

Research



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Transgenerational plasticity in the eye size of *Daphnia*

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It is well established that environmental signals can induce phenotypic responses that persist for multiple generations. The induction of such 'transgenerational plasticity' (TGP) depends upon the ability of organisms to accurately receive and process information from environmental signals. Thus, sensory systems are likely intertwined with TGP. Here we tested the link between an environmental stressor and transgenerational responses in a component of the sensory system (eye size) that is linked to enhanced vision and ecologically relevant behaviours. We reared 45 clones of *Daphnia pulicaria* in the presence and absence of a low-quality resource (cyanobacteria) and evaluated shifts in relative eye size in offspring. Our results revealed divergent shifts in relative eye size within- and across-generations. Parental *Daphnia* that were fed cyanobacteria produced a smaller eye than *Daphnia* fed high-quality algae. Such differences were then reversed in the offspring generation; *Daphnia* whose mothers were fed cyanobacteria produced larger eyes than *Daphnia* that were continually fed green algae. We discuss the extent to which this maternal effect on eye size is an adaptive response linked to improved foraging.

1. Introduction

It is well known that organisms exhibit the capacity to modify the expression of traits in response to a change in environmental conditions [1–5]. Such 'within-generation plasticity' occurs when environmental signals alter the expression of traits during development. It is also now clear that the environment can induce phenotypic changes that persist for multiple generations [6–15]. This 'transgenerational plasticity' (TGP) occurs when the environment experienced by parents induces phenotypic changes in offspring and future generations. TGP has been documented in a diverse array of organisms in response to many environmental stressors [6–15]. The empirical evaluation of TGP has almost exclusively focused on the life history, behavioural, morphological and physiological traits of organisms [16]. Given that the induction of TGP is dependent upon the ability of organisms to accurately receive information from environmental signals, it follows logically that components of the sensory system may also respond to environmental signals to ultimately enhance organismal performance. Yet, the link between the environment and transgenerational responses in sensory systems is largely unexplored [17].

Eye size is a feature of the visual sensory system that varies extensively across taxa [18,19]. Increased eye size is associated with improved aspects of vision [18,20–23] including visual acuity [24]. There are important ecological correlates of eye size; increased eye size or components of the eye (i.e. pupil size) are associated with shifts in foraging, mating and anti-predator behaviour [25–31]. Eye size has also been shown to be a key predictor of the foraging niche of birds [32]. A growing body of work has shown that eye size is phenotypically plastic in response to exposure to such factors as predator cues and resource

limitation [33–38]. Eye size can also diverge among populations [17,39–41]. The manner in which eye size is linked to the process of TGP is unknown.

Daphnia are a common feature of freshwater habitats and an important grazer on phytoplankton [42]. *Daphnia* are exposed to a diversity of phytoplankton ranging from high-quality green algae to grazer-resistant cyanobacteria [43]. Cyanobacteria is a low-quality resource because they are filamentous [44,45], nutritionally deficient [46,47], and some are toxic [48,49]. Research has shown that cyanobacteria negatively impact the survival, growth and reproduction of *Daphnia* [50–52]. There is also evidence for transgenerational effects of exposure to cyanobacteria on the fitness of *Daphnia* and other zooplankton. This includes some studies revealing compounding negative fitness consequences of cyanobacteria that spanned multiple generations [53–55] while other studies provide evidence for adaptive responses that lessen the negative impacts of cyanobacteria [56–61]; see also [62].

The visual system of *Daphnia* is characterized by a sac-like compound eye [63]. Research has shown that *Daphnia* can change the orientation of their eye and that the eye is capable of responding to shifts in light and motion [64]. *Daphnia* can also behaviourally respond to visual features of the environment (i.e. exhibit an optomotor response) [65]. As a result, researchers have proposed that eye size is potentially important for assessing food quality and predator avoidance [65]. There is also growing evidence that variation in environmental conditions can influence investment in eye tissue in *Daphnia* [17,35]. This includes a study documenting plasticity in eye size in response to resource limitation [35]. Given that eye size may be important for foraging, that resources can influence eye size [33,35], and that cyanobacteria can induce transgenerational plasticity (see above), it follows logically that cyanobacteria may modify transgenerational investment in eye tissue. On the one hand, exposure to a low-quality resource (i.e. cyanobacteria) may result in *Daphnia* increasing allocation towards other components of fitness at the expense of eye tissue. The alternative perspective is that *Daphnia* may increase investment in eye tissue when exposed to cyanobacteria because a larger eye may improve foraging capabilities. Research in other invertebrates have shown that increases in eye size may be mediated by shifts in the size or number of light-collecting units (ommatidia) [66].

Here we tested the influence of cyanobacteria on transgenerational plasticity in eye size. We reared 45 clones of *Daphnia pulicaria* in the presence and absence of cyanobacteria (*Anabaena*) and evaluated variation in relative eye size in the parental and offspring generations [67]. If exposure to cyanobacteria results in a trade-off between investment in life history versus eye tissue, then we expect to observe a decline in relative eye size and the production of smaller eyes will continue in the offspring generation. An alternative possibility is that exposure to cyanobacteria induces an adaptive response that enhances fitness (e.g. [58–62]). Such a result would potentially be supported if parents respond to exposure to cyanobacteria by increasing allocation to eye tissue in offspring.

