphospace occupancy to assess the overlap and differences in phenotypic diversity between diurnal and nocturnal teleosts. Our results reveal how optic morphology drives investment and divestment in the optic tecta, providing a much-needed macroevolutionary perspective on how dim-light vision has impacted this region of the teleost brain.

Materials and methods

Specimens

Eye measurements and micro-CT (X-ray microtomography) brain scans were collected for 111 individuals from 60 species (Data archived on DRYAD, doi:10.5061/dryad.br097sc). Body mass was collected at the time of capture for all specimens scanned except *Orthopristis chrysoptera*. Eye measurements for 39 species were acquired from Schmitz & Wainwright (2011b) with measurements from an additional 21 species acquired from specimens collected in Hawaii. All fish were collected on scuba using dip nets or via rod and reel in Curaçao, Hawaii or North Carolina in accordance with conditions stipulated in permits and in compliance with university standards of animal care and use (Macquarie University animal ethics permit 5201500020). Of the 60 species used in this study, 44 are diurnal and 16 nocturnal (Schmitz & Wainwright, 2011b; Dornburg *et al.*, 2017a). With regard to feeding guilds, the diurnal group is composed of 66% benthivores (29), 11% piscivores (5), 14% planktivores (6) and 9% herbivores (4); the nocturnal group is composed of 63% benthivores (10), 31% piscivores (5) and 6% planktivores (1) (Fig. S1) (Froese & Pauly, 2014). Voucher photos or tissue samples of specimens were deposited in the Yale Peabody Museum of Natural History and the North Carolina Museum of Natural Sciences.

Eye measurements

Both left and right eyes for 1–4 individuals per species were measured following the methods described in Schmitz & Wainwright (2011b). Briefly, fish were deeply anesthetized in a solution of tricaine methanesulfonate (MS-222) in seawater, and each eye was photographed prior to removal to determine maximum and minimum pupil diameters. To measure eye diameter, eyes were individually removed and photographed next to a micrometer using a USB dissecting microscope attached to a laptop. Next, the lens was excised and photographed to determine lens diameter. Once both eyes had been removed and photographed, fish were rapidly decapitated and the head placed in a 10% formalin solution (mixed with seawater). All eye measurements were taken from photographs after decapitation to ensure that the fish would remain alive until brain preservation.

Fixation, staining and micro-CT scanning

Heads or dissected brains were fixed in 10% formalin (in seawater) for at least three weeks before staining. Large heads (widest dimension >40 mm) were kept in 5% iodine potassium iodide (IKI). The remaining smaller heads were kept in 3.75% IKI and dissected brains were kept in 1.5% IKI. Heads remained in stain for approximately four weeks, dissected brains one week. Just prior to micro-CT scanning, tissues were removed from stain and blot dried, then wrapped in low-density polyethylene plastic wrap to prevent desiccation and eliminate the interference of in-liquid leaching of IKI. Wrapped specimens were placed snugly inside polypropylene tubes, which were secured to the micro-CT scanner base. Specimens were scanned using a Zeiss Xradia Versa XRM 510 micro-CT scanner housed at the Okinawa Institute for Science and Technology Graduate University (OIST). All scans were set for 1-s exposure and 1001 projections with brains scanned at 50–60 kV, 4–5 W, and heads at 80–160 kV, 7–10 W. Scans were approximately 50 min in duration. After scanning, specimens were returned to 10% formalin.

Brain segmentation

Micro-CT scans were visualized and virtually segmented using AMIRA software (version 6.0.0, FEI SAS, Bordeaux, France). Segmentation allows regions of interest in the image layers to be labelled and volumetrically quantified. Total brain volume included from the olfactory bulbs (anterior) to the medulla (posterior) at the point where medullary structures fuse dorsally, which tends to coincide where cranial nerve X exits the brainstem or slightly posterior to this location. The left and right optic tecta were segmented independently. Volume was calculated using AMIRA software using metadata embedded within the micro-CT file.

Comparative analyses

Eyes of nocturnal fish are not only larger in diameter than those of diurnal fish; they also have greater depth, larger lenses and changes in pupil shape (Schmitz & Wainwright, 2011b). By combining these axes of visual morphology, Schmitz & Wainwright (2011b) developed a metric (termed OPT3) that approximates where along the spectrum species lie with respect to photopic (bright light) and scotopic (dim light) vision. OPT3 is the product of the ratio of lens diameter to eye diameter and the ratio of minimum to maximum pupil diameter

$$\mathrm{OPT3} = (\mathrm{ld} \times \min(\mathrm{pd}))/(\mathrm{ed} \times \max(\mathrm{pd})) \qquad (1)$$

where ld is the lens diameter, pd the pupil diameter, and ed the eye diameter. We use this metric to quantify eye morphology for our comparative analyses.

Given that OPT3 was developed to distinguish between nocturnal and diurnal species, OPT3 and diel activity pattern are expected to be highly correlated variables (Figs S2 and S3). Because OPT3 integrates eye morphology related to light-gathering efficiency, we expect this continuous variable to be more informative

than a dichotomous activity assignment (e.g. nocturnal, diurnal). We therefore use OPT3 and not diel activity in our models. Activity data were compiled from Schmitz & Wainwright (2011b) and Dornburg *et al.* (2017a).

For all comparative analyses, we used the time-calibrated phylogeny estimated by Rabosky *et al.* (2013) as an evolutionary framework. This phylogeny is based on an analysis of 13 genes that capture the evolutionary divergences of 7822 fish species, including all but three lineages of our study. These species comprise *Equetus punctatus*, *Mulloidichthys flavolineatus* and *Bothus mancus*, and represent recently diverged tipward lineages within the taxon sampling strategy of Rabosky *et al.* (2013). To incorporate these missing lineages into our time-calibrated framework, we assembled cytochrome c oxidase subunit one (COI) sequences from GenBank that included the missing species and a subset of their close relatives including at least two lineages that represent a divergence within the tree estimated by Rabosky *et al.* (2013); Table S1. Divergences were time calibrated using secondary calibrations based on posterior distributions taken from the literature (e.g. (Near *et al.*, 2012, 2013); See Appendix S1 for more details), and divergence times were estimated using BEAST v. 2.4.5. (Bouckaert *et al.*, 2014) (see Appendix S1 for details). Although mitochondrial markers such as COI have been shown to impact evolutionary divergences at deep timescales in fishes, quantifications of phylogenetic information content for mitochondrial genomes (Dornburg *et al.*, 2014) suggest that the tipward sampling of this strategy poses minimal risk of saturation-based branch length errors while providing enough variable sites to achieve topological resolution and power for parameter estimation (Dornburg *et al.*, 2014, 2017b). Resulting trees were grafted onto the phylogeny of Rabosky *et al.* (2013) and pruned to only include lineages sampled in our study.

