

Out of water in the dark: Plasticity in visual structures and function in an amphibious fish

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Abstract

Many fishes encounter periods of prolonged darkness within their lifetime, yet the consequences for the visual system are poorly understood. We used an amphibious fish (*Kryptolebias marmoratus*) that occupies dark terrestrial environments during seasonal droughts to test whether exposure to prolonged darkness diminishes visual performance owing to reduced optic tectum (OT) size and/or neurogenesis. We performed a 3-week acclimation with a 2 × 2 factorial design, in which fish were either acclimated to a 12 h:12 h or 0 h:24 h light:dark photoperiod in water or in air. We found that water-exposed fish had poorer visual acuity when acclimated to the dark, while air-acclimated fish had poorer visual acuity regardless of photoperiod. The ability of *K. marmoratus* to capture aerial prey from water followed a similar trend, suggesting that good vision is important for hunting effectively. Changes in visual acuity did not result from changes in OT size, but air-acclimated fish had 37% fewer proliferating cells in the OT than water-acclimated fish. As *K. marmoratus* are unable to eat on land, reducing cell proliferation in the OT may serve as a mechanism to reduce maintenance costs associated with the visual system. Overall, we suggest that prolonged darkness and air exposure can impair vision in *K. marmoratus*, and that changes in visual performance may be mediated, in part, by OT neurogenesis. More broadly, we show that plastic changes to the visual system of fishes can have potential consequences for organismal performance and fitness.

KEYWORDS

brain, eyeless fish, neurogenesis, optic tectum, optokinetic response, PCNA

1 | INTRODUCTION

The visual system of fishes can be highly energetically expensive, both while processing information and at rest. In some species, up to 15% of the resting metabolism is used to maintain visual structures (Moran et al., 2015), including the eyes that convert visual information to neural signals, the optic nerves that deliver these signals to the brain, and the optic tectum (OT), which is the brain region responsible for analyzing these signals (Ewert, 1974). Many fishes living in permanent

darkness have therefore evolved visual structures that are reduced or absent altogether (Moran et al., 2015; Niven & Laughlin, 2008). Several other species experience long periods of darkness temporarily throughout their lifetime (e.g., during estivation or polar night), yet the consequences for the structure and function of the visual system are poorly understood (Hammerschlag et al., 2017).

When fishes experience prolonged visual deprivation, they may use phenotypic plasticity to reduce the energetic costs associated with the visual system. For example, populations of the Atlantic molly

(*Poecilia mexicana*) living in the dark cave habitats had a smaller OT than populations in habitats with a natural light (L):dark (D) photoperiod (Eifert et al., 2015). Differences in OT size were reversed after fish from these populations were reared in the laboratory for a few generations, suggesting that OT differences in wild fish resulted from phenotypic plasticity rather than local adaptation. Visual deprivation can also influence neurogenesis in the OT and associated tissues (McKeown et al., 2013). For example, zebrafish (*Danio rerio*) maintained in dim light were found to have fewer proliferating cells in the torus longitudinalis (Lindsey et al., 2014), a brain region closely associated with the OT that is involved with processing changes in light intensity (Wulliman, 1994). Overall, it is not well known whether dark-induced changes to the OT can alter the visual performance of fishes and interfere with their ability to perform important visual behaviors.

Some fishes occupy habitats that dry periodically owing to receding tides or seasonal droughts (Sayer & Davenport, 1991; Turko et al., 2021). While many of these fishes remain highly active out of water (e.g., mudskippers; Ord & Cooke, 2016), others become relatively inactive and seek refuge in moist dark places until water returns. For example, marbled lungfish (*Protopterus aethiopicus*) burrow underground and estivate in a completely dark mucous cocoon for several months during the dry season (Smith, 1930). Similarly, amphibious mangrove rivulus (*Kryptolebias marmoratus*) nestle deep within insect tunnels in rotting logs where they can remain dormant for several weeks during seasonal droughts (Taylor et al., 2008). Importantly, fishes that enter an inactive and hypometabolic state on land are often unable to feed in terrestrial environments, which may exacerbate the need to reduce energetic costs associated with the visual system when it is not in use. When water returns, however, effective aquatic vision may be critical for accomplishing essential tasks, such as predator avoidance or the capturing of prey both above and below the waterline (Zahl et al., 1977; Temple et al., 2010).