2. Material and methods

We tested for an influence of cyanobacteria on the eye size of *Daphnia* using clones from two lakes in Wisconsin, USA (Allequash, Mendota). The experiments that generated the

images that we used to assess eye size are published [67]. Here we provide a summary of the protocols. In May 2016, we obtained sediment samples from each lake via an Ekman grab. We then hatched 45 *Daphnia* clones from these sediment samples. These clones were reared and maintained in COMBO media [68] and fed non-limiting quantities of green algae (*Scenedesmus obliquus*) prior to the start of the experiments. For the experiments, we first raised all clones under common garden conditions for three generations. In January 2018, we isolated one adult female per clone and placed each individual into separate 90-ml containers. We collected four newborn individuals and placed them into a new jar as soon as a female produced a clutch of offspring. All individuals were transferred to fresh media and algae (*Scenedesmus obliquus*; 2.0 mg C/L) every other day. The second and third common garden generations were generated using the second clutch of offspring from the previous generation. All generations experienced the same conditions (temperature: 20°C; photoperiod: 16 L : 8 D; feeding rate: 1.0 mg C^{-L-d}).

We evaluated the transgenerational effects of cyanobacteria using offspring from third-generation common garden-reared adults. We collected eight newborn individuals from the second clutch of each clone and randomly assigned each individual to one of the following resource treatments: (a) *Scenedesmus* or (b) *Anabaena* (in generation 1 only). Individuals in the *Scenedesmus* treatment received 100% *Scenedesmus* while individuals in the *Anabaena* treatment received 100% *A. inaequalis*. Each treatment was replicated 4× per clone and received a similar carbon content of algae (1.0 mg C^{-L-d}). All other experimental conditions mimicked the previous common garden generations. All *Daphnia* were then monitored for the release of the first clutch into the brood chamber (i.e. maturation). Upon maturation, all individuals were photographed for estimates of size at maturation. These images allowed us to assess eye size. Using ImageJ, we traced the outline of the body (excluding the tail spine) and eye for estimates of body length and eye diameter. Our experiment continued for a second generation to test for potential transgenerational consequences of cyanobacteria. The second experimental generation was initiated by collecting individuals from the third clutch of each clone. Importantly, all individuals were fed *Scenedesmus* in the second generation. Each treatment was replicated 3× per clone in generation 2. Individuals in the second generation were photographed at maturation, which allowed us to assess eye size.

(a) Statistical analyses

We evaluated the influence of cyanobacteria on absolute and relative eye size within- and across-generations using linear mixed models (SPSS v. 27 IBM Corp.). We entered food treatment, generation and the food × generation interaction as fixed effects. Body size (length in millimetre) was entered as a covariate for the analyses of relative eye size. To test for clonal variation in plasticity, we included the clone × food × generation interaction as a random effect. We also tested for trade-offs between investment in eye size and life-history traits using the published data [67] by performing multiple regressions with eye size entered as the dependent variable, life-history trait (age at maturation, clutch size) and length entered as the independent variables. We performed these regressions separately for each generation [69].

3. Results

(a) Absolute eye size

The influence of cyanobacteria on absolute eye size depended upon generation. We observed a significant ($p < 0.05$) food × generation interaction ($F_{1,176.2} = 35.19$, $p < 0.001$). Exposure to cyanobacteria in generation 1 resulted in an absolute eye size that was 7% smaller versus the eye size of *Daphnia* in the