We simultaneously visualized shared evolutionary history and patterns of convergence in the size of the optic tectum relative to OPT3 using a two-dimensional phylomorphospace (Sidlauskas, 2008). The internal nodes of the phylogeny were placed into the resulting morphospace using maximum likelihood-based ancestral states estimates for OPT3 and optic tectum. To assess how the resulting morphospace is partitioned between nocturnal and diurnal lineages, we used stochastic character mapping (Bollback, 2006) to reconstruct changes in diel activity across the phylogeny, mapping the resulting map onto the branch lengths of the phylomorphospace, selecting the best-fit model of the evolutionary transition rate matrix from the candidate pool of equal or asymmetric rates using corrected Akaike information criterion (AICc). For both nocturnal and diurnal lineages, a convex hull of morphospace occupancy was calculated and used to determine overall differences in trait diversity, coupled with a comparison of kernel density estimates (KDE) of the probability density of each trait for nocturnal and diurnal lineages. All analyses were conducted in phytools (Revell, 2012) using code from Federman *et al.* (2016) with the exception of KDE analyses conducted using the sm package in R (Bowman & Azzalini, 2014).

We conducted comparative analyses using phylogenetic generalized least squares (PGLS) as implemented in the ape and geiger packages for R (Paradis *et al.*, 2004; Pennell *et al.*, 2014, Pinheiro *et al.*, 2016; R Core Team, 2017). Volume and mass measurements were log transformed prior to analysis. We built models using both Brownian (BM) and Ornstein–Uhlenbeck (OU) error structures, with parameters for those models fit using the corBrownian and fitContinuous methods in ape and geiger, respectively. For each of these error structures, we constructed five models with optic tectum volume as the dependent variable: one intercept-only model to represent the null hypothesis, one model with brain volume as the only predictor, one model with OPT3 and brain volume, one with feeding guild and brain volume, and finally one model containing brain volume, OPT3 and feeding guild. For these models, brain volume was calculated excluding optic tectum. We compared model fit using sample size corrected Akaike information criterion scores, AICc, a metric that assesses model fit while penalizing the addition of excess parameters. Parameter estimates and standard errors were calculated using model averaging (Mazerolle, 2014).

We also conducted a second set of PGLS analyses using total brain volume (including optic tectum) as the dependent variable to assess differences in total brain volume based on OPT3 (a continuous proxy for diel activity). We included all species except *Orthopristis chrysoptera* in this analysis because body mass data were missing for these specimens. Models for this analysis included an intercept-only model, a body mass only model and a model with both body mass and OPT3. Models were built using both BM and OU error structures. In order to exclude the possibility that our results might be affected by the methods used to add species to the phylogeny (above), we repeated all analyses with the three additional species excluded. These results did not differ in any material way from the analysis of the full data set, and so only the results using the full data set will be discussed.

Results

Visualizing changes in optic tecta volume across the phylogeny of sampled lineages depicts numerous independent decreases and increases in tissue mass investment (Fig. 1a). In general, shifts in nocturnal activity correspond to decreases in the volume of the optic tectum (Fig. 1a). In particular, nocturnal lineages such as moray eels (Muraenidae) (Fig. 1b) have some of the

smallest optic tectum volumes (Fig. 1). In contrast, most diurnal lineages have larger optic tecta, with flatfishes demonstrating the largest of any sampled species (Fig. 1a,c). Although changes in diel activity are generally linked with decreases in tecta volume, there are several notable exceptions. Diurnal triggerfishes (Balistidae) have some of the smallest optic tecta of any diurnal or nocturnal fishes (Fig. 1a,d), although nocturnal silversides (Atherinidae) and squirrelfishes and soldierfishes (Holocentridae) possess optic tectum volumes that are on par with the larger volumes found in diurnal lineages (Fig. 1a,e).

Visualization of the neural–visual phylomorphospace indicates a substantial reduction in the overall morphospace occupancy of nocturnal relative to diurnal lineages, with only a minor degree of overlap between the two (Fig. 2). Quantification of the area of the convex hull area for diurnal vs. nocturnal corresponds to a 4.49-fold increase in combinations of OPT3 and optic tectum areas represented, with nonequal morphospace occupancy supported under a range of resampling strategies (Fig. S4). The majority of nocturnal lineages have converged in relative optic tecta volumes below 0.2 and OPT3 values as large or larger than those found in diurnal lineages (Fig. 2). Moray eels represent some of the lowest optic tecta volumes and most divergent OPT3 values of the nocturnal lineages. In contrast, squirrelfishes and soldierfishes and the hardyhead silverside (*Atherinomorus stipes*; Atherinidae) have optic tecta values that are on par with those found in diurnal lineages (Fig. 2). Of the diurnal lineages, most lineages appear closely clustered. Notable exceptions include the scythe triggerfish (*Sufflamen bursa*; Balistidae), with both a low OPT3 and low optic tecta volume and flounders, which possess the most divergent OPT3 to optic tectum