We used *K. marmoratus* to explore how prolonged darkness during air exposure can influence visual performance. *K. marmoratus* is a useful model to address this question because (a) they can survive out of water for weeks to months during the dry season by seeking refuge in moist dark areas (e.g., insect tunnels within rotting logs; Taylor et al., 2008), (b) they cannot eat while on land and thus lower their metabolic rate after 3 weeks in air to conserve energy (Rossi & Wright, 2020; Turko et al., 2019), and (c) they rely on their visual system to accomplish essential daily tasks, such as leaping out of water to capture terrestrial arthropods (Martin et al., 2020; Pronko et al., 2013; Taylor, 1992). Leaping out of water for terrestrial insects may be an especially challenging visual task given the distortions that occur at the air-water interface owing to refraction (Barta & Horváth, 2003; Dill, 1977). We used *K. marmoratus* to first test the hypothesis that exposure to prolonged darkness would alter OT size and neurogenesis, thereby altering visual performance (darkness hypothesis). We predicted that dark-acclimated fish (0 h L:24 h D photoperiod) would have a smaller OT, fewer proliferating cells in the OT, and poorer visual acuity compared to fish maintained on a 12 h L:12 h D photoperiod, regardless of medium (i.e., air or water).

We then tested the hypothesis that air exposure would similarly alter OT size and neurogenesis because of the reduced energy intake on land, thereby altering visual performance (air exposure hypothesis). We predicted that air-acclimated fish would have a smaller OT, fewer proliferating cells in the OT, and poorer visual acuity than fish maintained in water, regardless of photoperiod. Moreover, we expected that any decrement in visual acuity would be accompanied by an impaired ability to capture aerial prey from water given the presumed importance of vision for hunting in this species (Pronko et al., 2013; Taylor, 1992). We performed a 3-week acclimation with a 2×2 factorial design, in which *K. marmoratus* were either acclimated to a 12 h L:12 h D or 0 h L:24 h D photoperiod in water or in air.

2 | METHODS

2.1 | Experimental animals

All experimental fish ($n = 176$; 0.082 ± 0.001 g; 18.1 ± 0.1 mm, mean \pm SEM) were adult hermaphrodites of the self-fertilizing *K. marmoratus* (strain HON11, originating from the Bay Islands; Tatarenkov et al., 2010). Before experimentation, fish were individually maintained in 120 ml clear plastic holding cups under standard conditions (~60 ml water, 15‰ salinity, 25°C, 12 h L:12 h D) in the Hagen Aqualab at the University of Guelph. Fish were fed live *Artemia sp.* nauplii three times per week, as well as frozen bloodworms once per week in the months before experimentation. All experimental procedures were approved by the University of Guelph Animal Care Committee (AUP 3891 and 4752).

2.2 | Experimental protocol

Fish were randomly assigned to one of four 3-week acclimations: water (12 h L:12 h D) (control), water in darkness (0 h L:24 h D), air (12 h L:12 h D), or air in darkness (0 h L:24 h D). A 3-week acclimation period was chosen because it is sufficient to induce a significant metabolic depression in *K. marmoratus* (Rossi & Wright, 2020; Turko et al., 2019). We determined the approximate light level for each experimental photoperiod using a digital intensity luxmeter (QUMOX): ~200 lux (12 h L), ~0 lux (12 h D), and ~0 lux (24 h D). The water-exposed groups were fed bloodworms three times per week, whereas the air-exposed groups were fasted throughout the acclimation period. Although differences in feeding state introduce a confounding variable to the data, it more accurately reflects the natural history of *K. marmoratus*. During the dry season, fish can remain out of water for several weeks and are unable to feed, resulting in metabolic suppression (Rossi & Wright, 2020; Turko et al., 2019). During the rainy season, fish forage routinely (D. S. Taylor, pers. obs.). All acclimations were carried out in 120 ml holding cups at a constant 25°C. We acclimated fish to air as previously described (Ong et al., 2007) and acclimated fish to darkness by

wrapping the holding cups with at least two layers of opaque duct tape to prevent light penetration. The lid of each cup was also covered in duct tape to similarly prevent light penetration. We used one small hole in the lid (covered by a duct tape flap) to insert bloodworms for feeding as well as to perform water changes, which we accomplished by siphoning water in and out using airline aquarium tubing. We performed weekly water changes for all fish maintained in water during the acclimation period. Bloodworms were never recovered from these weekly water changes, suggesting that all water-exposed fish, including those in the dark, were feeding throughout the acclimation period. Air-acclimated fish were disturbed on these same days by briefly tilting their holding cup.