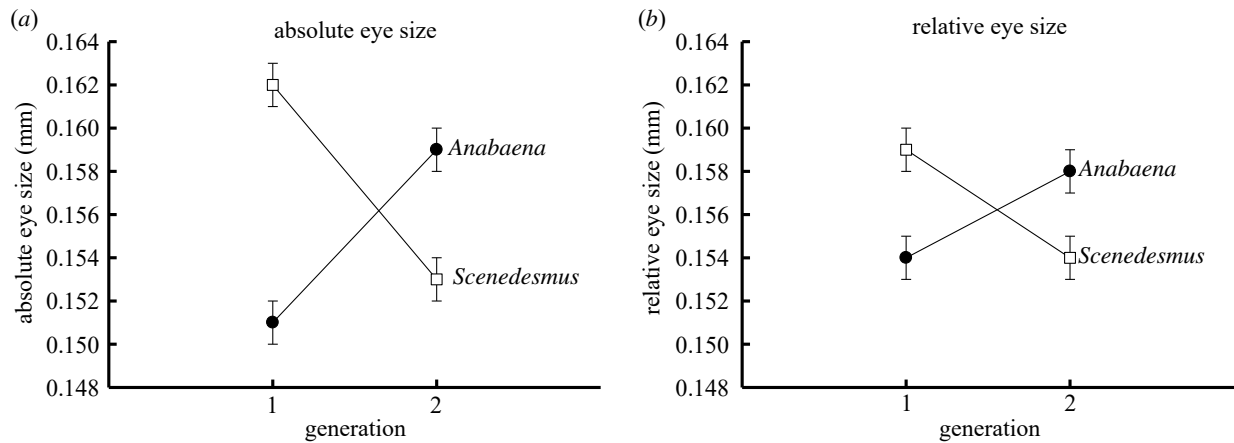


Figure 1. Exposure to cyanobacteria influences the expression of eye size within- and across-generations. (a) Absolute eye size, (b) relative eye size. The food treatment $\times$ generation interaction was significant for absolute (a) and relative (b) eye size. Note that all individuals were fed *Scenedesmus* in generation 2. Error = ± 1.0 s.e.

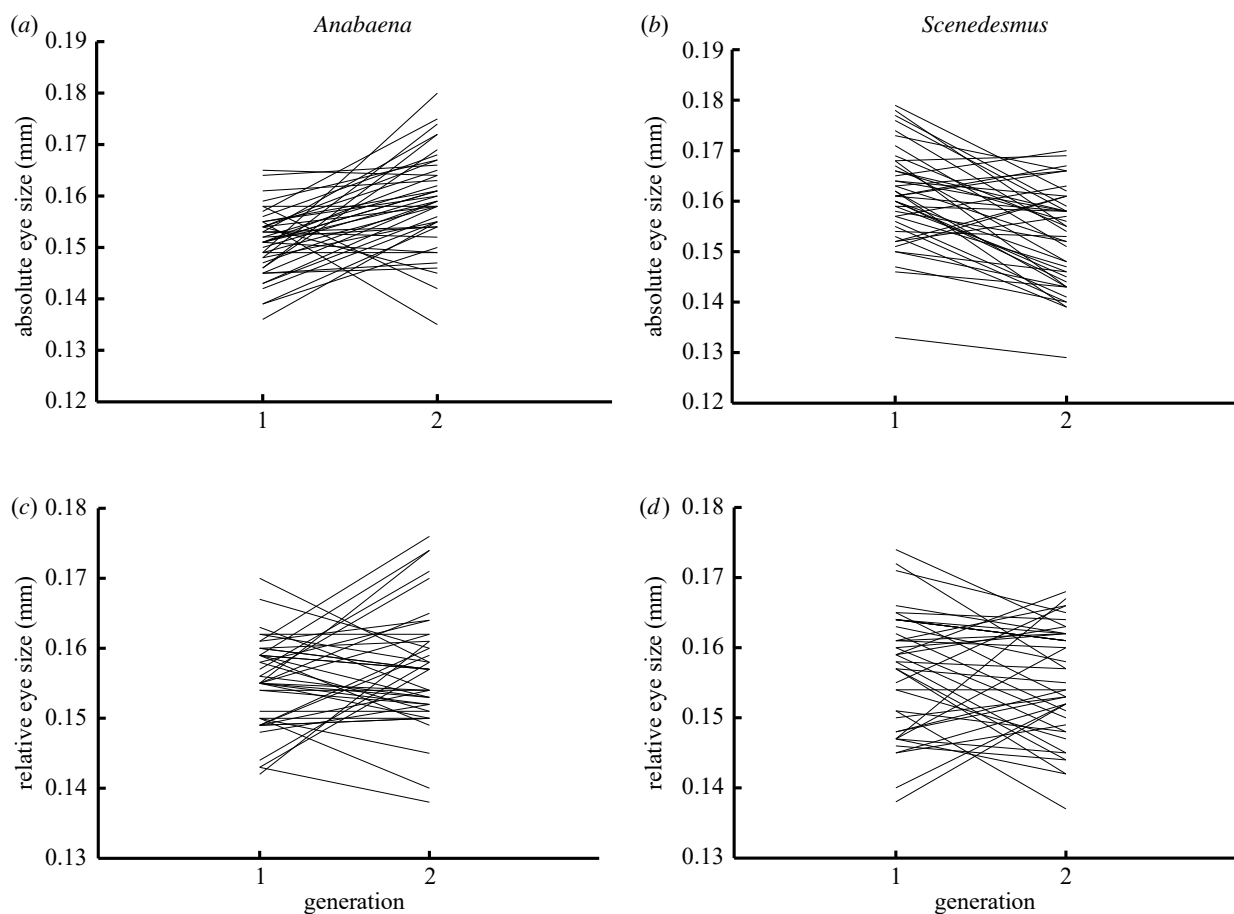


Figure 2. Clonal variation in responses to cyanobacteria. (a) Clonal variation in absolute eye size for the *Anabaena* treatment, (b) clonal variation in absolute eye size for the *Scenedesmus* treatment, (c) clonal variation in relative eye size for the *Anabaena* treatment, (d) clonal variation in relative eye size for the *Scenedesmus* treatment. For each panel, each line represents the shifts in eye size across generations for a given clonal lineage. The food treatment $\times$ generation $\times$ clone ID interaction was significant for absolute (a,b) and relative eye size (c,d).