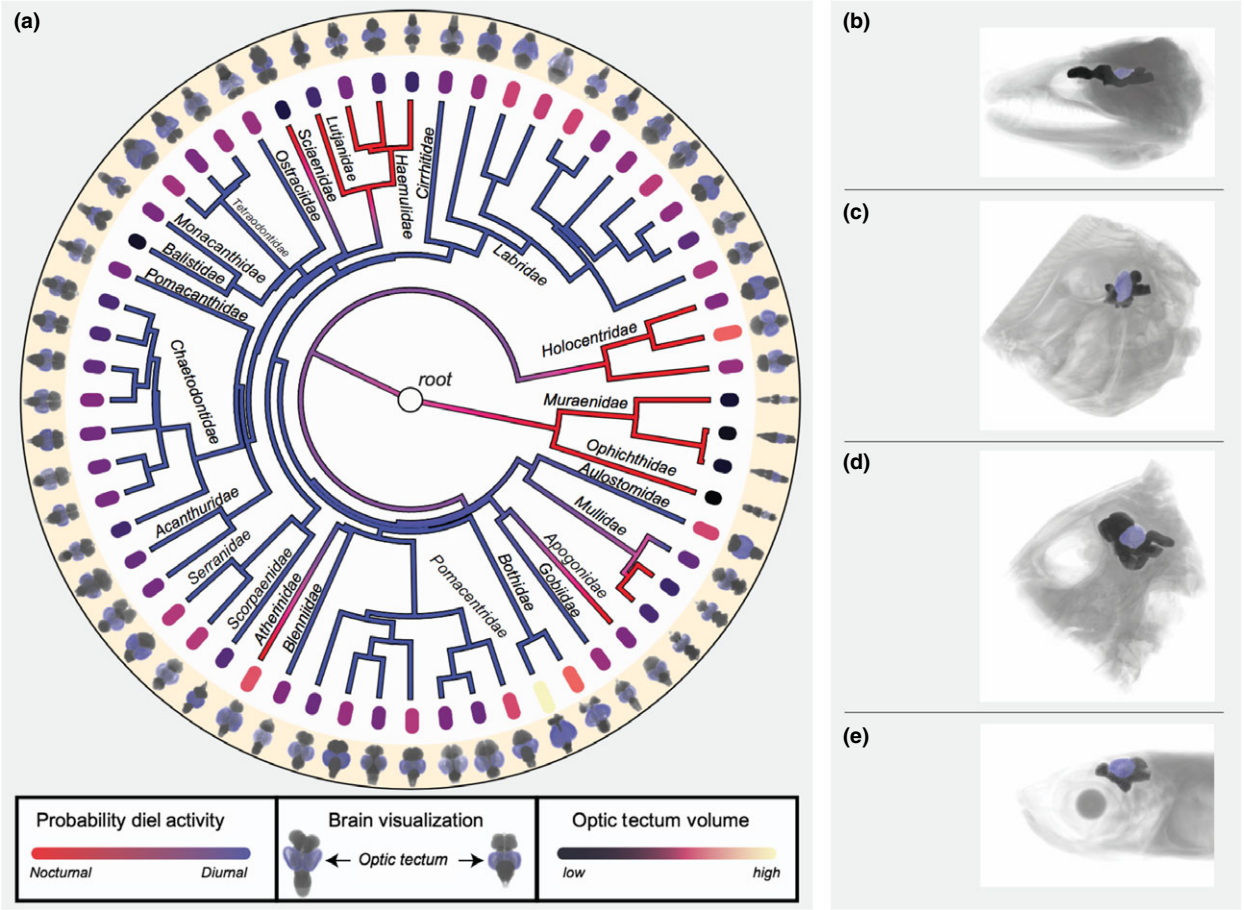

Fig. 1 (a) Phylogeny of species included in this study denoting diel activity patterns, relative investment in the optic tectum and a 2D dorsal view of 3D-rendered brains with optic tecta in translucent purple and the rest of the brain in translucent grey. (b–e) Translucent 3D-rendered heads with brain indicated in dark grey and optic tectum in purple for several key species discussed in the text: (b) *Gymnothorax javanicus*; giant moray eel. (c) *Bothus mancus*; peacock flounder. (d) *Sufflamen bursa*; scythe triggerfish. (e) *Atherinomorus stipes*; hardhead silverside.

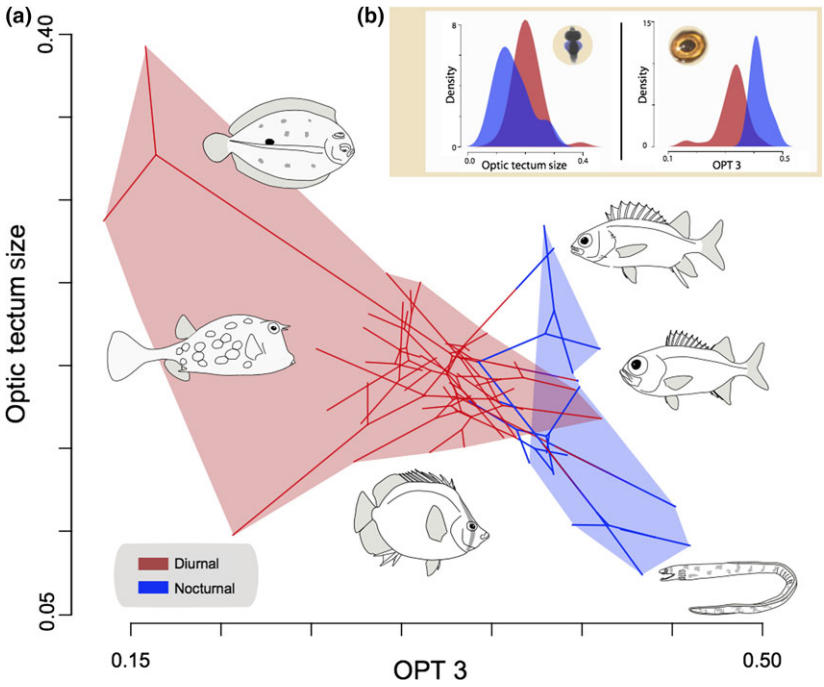

Fig. 2 (a) Neural–visual (Optic tectum-OPT3) phylomorphospace for nocturnal and diurnal lineages in our study. (b) A comparison of kernel density estimates (KDE) of the probability density of each trait for nocturnal and diurnal lineages.