2.3 | Visual acuity and hunting performance

Following the acclimation period, we subjected a random subset of fish from each group to either an optokinetic response (OKR) test to determine visual acuity ($n = 8-9$ per group) or a hunting test to assess their ability to capture aerial prey from water ($n = 24-25$ per group). Both tests were performed in water and in daylight. Therefore, air-exposed fish were returned to water in the dark the night before experimentation (8:00 p.m.), and all fish were exposed to ~6 h of daylight before the experimentation (8:00 a.m. to 2:00 p.m.). We placed fish assigned to the OKR test in clear 120 ml plastic holding cups overnight (~60 ml, 15‰ salinity, 25°C), whereas fish assigned to the hunting test were placed in their testing chamber the night before (clear 14 × 5.5 × 9.3 cm plastic containers; ~200 ml, 15‰, 25°C). We assessed visual acuity as previously described (Allore et al., 2021) using an OKR machine modified from existing designs (Cameron et al., 2013; Saidi et al., 2015; Znotinas & Standen, 2019) (Sporting Information: Figure S1). Briefly, we transferred fish into a cuvette plugged with mesh to restrict fish movement. The cuvette was then magnetically anchored to the bottom of a stationary water-filled beaker within the rotating drum of the OKR machine, with the fish's eyes ~6.5 cm from the edge of the drum. The drum was lined with a paper containing black and white lines of equal thickness (grating), which rotated along with the drum (10.5 rpm, clockwise). If the fish's

eyes consistently tracked the grating as it rotated, the fish was deemed to have elicited a visual response. We gradually decreased the size of black and white gratings (higher spatial frequency) to identify the smallest grating that elicited a visual response. We used the grating width to calculate visual acuity using the following equation:

$$\text{Visual acuity} = \frac{1}{2 \tan^{-1} \left(\frac{h}{2a} \right)}$$

Where a is the distance between the fish's eye and the grating (6.5 cm), and h is the length of the smallest cycle (the combined length of one black and one white line on the grating) to elicit a visual response. To assess hunting ability, we lowered a bloodworm to ~5 mm above the water surface in the testing chamber. We video-recorded the fish for 15 min and used the recordings to determine the latency to approach the bloodworm (second), the latency from approach to attack (second), and the number of times fish attacked the bloodworm before it was successfully captured. The "latency to approach" reflects the amount of time between when the bloodworm was lowered until the fish moved within striking distance (i.e., directly beneath the bloodworm with their head directed toward it). The "latency to attack" reflects the time between the first approach and the first time fish leapt out of water in an effort to capture the bloodworm. A capture was deemed successful when fish pulled the bloodworm into the water and consumed it.

Although 24–25 fish were subjected to the hunting test per group, not all fish approached and/or attacked the suspended bloodworm (Table 1). Following the hunting test, a random subset of fish ($n = 8-9$ per group) were euthanized via immersion in MS-222 (500 mg L⁻¹) and fixed in 10% buffered formalin for at least 2 weeks before brain morphology was assessed.

2.4 | Brain morphology and neurogenesis

To determine whether OT size was altered by our experimental acclimations, we carefully removed the skull cap of all fish fixed in

TABLE 1 Sample sizes for behavioral hunting tests

Treatment	N (total)	n (approached)	n (attacked)	(Attacked:approached)
Water				
12:12 light:dark	24	23	21	0.91
Water				
0:24 light:dark	24	19	11	0.58
Air				
12:12 light:dark	24	15	8	0.63
Air				
0:24 light:dark	25	20	9	0.45

Note: Not all fish subjected to the test approached and/or attacked the suspended bloodworm.