Scenedesmus treatment (figures 1 and 2). Such trends were reversed in generation 2; the absolute eye size in the cyanobacteria treatment was 4% larger than the eye size of *Daphnia* in the *Scenedesmus* treatment in generation 2 (figures 1 and 2). Overall, the influence of food treatment ($F_{1,176.2} = 2.07$, $p = 0.15$) and generation ($F_{1,176.2} = 0.09$, $p = 0.77$) were not significant ($p > 0.05$). The interaction between clone, food treatment and generation was significant (Wald $Z = 5.0$, $p < 0.001$) (figure 2).

(b) Relative eye size

The differences in relative eye size between the food treatments varied across-generations (figure 1) as the food treatment $\times$ generation interaction was significant ($F_{1,185.2} = 11.41$, $p = 0.001$). In generation 1, *Daphnia* from the cyanobacteria treatment exhibited a relative eye size that was 3% smaller than *Daphnia* from the *Scenedesmus* treatment (figure 1). The opposite pattern was observed in generation 2. Maternal exposure to cyanobacteria led to a relative eye size

in generation 2 that was 2.5% larger than *Daphnia* continually fed *Scenedesmus* (figures 1 and 2). Effects due to food treatment ($F_{1,180.2} = 0.55$, $p = 0.46$) and generation ($F_{1,179.8} = 0.12$, $p = 0.73$) were not significant. The clone $\times$ food treatment $\times$ generation interaction was significant (Wald $Z = 4.02$, $p < 0.001$) (figure 2).

(c) Regressions between eye size and life-history traits

The relationship between age at maturation and relative eye size was significantly negative in generation 1 ($\beta = -0.128$, $t = -2.7$, $p = 0.007$) but significantly positive in generation 2 ($\beta = 0.181$, $t = 3.39$, $p = 0.001$) (electronic supplementary material, figure S1). We observed a significant positive relationship between reproductive investment (in clutches 1–4) and relative eye size in generation 1 ($\beta = 0.377$, $t = 5.95$, $p < 0.001$) and generation 2 ($\beta = 0.237$, $t = 2.61$, $p = 0.01$) (electronic supplementary material, figure S1).

4. Discussion

Our results revealed divergent shifts in relative eye size within- and across-generations in response to exposure to cyanobacteria (figure 1). *Daphnia* that were fed a diet containing cyanobacteria in generation 1 produced a smaller eye than *Daphnia* fed green algae (figure 1). Given that we fed *Daphnia* a non-toxic strain of cyanobacteria, the production of a smaller eye in generation 1 likely stems from the reduced nutritional content of *Anabaena* versus *Scenedesmus* [67]. We examined whether the smaller eye size produced on the cyanobacteria diet in generation 1 is due to a fitness trade-off with some other trait. Even though we failed to find evidence for a trade-off with development rate or reproductive investment in generation 1 (electronic supplementary material, figure S1), this does not eliminate the possibility of a trade-off between eye size and some other component of fitness. Our results then demonstrated that maternal exposure to cyanobacteria led to a reversal of the differences in relative eye size between treatments in generation 2; *Daphnia* whose mothers were fed cyanobacteria produced larger eyes than *Daphnia* that were continually fed green algae (figure 1).

There are several possible explanations for the increase in relative eye size observed between parent and offspring generations in the cyanobacteria treatment. One possibility is that eye size is highly correlated with body size and constrained by shifts in body size. This is relevant because our previous study showed that body size increased between generation 1 and 2 in the cyanobacteria treatment [67]. Though, the regression between body size and eye size explains just 25% of the variation ($r^2 = 0.249$). This implies that there is ample opportunity for eye size to independently respond to shifts in selection.

Second, the increase in relative eye size may be an adaptive response to maternal exposure to cyanobacteria. That is, the shift in relative eye size between generations is potentially adaptive if a larger eye enhances the ability of *Daphnia* to forage or assess food quality [65]. This is plausible because *Anabaena* and *Scenedesmus* differ in size and morphology and variation in the density of different algal species can alter the light environment. Hathaway & Dudycha [65] proposed that *Daphnia* may use visual cues to identify micro-patches of resources that vary in quantity or quality. Furthermore, the distribution of green algae and cyanobacteria likely varies spatially and is well known to vary

temporally; cyanobacteria are much more prevalent during the summer in Lake Mendota [70]. As a result, seasonal shifts in algal composition will likely persist for multiple generations of *Daphnia* in lakes, which can favour the evolution of TGP [8]. Thus, one interpretation of our results is that maternal exposure to low-quality food leads to the production of a larger eye in offspring to aid in foraging.