Table 1 Model comparison results using the AICc information theoretic approach with the Brownian error structure. Brain: brain volume excluding optic tectum, OPT3: optic morphology, guild: piscivore, planktivore, herbivore or benthivore, intercept-only: null model.

Model	# parameters	AICc	ΔAICc	AICcWt	Cum. Wt
Brain + OPT3	4	6.18	0.00	0.91	0.91
Brain + OPT3 + Guild	7	12.26	6.08	0.04	0.96
Brain only	3	12.38	6.20	0.04	1.00
Brain + Guild	6	17.60	11.42	0.00	1.00
Intercept only	2	153.23	147.05	0.00	1.00

ratios and represent a major component of overall morphospace occupancy (Fig. 2).

In general, models fit using the BM error structure outperformed their Ornstein–Uhlenbeck counterparts (Table S2). Given the better fit of the BM-based models and the consistency of results between BM- and OU-based models, we only discuss models constructed using the BM error structure. The intercept-only model representing the null hypothesis had a delta AICc of >2 (147.04 ΔAICc) when compared to the best-supported model (Table 1), favouring rejection of the null hypothesis (Burnham & Anderson, 2013). Model comparison of all models in the candidate pool support OPT3 as a strong predictor of investment in optic tectum with an AICc model weight of 0.91 for the model including only OPT3 and total brain volume as predictors. This model also substantially outperforms the model with brain volume as the sole predictor, with a delta AIC of 6.2. There was no demonstrable effect of feeding guild (model weight <0.01).

There was support for an effect of visual morphology on optic tectum volume with a model-averaged coefficient of -1.72 ± 0.59 SE for OPT3 (95% CI -2.87, -0.57). Higher values of OPT3 correlated positively with scotopic vision (dim-light vision) providing evidence that fishes more reliant on scotopic vision invest relatively less in optic tectum. However, we did not find that overall brain size in marine fishes correlates with OPT3. The model containing OPT3 had an AICc model weight of 0.50 and the intercept-only model weight was also 0.50. The difference in AICc was <2 (0.02 ΔAICc), providing no convincing support for increased fit with the inclusion of OPT3. Feeding guild did not have an overall effect on the volume of the optic tectum across all fishes, and examination of diurnal and nocturnal species separately also showed no robust pattern.

Discussion

We find strong evidence that shifts to dim-light vision correspond with decreases in neural investment in the optic tectum. This finding is consistent with previous case studies focused on individual lineages of birds (Martin *et al.*, 2007; Corfield *et al.*, 2011; Gutierrez-Ibanez *et al.*, 2013), primates (Barton *et al.*, 1995; Barton & Harvey, 2000) and gadid fishes (Gadidae) (Evans, 1940). By examining the relationship between shifts in scotopic vision and neural investment across the largest clade within the vertebrates, teleost fishes, our findings,

taken with others (Wagner, 2001a,b), suggest that this shift in investment likely represents a general feature of vertebrate brain evolution.

Adjusting to the dark: lessons from the eyes of teleosts

Larger eyes can house more photoreceptors and may therefore be expected to collect larger amounts of sensory information. Under this scenario, the resulting increase in visual processing needs should drive a concomitant increase in the size of the optic tecta. Our results do not support this expectation. Instead, we find that despite having larger eyes for given body size, scotopic vision reliant teleosts invest less in the optic tectum than photopic-reliant fishes (Figs 1 and 2). This lack of investment may be partially explained by the fact that visual information detectable in bright conditions such as colour and ultra-violet are less detectable in dark conditions (Warrant & Johnsen, 2013). This precludes the need to invest greatly in neural tissue to process such information, suggesting that nocturnal fishes forego acuity and colour spectrum sensitivity in order to maximize sensitivity to light. However, many nocturnal species are also somewhat active or must occasionally avoid predators during the day, requiring these lineages to also be able to navigate a bright environment (Ménard *et al.*, 2008).

In contrast to nocturnal tetrapods, the majority of marine teleosts cannot cope with bright light by constricting their pupil. In essence, the aperture of the teleost optical centre is fixed, with only a few exceptions (Douglas *et al.*, 1998). Further, a larger pupil is negatively correlated with depth of field (Keating, 2002) limiting the ability to focus on close objects. Our findings are consistent with previous work supporting the idea that nocturnal lineages disproportionately occupy areas of morphospace that include the largest pupils (Fig. 2), suggesting a trade-off between maximizing light sensitivity and visual acuity for nocturnal lineages (Schmitz & Wainwright, 2011b). How then do nocturnal lineages navigate a bright world? One solution may be the ability of some lineages to switch their sensory mechanism through retinomotor movements, a process analogous to a photographer switching light sensitivity settings (i.e. switching the International Standards Organization (ISO) scale settings). Although not widely studied, several independent studies have found that marine teleosts have the ability to change the position of their rod and cone photoreceptors. In bright conditions, the rods are withdrawn from incoming light and deactivated as they are surrounded by pigment. Cones, however, are fully exposed and functional. The opposite is true in dim conditions: rods are exposed, although the cones are withdrawn and deactivated. Although intriguing, this physiological process is slow compared to pupillary light mediation, requiring minutes to hours to accomplish (Douglas *et al.*, 1998; Hodel *et al.*, 2006; Donatti & Fanta, 2007) and does not explain the systematic decrease in optic tectum investment found in our study.

We propose two nonmutually exclusive hypotheses that could underlie the decrease in optic tectum investment found in our study yet still allow teleosts to navigate bright environments. First, the lower investment in optic tecta suggests that species more specialized in scotopic vision reduce the density of cones and favour rod-vision with higher retinal convergence, rather than adding more receptors. Such a neurophysiological change would improve light sensitivity but reduce visual acuity not only as a result of increased convergence but also due to the inherent longer focal length of the larger eye. This strategy may explain the smaller optic tecta in scotopic-specialized species, as the information processing load of the optic tectum compared to more photopic-specialized species would be decreased. Second, it is possible that there are regional specializations of cell types across the retina. For example, eyes may feature an area with high densities of cones (photopic vision) surrounded by areas dominated by rods (scotopic vision) and/or different amounts of retinal convergence across the retina. This scenario is reminiscent of many-to-one mapping of form to function (Wainwright *et al.*, 2005) and would enable numerous possible physiological solutions to dim-light vision while keeping visual processing costs low. Further studies of how teleosts physiologically and behaviourally cope with changes in light exposure are not only an interesting research frontier but are also of high importance for predicting how altered light regimes impact near-shore species in many of the world's rapidly developing coastal environments.