formalin following the hunting test to expose the brain ($n=8-9$ per group). We photographed the dorsal surface of the brain under a Nikon SNZ1500 Stereoscopic Microscope (Nikon Instruments) and measured the OT surface area (mm^2) of both OT lobes from these photographs using ImageJ (<http://imagej.nih.gov/ij>) (Supporting Information: Figure S2A). It has been shown in other fishes that OT measurements obtained from dorsal view photographs can correlate strongly with those obtained from excised brains (Näslund, 2014). We standardized OT surface area to the surface area of the adjacent cerebrum (mm^2). We then excised brains as previously described (Moran et al., 2015), and dried them in an oven at 60°C for 24 h to obtain brain dry mass (mg). We standardized the brain dry mass to standard body length (mm) to account for any size differences between fish. Interestingly, fish in our breeding colony are occasionally born without eyes (~1% of the population)—a presumably fatal phenotype in the wild (Supporting Information: Figure S2B). We assessed the OT size and brain dry mass of eight eyeless fish to determine whether the brain of *K. marmoratus* is responsive to permanent visual deprivation. Finally, we used an additional random subset of fish ($n = 7$ per group) to assess neurogenesis in the OT. We stained $5\ \mu\text{m}$ -thick paraffin cross-sections through the OT (immediately anterior to the eyes) for the neurogenesis marker, proliferating cell nuclear antigen (PCNA), as previously described (Rossi and Wright, 2021; Supporting Information: Figure S3). We report the total number of PCNA⁺ cells in the OT proliferation zone on both the right and left sides of the brain.

2.5 | Statistical analysis

All data were initially tested for normality (Shapiro-Wilk) and homogeneity of variance (Levene's test), and appropriately transformed when necessary. We performed two-way analysis of variance (ANOVAs) to assess the influence of darkness and air exposure on visual acuity, hunting performance (i.e., latency to approach, latency to attack, and % success), OT size, and OT neurogenesis. When a significant air exposure \times photoperiod interaction was present in the data, we performed a Holm-Sidak post hoc test to reveal the differences between groups. Finally, we compared the OT size and brain mass of eyeless morphs to control fish (i.e., those acclimated to water on a standard photoperiod) using two-tailed *t*-tests. All statistical analyses were performed using RStudio (version 1.1.463) with R (version 3.6.1) and all graphs were generated using GraphPad Prism (version 8). Results were considered significant at $\alpha < 0.05$.

3 | RESULTS

3.1 | Visual acuity and hunting performance

Visual acuity was altered both by photoperiod and air exposure (two-way ANOVA, interaction; $F_{1,30} = 6.1, p = 0.02$). We found that fish maintained in water had poorer visual acuity when acclimated to the

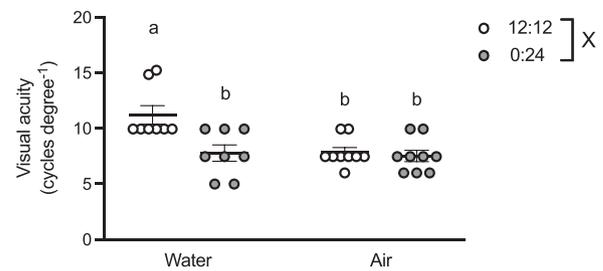


FIGURE 1 The visual acuity of *Kryptolebias marmoratus* following experimental acclimations. The X in the figure legend denotes a significant photoperiod \times air exposure interaction. Different lower case letters indicate significant differences between groups. Error bars denote the mean \pm SEM.

dark (Holm-Sidak; $F_{1,30} = 8.9, p < 0.01$), while air-acclimated fish had poorer visual acuity regardless of photoperiod (Holm-Sidak; $F_{1,30} = 8.2, p < 0.01$ for both photoperiods) (Figure 1). Photoperiod significantly altered the latency to approach the bloodworm (two-way ANOVA; $F_{1,73} = 8.0, p = 0.01$), as fish maintained in darkness were overall ~2.5 times slower to approach the bloodworm than fish maintained under standard light conditions (Figure 2a). On the other hand, air-acclimated fish were slower to attack the suspended bloodworm (two-way ANOVA; $F_{1,45} = 5.3, p = 0.03$) and less successful at attacking it (two-way ANOVA; $F_{1,45} = 8.8, p < 0.01$) (Figure 2b,c).