Finally, it is also plausible that there is no across-generational carry-over effect of feeding on cyanobacteria. In our experiments, parents were exposed to cyanobacteria but offspring were then fed green algae. Some studies have indeed found weak evidence for transgenerational responses to maternal exposure to cyanobacteria [62]. On the one hand, this latter possibility appears less likely to explain our results because the *Daphnia* developed in the brood chamber while mothers were fed cyanobacteria and the offspring then experienced cyanobacteria for approximately the first 12 h of life. *Daphnia* are very sensitive to environmental conditions during embryonic development [11,71] and during their first juvenile instar stage [72,73]. Though, it is also possible that exposure to cyanobacteria and then green algae resulted in 'nutritional upgrading' and, in turn, the production of a larger eye [74]. In general, the causes and consequences of plasticity in eye size warrant further study.

One surprising aspect of our results is that the eye size of *Daphnia* declined between generation 1 and 2 despite continual exposure to *Scenedesmus* (figure 1). It is unclear if this represents a maternally derived response to *Scenedesmus*. Though, it is important to highlight that there is little evidence that the quality of the green algae declined over time as rates of development were nearly identical in the *Scenedesmus* treatment between generations [67].

Our study contributes to a growing body of work demonstrating plasticity in eye size or a component of the eye. This includes several studies examining the link between resource availability and plasticity in eye size [33,35,37]. The trends revealed by these studies are mixed. Similar to the present study, Brandon & Dudycha [35] showed that low resource availability leads to declines in eye size. But other studies have observed the opposite [33] or no response to declines in resources [37]. The important advance observed in the current study is that we manipulated resource quality (and not just resource availability) and demonstrated a within-generational response and, possibly, an adaptive transgenerational response in relative eye size to poor food quality. In general, our understanding of the ecological and evolutionary significance of eye size is rapidly accumulating (e.g. [17,32,33–41]). This includes the link between eye size and many ecologically relevant behaviours [25–31]. Our study calls for more work aimed at furthering our understanding of the role of sensory systems in transgenerational plasticity.

Data accessibility. All data are located in the following Dryad Digital Repository: <https://doi.org/10.5061/dryad.34tmpg4kc> [69].

Authors' contributions. M.R.W. and M.K.G. conceived the study. M.K.G. collected all data. M.R.W. analysed the data. M.R.W. and M.K.G. wrote the manuscript. The authors approve the final version of the manuscript and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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References