Ecology and the evolution of the optic tectum

Evolutionary transitions in trophic level have been repeatedly highlighted as driving changes in fish optic tecta, with tectum size increasing along a trophic gradient from planktivore to piscivore (Evans, 1940; Huber & Rylander, 1991, 1992; Huber *et al.*, 1997; Gonzalez-Voyer *et al.*, 2009; Edmunds *et al.*, 2016). For the lineages examined in this study, this result is not supported (Fig. 1 and Table 1). However, it may be that this pattern is only true for lineages that share characteristics that are yet to be identified as relevant to this question. However, care should be taken to extrapolate the expectations of a trophic gradient as a general condition, as several environmental factors can offset or overturn this relationship.

Environmental factors such as turbidity, depth (a proxy for changes in light attenuation) and vegetation have all been suggested to erode the relationship between feeding ecology and optic tectum size (Evans, 1940; Davis & Miller, 1967; Gomahr *et al.*, 1992;

Kotrschal & Palzenberger, 1992; Edmunds *et al.*, 2016). For example, recent work has reported a decrease in tectum size for several common diurnal North American freshwater piscivores (e.g. trout and bass) that hunt in low-light conditions (Edmunds *et al.*, 2016). These predators rely on olfaction to locate prey, which corresponds with an increase in the brain's olfactory bulb. A similar trend is evident in the nocturnal piscivores sampled in our study. Moray eels possess an extremely reduced optic tectum (Figs 1 and 2), a condition that has been used as a conceptual framework for expectations of the nocturnal fish brain (Yamamoto, 2017). Feeding on drifting or floating plankton is considered to require high spatial or temporal visual acuity (Hobson, 1991; Schmitz & Wainwright, 2011a). Diurnal zooplanktivores visually identify individual plankton before striking, requiring the ability to process the identity of difficult to resolve small and semi-transparent prey items. It is unclear whether nocturnal planktivores use a similar strategy and therefore may require higher acuity than nocturnal species of other feeding guilds.

The majority of fishes sampled in our study occur on coral reefs, an environment characterized by asymmetrical predation risks across temporal intervals. Diurnal species are under far less predation pressure than crepuscular and nocturnal lineages (Danilowicz & Sale, 1999). Nocturnal planktivores must forage in exposed environments, requiring visual acuity to detect incoming motion and early detection of ambush predators. Such early detection has been hypothesized to initiate rapid C-start and escape responses in fishes (Kotrschal *et al.*, 2017). This 'flee-early' strategy could theoretically drive an increase in tectum size as processing motion is primarily the domain of the optic tectum (Guthrie, 1990). For example, visual detection of predators has been demonstrated to promote site fidelity in refuge selection in the nocturnal squirrelfish *Holocentrus*, favouring the selection of areas of the reef where incoming predators such as jacks, barracudas or snappers can be detected more readily (Ménard *et al.*, 2008). This raises a question: How generalizable is the hypothesis that predation impacts the evolutionary diversification of the optic tectum?

Recent investigations of how predation shapes the fish optic tectum have found evidence for an impact both at the species level (Kotrschal *et al.*, 2017) as well as between closely related species (White & Brown, 2015). Given that visual processing is required for early detection as well as effective predator avoidance when schooling, nocturnal fishes may be in an evolutionary arms race with predators optimizing olfaction and other regions of the brains for effective hunting. Further, predation pressure has been found to drive overall patterns of brain size evolution in several vertebrate groups (Kondoh, 2010; Moller & Erritzoe, 2014), with recent work across the evolutionary history of frogs (Anura) demonstrating a strong effect of predation pressure on positive changes in optic tectum volume (Liao *et al.*, 2015). As such, predation pressure may be a major force shaping the optic region of the vertebrate brain, and an under-appreciated axis of diversification driving general patterns of brain mosaicism.

Conclusion

It is increasingly clear that in vertebrates, spanning primates to fishes, common axes of diversification can promote repeated patterns of brain diversification within different neural regions (Barton & Harvey, 2000; Iwaniuk, 2004; Lefebvre & Sol, 2008; Hoops *et al.*, 2017). Our study demonstrates several major patterns of neural investment associated with the teleost visual system. First, despite driving the evolution of larger eyes, transitions to lifestyles characterized by dim-light vision generally drive a decrease in investment in the optic tectum. Second, there is a substantial shift and overall reduction in visual morphospace occupancy for nocturnal lineages, corresponding with convergence in large orbits and reductions in optic tectum size. These findings underscore the importance of considering diel activity patterns in comparative studies.

Across vertebrates, diel activity patterns are often deeply conserved over evolutionary timescales (Anderson & Wiens, 2017). As we continue to progress towards a synthetic understanding of the evolutionary pathways that have given rise to the compositional diversity of vertebrate brain, additional studies that consider transitions in temporal niche offer an exciting research frontier that promises new insights into patterns of neural investment and evolutionary trade-offs that have given rise to the diversity of the vertebrate brain. Such a perspective will not only illuminate general features of vertebrate evolution, but also be of potential high conservation importance for predicting the impact of environmental changes that alter the circadian rhythms of wildlife.

Acknowledgments

The authors would like to acknowledge the contribution of two anonymous reviewers and editor Michael Jennions, whose helpful comments significantly improved this manuscript. We thank Mark Vermeij and the entire staff of CARMABI for facilitating collection efforts and export permitting in Curaçao, Dan Dombrowski for help catching fish and facilitating boat access in North Carolina, and the Westpunt Syndicate for their advice and help in the field. We further would like to thank Greg Watkins-Colwell, Gabriela Hogue and Lindsay Roupe for help with specimen and tissue curation. TLI would like the acknowledge the Physics and Biology Unit at OIST. Special thanks to John Deyrup for early assistance with CT scanning.