3.2 | Brain morphology and neurogenesis

Photoperiod and air exposure had no effect on OT size (two-way ANOVA; $F_{1,28} = 0.05, p = 0.82$; $F_{1,28} = 0.01, p = 0.92$) or dry brain mass (two-way ANOVA; $F_{1,29} = 1.3, p = 0.26$; $F_{1,29} = 0.2, p = 0.69$) (Figure 3a,b). Eyeless fish had a significantly smaller OT than control fish (*t*-test; $t = 6.1, df = 14, p < 0.01$), although their brain dry mass did not differ from the control (*t*-test; $t = 1.9, df = 14, p = 0.15$) (Figure 3a,b). Air exposure significantly altered cell proliferation in the OT (two way ANOVA; $F_{1,24} = 9.2, p < 0.01$), as fish in air had 37% fewer proliferating cells in the OT compared to fish maintained in water (Figure 3c).

4 | DISCUSSION

Amphibious *K. marmoratus* spend weeks to months out of water in the dark moist refuges. Here, we show that darkness and air exposure significantly reduced their visual acuity and hunting performance. The brain region responsible for visual processing, the OT, showed a marked reduction in PCNA⁺ cells (marker for neurogenesis, Bertapelle et al., 2017; Rankin et al., 2004) in air-acclimated, but not in aquatic dark-acclimated fish. Since air-exposed *K. marmoratus* were fasted during the acclimation period, reducing cell proliferation in the OT may serve as a mechanism to reduce maintenance costs associated with the visual system. Reduced OT neurogenesis may have influenced the visual acuity of air-acclimated