- West-Eberhard MJ. 2003 *Developmental plasticity and evolution*. New York, NY: Oxford University Press.
- Crispo E. 2007 The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. *Evolution* **61**, 2469–2479. (doi:10.1111/j.1558-5646.2007.00203.x)
- Ghalambor CK, McKay JK, Carroll SP, Reznick DN. 2007 Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* **21**, 394–407. (doi:10.1111/j.1365-2435.2007.01283.x)
- Hendry AP. 2016 Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *J. Heredity* **107**, 25–41. (doi:10.1093/jhered/esv060)
- Levis NA, Pfennig DW. 2016 Evaluating 'plasticity-first' evolution in nature: key criteria and empirical approaches. *Trends Ecol. Evol.* **31**, 563–574. (doi:10.1016/j.tree.2016.03.012)
- Galloway LF, Etterson JR. 2007 Transgenerational plasticity is adaptive in the wild. *Science* **318**, 1134–1136. (doi:10.1126/science.1148766)
- Jablonka E, Raz G. 2009 Transgenerational epigenetic inheritance: prevalence, mechanisms, and implications for the study of heredity and evolution. *Q. Rev. Biol.* **84**, 131–176. (doi:10.1086/598822)
- Bonduriansky R, Crean AJ, Day T. 2012 The implications of nongenetic inheritance for evolution in changing environments. *Evol. Appl.* **5**, 192–201. (doi:10.1111/j.1752-4571.2011.00213.x)
- Bashey F. 2006 Cross-generational environmental effects and the evolution of offspring size in the Trinidadian guppy *Poecilia reticulata*. *Evolution* **60**, 348–361. (doi:10.1111/j.0014-3820.2006.tb01111.x)
- Salinas S, Munch SB. 2012 Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. *Ecol. Lett.* **15**, 159–163. (doi:10.1111/j.1461-0248.2011.01721.x)
- Walsh MR, Cooley F, Biles K, Munch SB. 2015 Predator-induced phenotypic plasticity within-and across-generations: a challenge for theory? *Proc. R. Soc. B* **282**, 20142205. (doi:10.1098/rspb.2014.2205)
- Walsh MR, Castoe T, Holmes J, Packer M, Biles K, Walsh M, Munch SB, Post DM. 2016 Local adaptation in transgenerational responses to predators. *Proc. R. Soc. B* **283**, 20152271. (doi:10.1098/rspb.2015.2271)
- Heckwolf MJ, Meyer BS, Döring T, Eizaguirre C, Reusch TB. 2018 Transgenerational plasticity and selection shape the adaptive potential of sticklebacks to salinity change. *Evol. Appl.* **11**, 1873–1885. (doi:10.1111/eva.12688)
- Wadgymar SM, Mactavish RM, Anderson JT. 2018 Transgenerational and within-generation plasticity in response to climate change: insights from a manipulative field experiment across an elevational gradient. *Am. Nat.* **192**, 698–714. (doi:10.1086/700097)
- Donelan SC, Hellmann JK, Bell AM, Luttbegg B, Orrock JL, Sheriff MJ, Sih A. 2020 Transgenerational plasticity in human-altered environments. *Trends Ecol. Evol.* **35**, 115–124. (doi:10.1016/j.tree.2019.09.003)
- Tariel J, Plénet S, Luquet É. 2020 Transgenerational plasticity in the context of predator–prey interactions. *Front. Ecol. Evol.* **8**, 548660. (doi:10.3389/fevo.2020.548660)
- Beston SM, Dudycha JL, Post DM, Walsh MR. 2019 The evolution of eye size in response to increased fish predation in *Daphnia*. *Evolution* **73**, 792–802. (doi:10.1111/evo.13717)
- Fernald RD. 2004 Eyes: variety, development and evolution. *Brain Behav. Evol.* **64**, 141–147. (doi:10.1159/000079743)
- Land MF, Nilsson DE. 2012 *Animal eyes*. Oxford, UK: Oxford University Press.
- Rittland SM. 1982 The allometry of the vertebrate eye. PhD thesis, University of Chicago, Chicago, IL.
- Motani R, Rothschild BM, Wahl W. 1999 Large eyeballs in diving ichthyosaurs. *Nature* **402**, 747–747. (doi:10.1038/45435)
- Møller AP, Erritzøe J. 2010 Flight distance and eye size in birds. *Ethology* **116**, 458–465. (doi:10.1111/j.1439-0310.2010.01754.x)
- Caves EM, Sutton TT, Johnsen S. 2017 Visual acuity in ray-finned fishes correlates with eye size and habitat. *J. Exp. Biol.* **220**, 1586–1596. (doi:10.1242/jeb.151183)