Competing interests

The authors declare no competing financial interests.

Author contributions

TLI, AD, DLW and EPE conceived of the study. DLW, TLI and AD collected samples. TLI, AD, LS, PCW, EPE and DLW collected data. TLI, DW and AD performed analyses. All authors contributed the writing and development of the manuscript.

Funding

This work was supported by subsidy funding to OIST and a Macquarie Research Development Grant (MQRDG) to DLW and TLI.

References

Anderson, S.R. & Wiens, J.J. 2017. Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates. *Evolution* **71**: 1944–1959.

Angielczyk, K.D. & Schmitz, L. 2014. Nocturnality in synapsids predates the origin of mammals by over 100 million years. *Proc. R. Soc. B Biol. Sci.* **281**: 20141642.

Barton, R.A. & Harvey, P.H. 2000. Mosaic evolution of brain structure in mammals. *Nature* **405**: 1055–1058.

Barton, R.A., Purvis, A. & Harvey, P.H. 1995. Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **348**: 381–392.

Bollback, J.P. 2006. SIMMAP: stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics* **7**: 88.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D. *et al.* 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol.* **10**: e1003537.

Bowman, A.W. & Azzalini, A. 2014. R package 'sm': nonparametric smoothing methods (version 2.2-5.4). http://www.stats.gla.ac.uk/~adrian/sm

Burnham, K.P. & Anderson, D.R. 2013. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer, New York.

Corfield, J.R., Gsell, A.C., Brunton, D., Heesy, C.P., Hall, M.I., Acosta, M.L. *et al.* 2011. Anatomical specializations for nocturnality in a critically endangered parrot, the Kakapo (*Strigops habroptilus*). *PLoS ONE* **6**: e22945.

Danilowicz, B.S. & Sale, P.F. 1999. Relative intensity of predation on the French grunt, *Haemulon flavolineatum*, during diurnal, dusk, and nocturnal periods on a coral reef. *Mar. Biol.* **133**: 337–343.

Davis, B.J. & Miller, R.J. 1967. Brain patterns in minnows of genus *Hybopsis* in relation to feeding habits and habitat. *Copeia* **1967**: 1.

Donatti, L. & Fanta, E. 2007. Retinomotor movements in the Antarctic fish *Trematomus newnesi* Boulenger submitted to different environmental light conditions. *Rev. Bras. Zool.* **24**: 457–462.

Dornburg, A., Townsend, J.P., Friedman, M. & Near, T.J. 2014. Phylogenetic informativeness reconciles ray-finned fish molecular divergence times. *BMC Evol. Biol.* **14**: 169.

Dornburg, A., Forrestel, E.J., Moore, J.A., Iglesias, T.L., Jones, A., Rao, L. *et al.* 2017a. An assessment of sampling biases across studies of diel activity patterns in marine ray-finned fishes (Actinopterygii). *Bull. Mar. Sci.* **93**: 611–639.

Dornburg, A., Townsend, J.P. & Wang, Z. 2017b. Chapter one - maximizing power in phylogenetics and phylogenomics: a perspective illuminated by fungal big data. In: *Advances in Genetics*, Vol. **100** (J.P. Townsend & Z. Wang eds), pp. 1–47. Academic Press, Cambridge, MA, USA.

Douglas, R.H., Harper, R.D. & Case, J.F. 1998. The pupil response of a teleost fish, *Porichthys notatus*: description and comparison to other species. *Vision. Res.* **38**: 2697–2710.

Edmunds, N.B., McCann, K.S. & Laberge, F. 2016. Food web structure shapes the morphology of teleost fish brains. *Brain Behav. Evol.* **87**: 128–138.

Evans, H.M. 1940. *Brain and Body of Fish; A Study of Brain Pattern in Relation to Hunting and Feeding in Fish, by H. Muir Evans*. The Blakiston Company, Philadelphia.

Federman, S., Dornburg, A., Daly, D.C., Downie, A., Perry, G.H., Yoder, A.D. *et al.* 2016. Implications of lemuriform extinctions for the Malagasy flora. *Proc. Natl Acad. Sci.* **113**: 5041–5046.

Fishelson, L., Ayalon, G., Zverdling, A. & Holzman, R. 2004. Comparative morphology of the eye (with particular attention to the retina) in various species of cardinal fish (Apogonidae, Teleostei). *Anat. Rec. A Discov. Mol. Cell Evol. Biol.* **277**: 249–261.

Froese, R. & Pauly, D. (Eds). 2014. FishBase. World Wide Web electronic publication. http://www.fishbase.org, version (04/2014),

Gerkema, M.P., Davies, W.I.L., Foster, R.G., Menaker, M. & Hut, R.A. 2013. The nocturnal bottleneck and the evolution of activity patterns in mammals. *Proc. R. Soc. B Biol. Sci.* **280**: 20130508.

Goatley, C.H.R. & Bellwood, D.R. 2009. Morphological structure in a reef fish assemblage. *Coral Reefs* **28**: 449–457.

Goatley, C.H.R., Bellwood, D.R. & Bellwood, O. 2010. Fishes on coral reefs: changing roles over the past 240 million years. *Paleobiology* **36**: 415–427.

Gomahr, A., Palzenberger, M. & Kotraschal, K. 1992. Density and distribution of external taste-buds in cyprinids. *Environ. Biol. Fishes* **33**: 125–134.

Gonzalez-Voyer, A., Winberg, S. & Kolm, N. 2009. Social fishes and single mothers: brain evolution in African cichlids. *Proc. R. Soc. Lond. B Biol. Sci.* **276**: 161–167.

Guthrie, S.D.M. 1990. The physiology of the teleostean optic tectum. In: *The Visual System of Fish* (R. Douglas, M. Djamgoz, eds), pp. 279–343. Springer, Netherlands, Dordrecht.