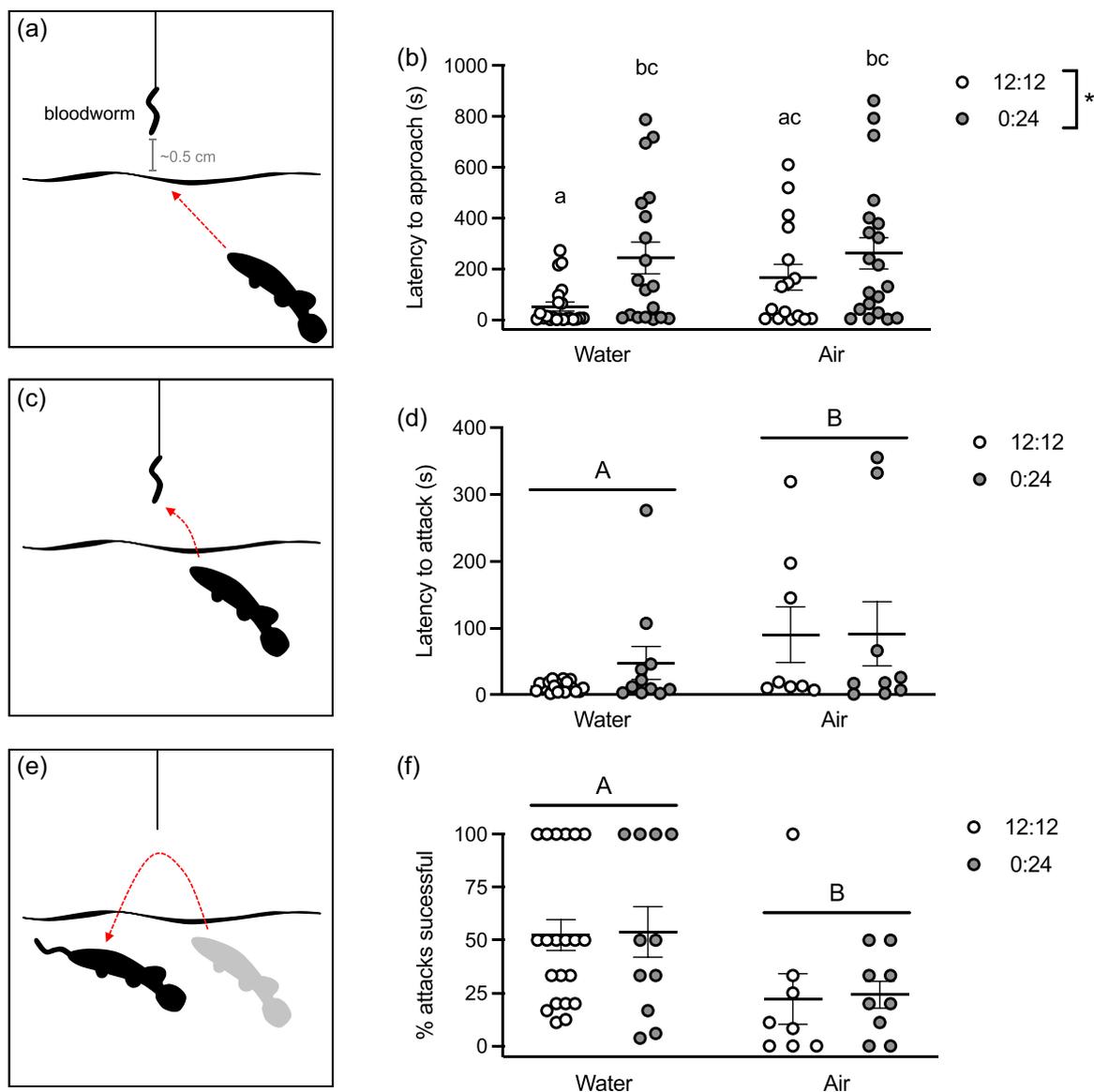


FIGURE 2 The hunting performance of *Kryptolebias marmoratus*. (a, b) Latency to approach the suspended bloodworm. The asterisks in the legend denote a significant main effect of photoperiod. (c, d) Latency to attack the bloodworm after approach, and (e, f) percentage of attacks successful. Lowercase letters denote significant differences between all groups. Uppercase letters denote a significant main effect of air exposure. Error bars denote the mean \pm SEM.

fish. However, it is likely that other factors are also at play given that fish in aquatic darkness exhibited impaired visual acuity with no concomitant changes in OT neurogenesis. Overall, our findings suggest that prolonged darkness and air exposure can cause plastic changes to the structure and function of the visual system of fishes that can interfere with their ability to perform ecologically-important visual behaviors.

5 | DARKNESS HYPOTHESIS

Like most fishes, *K. marmoratus* rely on vision to capture prey, avoid predators, and navigate to new environments. Yet, we found that exposure to prolonged darkness readily impaired visual acuity in *K.*

marmoratus maintained in water, consistent with the “darkness hypothesis.” We found no evidence that dark-related changes in visual acuity were mediated by OT size or neurogenesis, suggesting that other components of the visual system in *K. marmoratus* are sensitive to dark-acclimation (e.g., retina). In most fishes, the retina contains two photoreceptor types: rods for dim-light (scotopic) vision and cones for bright-light (photopic) vision (de Busserolle et al., 2017; Fernald, 1990). When fishes experience changes in ambient light (e.g., night to day), they can maintain visual performance by rapidly altering the position and morphology of these rod and cone photoreceptors (Braekevelt, 1982; Burnside et al., 1982; McFarland et al., 1979), among other changes to the visual system (Kurz-Isler & Wolburg, 1986; Siebeck et al., 2003). The poorer visual acuity of water-exposed *K. marmoratus* on the 0 h L:24 h D photoperiod is