- Caves EM, Brandley NC, Johnsen S. 2018 Visual acuity and the evolution of signals. *Trends Ecol. Evol.* **33**, 358–372. (doi:10.1016/j.tree.2018.03.001)
- Garamszegi LZ, Møller AP, Erritzøe J. 2002 Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proc. R. Soc. Lond. B* **269**, 961–967. (doi:10.1098/rspb.2002.1967)
- Jander U, Jander R. 2002 Allometry and resolution of bee eyes (Apoidea). *Arthropod. Struct. Dev.* **30**, 179–193. (doi:10.1016/S1467-8039(01)00035-4)
- Hall MI, Ross CF. 2007 Eye shape and activity pattern in birds. *J. Zool.* **271**, 437–444. (doi:10.1111/j.1469-7998.2006.00227.x)
- Somanathan H, Kelber A, Borges RM, Wallén R, Warrant EJ. 2009 Visual ecology of Indian carpenter bees II: adaptations of eyes and ocelli to nocturnal and diurnal lifestyles. *J. Comp. Physiol. A* **195**, 571–583. (doi:10.1007/s00359-009-0432-9)
- Brischoux F, Pizzato L, Shine R. 2010 Insights into the adaptive significance of vertical pupil shape in snakes. *J. Evol. Biol.* **23**, 1878–1885. (doi:10.1111/j.1420-9101.2010.02046.x)
- Liu Y, Ding L, Lei J, Zhao E, Tang Y. 2012 Eye size variation reflects habitat and daily activity patterns in colubrid snakes. *J. Morphol.* **273**, 883–893. (doi:10.1002/jmor.20028)
- McCoy VE, Lamsdell JC, Poschmann M, Anderson RP, Briggs DE. 2015 All the better to see you with: eyes and claws reveal the evolution of divergent ecological roles in giant pterygotid eurypterids. *Biol. Lett.* **11**, 20150564. (doi:10.1098/rsbl.2015.0564)
- Ausprey IJ, Newell FL, Robinson SK. 2021 Adaptations to light predict the foraging niche and disassembly of avian communities in tropical countrysides. *Ecology* **102**, e03213. (doi:10.1002/ecy.3213)
- Merry JW, Kemp DJ, Rutowski RL. 2011 Variation in compound eye structure: effects of diet and family. *Evolution* **65**, 2098–2110. (doi:10.1111/j.1558-5646.2011.01285.x)
- Lönnstedt OM, McCormick MI, Chivers DP. 2013 Predator-induced changes in the growth of eyes and false eyespots. *Sci. Rep.* **3**, 1–5. (doi:10.1038/srep02259)
- Brandon CS, Dudycha JL. 2014 Ecological constraints on sensory systems: compound eye size in *Daphnia* is reduced by resource limitation. *J. Comp. Physiol. A* **200**, 749–758. (doi:10.1007/s00359-014-0918-y)
- Brandon CS, James T, Dudycha JL. 2015 Selection on incremental variation of eye size in a wild population of *Daphnia*. *J. Evol. Biol.* **28**, 2112–2118. (doi:10.1111/jeb.12711)
- Svanbäck R, Johansson F. 2019 Predation selects for smaller eye size in a vertebrate: effects of environmental conditions and sex. *Proc. R. Soc. B* **286**, 20182625. (doi:10.1098/rspb.2018.2625)
- Vinterstare J, Hulthén K, Nilsson DE, Nilsson PA, Brönmark C. 2020 More than meets the eye: predator-induced pupil size plasticity in a teleost fish. *J. Anim. Ecol.* **89**, 2258–2267. (doi:10.1111/1365-2656.13303)
- Beston SM, West E, Walsh MR. 2017 The evolution of vertebrate eye size across an environmental gradient: phenotype does not predict genotype in a Trinidadian killifish. *Evolution* **71**, 2037–2049. (doi:10.1111/evo.13283)
- Beston SM, Walsh MR. 2019 Natural selection favours a larger eye in response to increased competition in natural populations of a vertebrate. *Funct. Ecol.* **33**, 1321–1331. (doi:10.1111/1365-2435.13334)
- Glazier DS, Deptola TJ. 2011 The amphipod *Gammarus minus* has larger eyes in freshwater springs with numerous fish predators. *Invert. Biol.* **130**, 60–67. (doi:10.1111/j.1744-7410.2010.00220.x)
- Carpenter SR, Cottingham KL, Schindler DE. 1992 Biotic feedbacks in lake phosphorus cycles. *Trends Ecol. Evol.* **7**, 332–336. (doi:10.1016/0169-5347(92)90125-U)
- Vijverberg J. 1989 Culture techniques for studies on the growth, development, and reproduction of copepods and cladocerans under laboratory and *in situ* conditions. *Freshw. Biol.* **21**, 317–373. (doi:10.1111/j.1365-2427.1989.tb01369.x)
- Gilbert JJ. 1990 Differential effects of *Anabaena affinis* on cladocerans and rotifers: mechanisms and