Gutierrez-Ibanez, C., Iwaniuk, A.N., Lisney, T.J. & Wylie, D.R. 2013. Comparative study of visual pathways in owls (Aves: Strigiformes). *Brain Behav. Evol.* **81**: 27–39.

Hall, M.I., Kamilar, J.M. & Kirk, E.C. 2012. Eye shape and the nocturnal bottleneck of mammals. *Proc. Biol. Sci.* **279**: 4962–4968.

Hobson, E.S. 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: *The Ecology of Fishes on Coral Reefs* (P.F. Sale, ed.), pp. 69–95. Academic Press, San Diego.

Hodel, C., Neuhauss, S.C.F. & Biehlmaier, O. 2006. Time course and development of light adaptation processes in the outer zebrafish retina. *Anat. Rec. Part A Discov. Mol. Cell. Evol. Biol.* **288A**: 653–662.

Hoops, D., Vidal-García, M., Ullmann, J.F.P., Janke, A.L., Stait-Gardner, T., Duchêne, D.A. *et al.* 2017. Evidence for concerted and mosaic brain evolution in dragon lizards. *Brain Behav. Evol.* **90**: 211–223.

Huber, R. & Rylander, M.K. 1991. Quantitative histological studies of the optic tectum in six species of *Notropis* and *Cyprinella* (Cyprinidae, Teleostei). *J. Hirnforsch.* **32**: 309–316.

Huber, R. & Rylander, M.K. 1992. Quantitative histological study of the optic-nerve in species of minnows (Cyprinidae, Teleostei) inhabiting clear and turbid water. *Brain Behav. Evol.* **40**: 250–255.

Huber, R., vanStaaden, M.J., Kaufman, L.S. & Liem, K.F. 1997. Microhabitat use, trophic patterns, and the evolution of brain structure in African cichlids. *Brain Behav. Evol.* **50**: 167–182.

Hughes, A. 1977. The topography of vision in mammals of contrasting life style: comparative optics and retinal organisation. In: *The Visual System in Vertebrates* (F. Crescitelli, ed.), pp. 613–756. Springer, Berlin Heidelberg, Berlin, Heidelberg.

Iwaniuk, A.N. 2004. Brood parasitism and brain size in cuckoos: a cautionary tale on the use of modern comparative methods. *Int. J. Comp. Psychol.* **17**: 17.

Joselevitch, C. & Kamermans, M. 2009. Retinal parallel pathways: seeing with our inner fish. *Vision. Res.* **49**: 943–959.

Keating, M.P. 2002. *Geometric, Physical, and Visual Optics*, 2nd edn. Butterworth-Heinemann, Boston.

Kolb, H. & Dekorver, L. 1991. Midget ganglion cells of the parafovea of the human retina: a Study by electron microscopy and serial section reconstructions. *J. Comp. Neurol.* **303**: 617–636.

Kondoh, M. 2010. Linking learning adaptation to trophic interactions: a brain size-based approach. *Funct. Ecol.* **24**: 35–43.

Kotrschal, K. & Palzenberger, M. 1992. Neuroecology of cyprinids - comparative, quantitative histology reveals diverse brain patterns. *Environ. Biol. Fishes* **33**: 135–152.

Kotrschal, K., Van Staaden, M.J. & Huber, R. 1998. Fish brains: evolution and environmental relationships. *Rev. Fish Biol. Fisheries* **8**: 373–408.

Kotrschal, A., Deacon, A.E., Magurran, A.E. & Kolm, N. 2017. Predation pressure shapes brain anatomy in the wild. *Evol. Ecol.* **31**: 619–633.

Land, M.F. & Nilsson, D.E. 2012. *Animal Eyes*. OUP Oxford, Oxford, UK.

Lefebvre, L. & Sol, D. 2008. Brains, lifestyles and cognition: are there general trends? *Brain Behav. Evol.* **72**: 135–144.

Liao, W.B., Lou, S.L., Zeng, Y. & Merila, J. 2015. Evolution of anuran brains: disentangling ecological and phylogenetic sources of variation. *J. Evol. Biol.* **28**: 1986–1996.

Losey, G.S., McFarland, W.N., Loew, E.R., Zamzow, J.P., Nelson, P.A., Marshall, N.J. *et al.* 2003. Visual biology of Hawaiian coral reef fishes. I. Ocular transmission and visual pigments. *Copeia* **2003**: 433–454.

Maor, R., Dayan, T., Ferguson-Gow, H. & Jones, K.E. 2017. Temporal niche expansion in mammals from a nocturnal ancestor after dinosaur extinction. *Nat. Ecol. Evol.* **1**: 1889–1895.

Martin, G.R., Wilson, K.J., Wild, J.M., Parsons, S., Kubke, M.F. & Corfield, J. 2007. Kiwi forego vision in the guidance of their nocturnal activities. *PLoS ONE* **2**: e198.

Mazerolle, M.J. 2014. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.00. http://CRAN.R-project.org/package=AICcmodavg.

Ménard, A., Turgeon, K. & Kramer, D.L. 2008. Selection of diurnal refuges by the nocturnal squirrelfish, Holocentrus rufus. *Environ. Biol. Fishes* **82**: 59–70.

Moller, A.P. & Erritzoe, J. 2014. Predator-prey interactions, flight initiation distance and brain size. *J. Evol. Biol.* **27**: 34–42.

Narendra, A., Reid, S.F. & Raderschall, C.A. 2013. Navigational efficiency of nocturnal *Myrmecia* ants suffers at low light levels. *PLoS ONE* **8**: e58801.

Narendra, A., Kamhi, J.F. & Ogawa, Y. 2017. Moving in dim light: behavioral and visual adaptations in nocturnal ants. *Integr. Comp. Biol.* **57**: 1104–1116.

Near, T.J., Eytan, R.I., Dornburg, A., Kuhn, K.L., Moore, J.A., Davis, M.P. *et al.* 2012. Resolution of ray-finned fish phylogeny and timing of diversification. *Proc. Natl Acad. Sci.* **109**: 13698–13703.