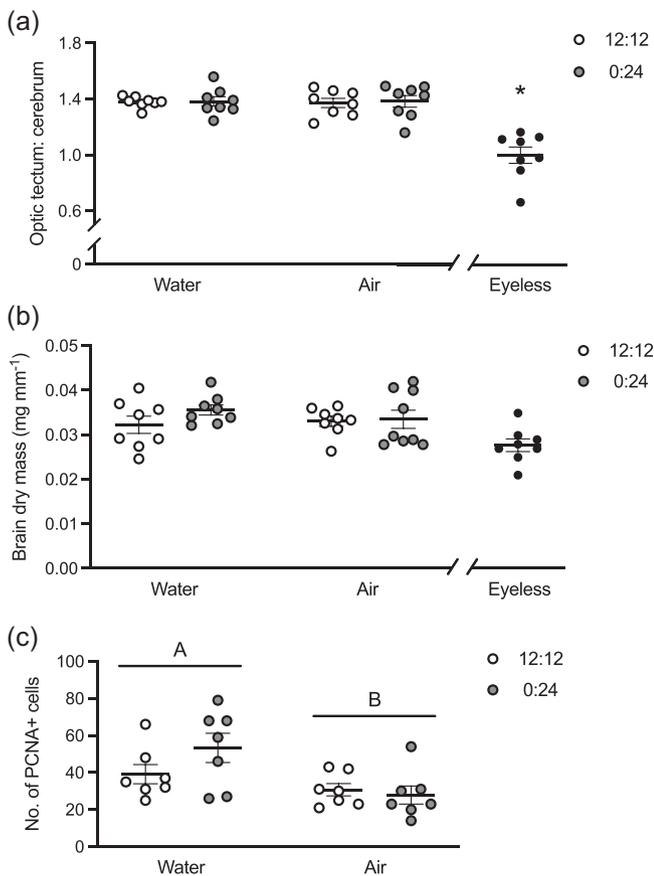


FIGURE 3 (a) Optic tectum (OT) to cerebrum surface area (mm^2) ratio. An asterisk denotes a significant difference between the OT size of eyeless and control (water, 12 h L:12h D) fish. (b) Dry brain mass standardized to standard body length. (c) The number of PCNA+ cells in the OT of *Kryptolebias marmoratus*. Uppercase letters denote a significant main effect of air exposure. Error bars denote the mean \pm SEM.

suggestive of a slower and/or impaired ability to shift between a scotopic- and photopic-adapted state. Indeed, mammalian studies have demonstrated that it can take several days for vision to be restored following weeks or months of dark-acclimation (Timney et al., 1978). Although some fishes can encounter long periods of darkness within their lifetime, investigations into their capacity for photopic adaptation are extremely limited.

We used a visually-demanding hunting test to assess organismal performance in a more ecologically-relevant context. Terrestrial insects and arachnids have been found in the gut content of wild *K. marmoratus* (Huehner et al., 1985; Taylor, 1992), suggesting that terrestrial prey capture is an important foraging behavior. Although this behavior is seldom observed in the wild owing to the cryptic nature of this species, captive *K. marmoratus* routinely leap out of water to capture food (Rossi, pers. obs.) (Huehner et al., 1985). In support of the “darkness hypothesis,” we found that dark-acclimated fish were overall slower to approach the suspended bloodworm during the hunting tests, which may reflect a reduced ability to initially detect prey above water. Interestingly,

dark-acclimation slowed the approach of both water- and air-exposed fish, although darkness only had a marked effect on the visual acuity of water-exposed fish, since air-exposed fish had low visual acuity regardless of photoperiod. Thus, aerial darkness may alter other aspects of visual performance important for aerial prey detection, such as the ability to detect subtle shadows (i.e., contrast sensitivity; Santon et al., 2019). Alternatively, the latency to approach aerial prey may be related to feeding motivation rather than prey detection. We found that across both water- and air-exposed groups, a lower proportion of fish on the 0 h L:24 h D photoperiod attacked the suspended bloodworm following approach relative to fish on the 12 h L:12 h D photoperiod. A lower motivation to feed may result from metabolic changes caused by dark-acclimation (e.g., metabolic depression) (Milsom et al., 2008; Zhang et al., 2006). Moreover, if *K. marmoratus* become inactive during periods of darkness owing to a lower metabolic rate, then muscle disuse atrophy may impair their ability to leap for prey out of water—an interesting avenue for future investigation.

6 | AIR EXPOSURE HYPOTHESIS

A few fishes, including *K. marmoratus*, occupy dark terrestrial environments for weeks or months during seasonal droughts (Smith, 1930; Taylor et al., 2008). Since *K. marmoratus* are unable to swallow food out of water, metabolic depression is critical for slowing the use of endogenous energy stores during these long periods on land (Rossi & Wright, 2020; Turko et al., 2019). In support of the “air exposure hypothesis,” we found that air-acclimated fish had fewer proliferating cells in their OT, possibly to reduce maintenance costs associated with the visual system while in a fasted and metabolically depressed state. To our knowledge, we are among the first to demonstrate that periods of dormancy can attenuate neurogenesis in fishes, albeit in hibernating mammals, reduced rates of neurogenesis have been reported in the subventricular zone and hippocampus (e.g., *Mesocricetus auratus*; León-Espinosa et al., 2016). Interestingly, repeated short-term periods of air exposure increased neurogenesis in the telencephalon of *K. marmoratus* and enhanced their ability to learn the location of important environmental features (Rossi & Wright, 2021). The differential effects of intermittent and prolonged air exposure on neurogenesis suggest that different brain-related functions may be important for *K. marmoratus* during brief versus extended terrestrial episodes. Understanding how air exposure impacts neural processes in amphibious fishes more broadly is a fascinating area for future work.