- implications. *Ecology* **71**, 1727–1740. (doi:10.2307/1937581)
45. DeMott WR. 1989 The role of competition in zooplankton succession. In *Plankton ecology: succession in plankton communities* (ed. U Sommer), pp. 195–252. Berlin, Germany: Springer.
 46. Von Elert E, Wolffrom T. 2001 Supplementation of cyanobacterial food with polyunsaturated fatty acids does not improve growth of *Daphnia*. *Limnol. Oceanogr.* **46**, 1552–1558. (doi:10.4319/lo.2001.46.6.1552)
 47. Von Elert E, Martin-Creuzburg D, Le Coz JR. 2002 Absence of sterols constrains carbon transfer between cyano-bacteria and a freshwater herbivore (*Daphnia galeata*). *Proc. R. Soc. Lond. B* **270**, 1209–1214. (doi:10.1098/rspb.2003.2357)
 48. DeMott WR, Zhang QX, Carmichael WW. 1991 Effects of toxic cyanobacteria and purified toxins on the survival and feeding of a copepod and 3 species of *Daphnia*. *Limnol. Oceanogr.* **36**, 1346–1357. (doi:10.4319/lo.1991.36.7.1346)
 49. Rohrlack TK, Henning M, Kohl JG. 1999 Mechanisms of the inhibitory effect of the cyanobacterium *Microcystis aeruginosa* on *Daphnia galeata*'s ingestion rate. *J. Plankton Res.* **21**, 1489–1500. (doi:10.1093/plankt/21.8.1489)
 50. Hairston NG Jr, Lampert W, Caceres CE, Holtmeier CL, Weider LJ, Gaedke U, Fischer JM, Fox JA, Post DM. 1999 Rapid evolution revealed by dormant eggs. *Nature* **401**, 446. (doi:10.1038/46731)
 51. Lurling L. 2003 *Daphnia* growth on microcystin-producing and microcystin-free *Microcystis aeruginosa* in different mixtures with the green alga *Scenedesmus obliquus*. *Limnol. Oceanogr.* **48**, 2214–2220. (doi:10.4319/lo.2003.48.6.2214)
 52. Sarnelle O, Gustafsson S, Hansson L. 2010 Effects of cyanobacteria on fitness components of the herbivore *Daphnia*. *J. Plankton Res.* **32**, 471–477. (doi:10.1093/plankt/fbp151)
 53. Faassen EJ, García-Altares M, Mendes e Mello M, Lüring M. 2015 Trans generational effects of the neurotoxin BMAA on the aquatic grazer *Daphnia magna*. *Aquat. Toxic.* **168**, 98–107. (doi:10.1016/j.aquatox.2015.09.018)
 54. Zhu X, Wang Q, Zhang L, Liu J, Zhu C, Yang Z. 2015 Offspring performance of *Daphnia magna* after short-term maternal exposure to mixtures of microcystin and ammonia. *Environ. Sci. Pollut. R* **22**, 2800–2807. (doi:10.1007/s11356-014-3520-5)
 55. Dao TS, Wiegand C, Bui BT, Dinh KV. 2018 Transgenerational effects of cyanobacterial toxins on a tropical micro-crustacean *Daphnia lumholtzi* across three generations. *Environ. Pollut.* **243**, 791–799. (doi:10.1016/j.envpol.2018.09.055)
 56. Ortiz-Rodríguez R, Dao TS, Wiegand C. 2012 Transgenerational effects of microcystin-LR on *Daphnia magna*. *J. Exp. Biol.* **215**, 2795–2805. (doi:10.1242/jeb.069211)
 57. Gustafsson S, Rengefors K, Hansson L. 2005 Increased consumer fitness following transfer of toxin tolerance to offspring via maternal effects. *Ecology* **86**, 2561–2567. (doi:10.1890/04-1710)
 58. Jiang X, Yang W, Zhao S, Liang H, Zhao Y, Chen L, Li R. 2013 Maternal effects of inducible tolerance against the toxic cyanobacterium *Microcystis aeruginosa* in the grazer *Daphnia carinata*. *Environ. Pollut.* **178**, 142–146. (doi:10.1016/j.envpol.2013.03.017)
 59. Schwarzenberger A, Von Elert E. 2013 Cyanobacteria protease inhibitors lead to maternal transfer of increased protease gene expression in *Daphnia*. *Oecologia* **172**, 11–20. (doi:10.1007/s00442-012-2479-5)
 60. Lyu K, Guan H, Wu C, Wang X, Wilson AE, Yang Z. 2016 Maternal consumption of non-toxic *Microcystis* by *Daphnia magna* induces tolerance to toxic *Microcystis* in offspring. *Freshw. Biol.* **61**, 219–228. (doi:10.1111/fwb.12695)
 61. Peng S, Deng D, He P, Xu X, Zhang C, Cao J, Liu Q, Zhang T. 2018 Effects of *Microcystis aeruginosa* on the life history traits and SOD activity of *Daphnia similoides sinensis*. *Environ. Sci. Pollut. R* **25**, 30 696–30 707. (doi:10.1007/s11356-018-3040-9)
 62. Radersma R, Hegg A, Noble DW, Uller T. 2018 Timing of maternal exposure to toxic cyanobacteria and offspring fitness in *Daphnia magna*: implications for the evolution of anticipatory maternal effects. *Ecol. Evol.* **8**, 12 727–12 736. (doi:10.1002/ece3.4700)
 63. Ringelberg J. 1987 Light induced behavior in *Daphnia*. *Memorie dell'Istituto Italiano di Idrobiologia* **45**, 285–323.
 64. Frost BJ. 1975 Eye movements in *Daphnia pulex*. *J. Exp. Biol.* **62**, 175–187. (doi:10.1242/jeb.62.1.175)
 65. Hathaway CR, Dudyca JL. 2018 Quantitative measurement of the optomotor response in free-swimming *Daphnia*. *J. Plankton Res.* **40**, 222–229. (doi:10.1093/plankt/fby014)
 66. Casares F, McGregor AP. 2020 The evolution and development of eye size in flies. *Wiley Interdiscip. Rev. Dev. Biol.* **10**, e380.
 67. Gillis MK, Walsh MR. 2019 Individual variation in plasticity dulls transgenerational responses to stress. *Funct. Ecol.* **33**, 1993–2002. (doi:10.1111/1365-2435.13409)
 68. Kilham SS, Kreeger DA, Lynn SG, Goulden CE, Herrera L. 1998 COMBO: a defined freshwater culture medium for algae and zooplankton. *Hydrobiologia* **377**, 147–159. (doi:10.1023/A:1003231628456)
 69. Walsh MR, Gillis MK. 2021 Data from: Transgenerational plasticity in eye size in *Daphnia*. Dryad Digital Repository. (doi:10.5061/dryad.34tmpg4kc)
 70. Carpenter SR. 1989 Temporal variance in lake communities: blue-green algae and the trophic cascade. *Landsc. Ecol.* **3**, 175–184. (doi:10.1007/BF00131536)
 71. Laforsch C, Tollrian R. 2004 Embryological aspects of inducible morphological defenses in *Daphnia*. *J. Morphol.* **262**, 701–707. (doi:10.1002/jmor.10270)
 72. Weiss LC, Leimann J, Tollrian R. 2015 Predator-induced defenses in *Daphnia longicephala*: location of kairomone receptors and timeline of sensitive phases to trait formation. *J. Exp. Biol.* **218**, 2918–2926. (doi:10.1242/jeb.124552)
 73. Imai M, Naraki Y, Tochinali S, Miura T. 2009 Elaborate regulations of the predator-induced polyphenism in the water flea *Daphnia pulex*: kairomone-sensitive periods and life-history tradeoffs. *J. Exp. Zool. A* **311**, 788–795. (doi:10.1002/jez.565)
 74. Freese HM, Martin-Creuzburg D. 2013 Food quality of mixed bacteria–algae diets for *Daphnia magna*. *Hydrobiologia* **715**, 63–76. (doi:10.1007/s10750-012-1375-7)