Near, T.J., Dornburg, A., Eytan, R.I., Keck, B.P., Smith, W.L., Kuhn, K.L. *et al.* 2013. Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proc. Natl Acad. Sci.* **110**: 12738–12743.

Nørgaard, T., Nilsson, D.-E., Henschel, J.R., Garm, A. & Wehner, R. 2008. Vision in the nocturnal wandering spider *Leucorchestris arenicola* (Araneae: Sparassidae). *J. Exp. Biol.* **211**: 816.

Northmore, D.P.M. 2011. Optic tectum. In: *Encyclopedia of Fish Physiology: From Genome to Environment*, (Farrell, A., ed.). pp. 131–142. Cambridge, MA: Elsevier.

Palmer, B.A., Taylor, G.J., Brumfeld, V., Gur, D., Shemesh, M., Elad, N. *et al.* 2017. The image-forming mirror in the eye of the scallop. *Science* **358**: 1172.

Paradis, E., Claude, J. & Strimmer, K. 2004. APE: analyses of Phylogenetics and Evolution in R language. *Bioinformatics* **20**: 289–290.

Pennell, M.W., Eastman, J.M., Slater, G.J., Brown, J.W., Uyeda, J.C., FitzJohn, R.G. *et al.* 2014. geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* **30**: 2216–2218.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & Team R. D. C. 2016. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-128, http://CRAN.R-project.org/package=nlme. R Foundation for Statistical Computing, Vienna.

Querubin, A., Lee, H.R., Provis, J.M. & O'Brien, K.M.B. 2009. Photoreceptor and ganglion cell topographies correlate with information convergence and high acuity regions in the adult pigeon (*Columba livia*) retina. *J. Comp. Neurol.* **517**: 711–722.

R Core Team 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabosky, D.L., Santini, F., Eastman, J., Smith, S.A., Sidlauskas, B., Chang, J. *et al.* 2013. Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nat. Commun.* **4**: 1958.

Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223.

Schmitz, L. & Motani, R. 2011. Nocturnality in dinosaurs inferred from scleral ring and orbit morphology. *Science* **332**: 705.

Schmitz, L. & Wainwright, P.C. 2011a. Ecomorphology of the eyes and skull in zooplanktivorous labrid fishes. *Coral Reefs* **30**: 415–428.

Schmitz, L. & Wainwright, P.C. 2011b. Nocturnality constrains morphological and functional diversity in the eyes of reef fishes. *BMC Evol. Biol.* **11**: 338.
Sidlauskas, B. 2008. Continuous and arrested morphological diversification in sister clades of characiform fishes: a phylomorphospace approach. *Evolution* **62**: 3135–3156.
Tierney, S.M., Friedrich, M., Humphreys, W.F., Jones, T.M., Warrant, E.J. & Wcislo, W.T. 2017. Consequences of evolutionary transitions in changing photic environments. *Aust. Entomol.* **56**: 23–46.
Viets, K., Eldred, K. & Johnston, R.J. Jr 2016. Mechanisms of photoreceptor patterning in vertebrates and invertebrates. *Trends Genet.* **32**: 638–659.
Wagner, H.J. 2001a. Brain areas in abyssal demersal fishes. *Brain Behav. Evol.* **57**: 301–316.
Wagner, H.J. 2001b. Sensory brain areas in mesopelagic fishes. *Brain Behav. Evol.* **57**: 117–133.
Wainwright, P.C., Alfaro, M.E., Bolnick, D.I. & Hulsey, C.D. 2005. Many-to-one mapping of form to function: a general principle in organismal design? *Integr. Comp. Biol.* **45**: 256–262.
Warrant, E.J. 1999. Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vision. Res.* **39**: 1611–1630.
Warrant, E. 2004. Vision in the dimmest habitats on earth. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **190**: 765–789.
Warrant, E.J. & Johnsen, S. 2013. Vision and the light environment. *Curr. Biol.* **23**: R990–R994.
White, G.E. & Brown, C. 2015. Microhabitat use affects brain size and structure in intertidal gobies. *Brain Behav. Evol.* **85**: 107–116.
Wu, Y., Hadly, E.A., Teng, W., Hao, Y., Liang, W., Liu, Y. *et al.* 2016. Retinal transcriptome sequencing sheds light on the adaptation to nocturnal and diurnal lifestyles in raptors. *Sci. Rep.* **6**: 33578.
Wu, Y., Wang, H. & Hadly, E.A. 2017. Invasion of ancestral mammals into dim-light environments inferred from adaptive evolution of the phototransduction genes. *Sci. Rep.* **7**: 46542.
Yamamoto, N. 2017. Adaptive radiation and vertebrate brain diversity: cases of teleosts. In: *Brain Evolution by Design. Diversity and Commonality in Animals* (S. Shigeno, Y. Murakami & T. Nomura eds), pp. 253–271. Springer, Tokyo.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article

Appendix S1 Methods and Results.

Figure S1 Trophic guild membership and species averages for eye morphology (OPT3) related to photopic (lower numbers) and scotopic (higher numbers) vision and how it relates to investment in the optic tectum relative to total brain.

Figure S2 Diel activity pattern and species averages for eye morphology (OPT3) related to photopic (lower numbers) and scotopic (higher numbers) vision and how it relates to investment in the optic tectum relative to total brain.

Figure S3 Distribution of measures of OPT3 for diurnal and nocturnal species of teleost fishes with white lines indicting the species average OPT3.

Figure S4 Variables used in PGLS analysis, coded by diel activity period.

Figure S5 Variables used in PGLS analysis, coded by trophic guild.

Figure S6 Results of subsampling procedure assessing the impact of decreased taxon sampling on quantification of the convex hulls of morphospace occupancy for diurnal vs. nocturnal lineages.

Table S1 Genbank identifiers for additional sequences used in this study.

Table S2 Model comparison using the AICc information theoretic approach for small sample size to determine the best fit error structure for our analyses explaining optic tectum volume: brownian motion (bm) or Ornstein-Uhlenbeck (ou) error structure.

Data deposited at Dryad: https://doi.org/10.5061/dryad.br097sc

Received 19 February 2018; revised 13 May 2018; accepted 25 May 2018