The reduced OT neurogenesis in air-acclimated *K. marmoratus* coincided with poorer visual acuity. Our findings are consistent with that of previous studies linking OT neurogenesis with visual performance. For example, McKeown and colleagues demonstrated that following an OT injury, a high rate of OT neurogenesis was required to restore visually-mediated avoidance behaviors in African clawed frogs (*Xenopus laevis*; McKeown et al., 2013). Alternatively, it is well-established that different eye morphologies are required for fish vision in water and in air (Colicchia, 2007; Sayer, 2005). Thus, air-

induced changes to the eyes of *K. marmoratus* may have improved aerial vision at the expense of visual performance upon return to water. Many studies have explored the adaptations that facilitate aerial and aquatic vision in amphibious fishes (Graham, 1970; Graham and Rosenblatt, 1970; Perez et al., 2017;) but the idea that plastic changes may play a role warrants further investigation. Regardless of the mechanism(s) underlying the low visual acuity of air-acclimated fish, their impaired vision may have led to the slower attack of aerial prey, as well as the lower proportion of successful attacks given that detecting and capturing aerial prey from water are likely visually-demanding tasks. Indeed, many studies have shown that conditions that impair visual acuity (e.g., high water turbidity) can dramatically alter predator-prey interactions (Hess et al., 2019; Wenger et al., 2013, 2017), including the effectiveness of predator strikes (Ortega et al., 2020). Overall, we suggest that following long periods of terrestrial exposure, *K. marmoratus* may be less effective at foraging, escaping predators, and navigating the environment. It is unknown whether other amphibious fishes similarly exhibit visual impairment following long periods in air, or whether strategies exist to maintain the integrity of their visual system.

7 | PERSPECTIVES

Many fishes encounter periods of prolonged darkness within their lifetime, including a handful of amphibious species that seek refuge in underground burrows, rotting logs, or moist detritus during seasonal droughts (Eldon, 1979; Smith, 1930; Taylor et al., 2008). We demonstrated that dark-acclimation could impair visual performance in the amphibious *K. marmoratus*, but that air acclimation had more serious consequences for their visual system. Our findings suggest that fishes that return to water after several weeks of inactivity on land may perceive the aquatic environment with less detail, which can negatively impact their foraging ability. It is unknown whether this visual impairment can be reversed or whether fish can compensate for poor vision by enhancing other senses (e.g., olfaction). Interestingly, the eyeless fish in our laboratory colony provide some insight into the capacity for *K. marmoratus* to compensate for visual impairment. The brains of eyeless fish were similar in mass to those of control fish despite having significantly smaller OT lobes, possibly owing to a compensatory increase in another brain region (e.g., olfactory bulbs). Investigating the interplay between different sensory systems may therefore be critical for understanding how animals effectively perform ecologically-relevant tasks in the face of environmental change.

Finally, our study highlights the potentially deleterious effects of prolonged food deprivation and metabolic depression on neural and visual processes. In this study, we induced a metabolic depression in *K. marmoratus* via air acclimation, but several other fishes enter a hypometabolic state in response to cold temperatures and food scarcity during winter months (Sayer & Davenport, 1996; Speers-Roesch et al., 2018). Do other fishes similarly exhibit reduced neurogenesis and visual performance during long periods of metabolic depression? Many studies have explored how energy-limitation can

alter the visual system of fishes over evolutionary time (Krishnan & Rohner, 2017), but relatively few have focused on plastic changes that can occur within an individual's lifetime. Overall, we suggest that phenotypic plasticity in the visual system can govern individual fitness by influencing how well fishes perform important visual behaviors.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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