JOURNAL OF Evolutionary Biology

doi: 10.1111/jeb.12711

SHORT COMMUNICATION

Selection on incremental variation of eye size in a wild population of *Daphnia*

C. S. BRANDON, T. JAMES & J. L. DUDYCHA

Department of Biological Sciences, University of South Carolina, Columbia, SC, USA

Keywords:

Daphnia obtusa;
eyes;
heritability;
ponds;
selection gradient;
vision.

Abstract

Several studies of eye morphology have analysed macroevolutionary patterns in the diversity of eyes, and although these studies are often linked to environment or behaviour, they provide only indirect evidence of selection. Specific data to show the microevolutionary potential for adaptation by natural selection in eye morphology have been lacking. We document directional selection on eye size, an important determinant of visual capabilities, in a wild population of the freshwater microcrustacean *Daphnia*. We show that even slight changes in eye size may have major consequences for fitness. An increase in eye diameter of 19.9 μm – slightly more than one standard deviation – is associated with an increase in clutch size of one egg, or an increase of nearly 20% of the mean clutch size. Furthermore, relative eye size is genetically variable and thus could evolve in response to the observed selective pressure. We conclude that selection on incremental variation in eye size may have led to differences observed on broader taxonomic scales.

Introduction

Eyes are complex structures that historically have been used to call into question the entire theory of evolution, by arguing that the incremental process of adaptation by natural selection could not produce such structures. Nilsson & Pelger (1994) provided a theoretical counterpoint to this argument by showing that highly conservative models of natural selection could produce complex eyes from simple pigmented eye spots in only a few hundred thousand generations. Furthermore, the structural varieties of eyes that lie along this simple to complex continuum are all still functional in terms of obtaining light information and in fact are represented by numerous forms that exist in nature (Salvini-Plawen & Mayr, 1977). Even so, evolutionary biologists have lacked empirical data to demonstrate directly the microevolutionary potential for adaptation in eye morphology.

Eyes provide environmental information that informs critical behaviours ranging from finding food and mates to avoiding threats and predators. Their importance among animals is underscored by their near ubiquity in any environment where light is present. Morphological and physiological components of eyes define the bounds of an animal's visual capabilities (Land & Nilsson, 2012) and thus reveal a great deal about what aspects of the visual environment are important to an animal. An astonishing array of visual system diversity has been catalogued on broad taxonomic scales (Salvini-Plawen & Mayr, 1977). This variation is often argued to be driven by differences in selection by environmental differences (Garamszegi *et al.*, 2002; Ross & Kirk, 2007; Hall, 2008; Somanathan *et al.*, 2009; Veilleux & Lewis, 2011), or by differences in visually mediated behaviours (Nilsson, 2009; Møller & Erritzøe, 2010). This research has focused on patterns at macroevolutionary scales and thus is limited to indirect inferences about the selective value of small changes in visual structures.

To address this gap, we sought to examine the reproductive consequences of eye size variation in the freshwater crustacean *Daphnia obtusa* Kurz. Eye size is a

Correspondence: Jeffry L. Dudycha, Department of Biological Sciences, University of South Carolina, 715 Sumter St, Columbia, SC 29208, USA.
Tel.: +1 803 777 3987; fax: +1 803 777 4002; e-mail: dudycha@biol.sc.edu

general indicator of visual capability (Land, 1997; Land & Nilsson, 2012). Larger eyes typically enhance resolution and/or visual sensitivity, two key aspects of vision (Land & Nilsson, 2012). Indeed, many studies have demonstrated that macroevolutionary-scale variation in eye size often covaries with the light environment and/or behaviour (Hiller-Adams & Case, 1988; Bauer *et al.*, 1998; Garamszegi *et al.*, 2002; Thomas *et al.*, 2002, 2006; Lisney & Collin, 2007; Somanathan *et al.*, 2009; Møller & Erritzøe, 2010; Schmitz & Wainwright, 2011; Veilleux & Lewis, 2011).

The optimal size of an eye for a given organism depends on its environment. In *Daphnia,* eyes likely benefit the animal by providing critical information for navigation (Schwind, 1999), orientation (Baylor & Smith, 1953; Ringelberg *et al.*, 1974; Novales Flamarique & Browman, 2000) and resource location (Smith & Baylor, 1953; Young *et al.*, 1984; Hamza & Ruggiu, 2000). However, eyes come at a cost as well. Eyes are expensive in terms of building materials used during development, and they also demand a sizeable slice of an animal's energy budget (Niven & Laughlin, 2008). For example, Laughlin *et al.* (1998) showed that the retina of the blowfly *Calliphora vicina* accounted for 10% of its resting metabolic rate. In *Daphnia*, prolonged resource limitation leads to the development of disproportionately smaller eyes relative to body size (Brandon & Dudycha, 2014). Evidence from studies on related and morphologically similar zooplankton to *Daphnia* suggests that the darkly pigmented eye in an otherwise transparent body can act as a visual target for zooplanktivorous fish (Zaret & Kerfoot, 1975; Branstrator & Holl, 2000). Additionally, compound eyes in *Daphnia* have been shown to display phenotypic plastic responses to fish kairomones, where eyes are relatively smaller in fish-scent environments (Boersma *et al.*, 1998). Selection can therefore potentially act from multiple angles on eye size in *Daphnia.*

In this report, we present an observational study in which we measure a reproductive selection gradient on eye size from a wild population of *D. obtusa*. We estimate reproductive fitness by measuring the number of eggs present in the brood chamber (Vanni & Lampert, 1992). Eye size is positively correlated with body size in *Daphnia* (Brandon & Dudycha, 2014); we therefore analysed both eye size and body size and considered their correlated effects in our analyses of selection (Lande & Arnold, 1983). We also considered the potential of eye size to evolve in response to selection by measuring genetic variation of relative eye size in a laboratory-based common garden experiment.

Study site and methods

We measured selection on a wild population of *D. obtusa* in an ephemeral pond, Knobby Knees (KNB; 33°47′42″N, 80°45′18″), in Congaree National Park, an old-growth floodplain forest in South Carolina, USA. KNB is 20 metres from an intermittent creek with steep banks. Depth varies depending on rainfall and season, but has been measured as deep as 70 cm. Like most ponds in the *D. obtusa* metapopulation at Congaree, KNB is heavily shaded under forest canopy cover. Although *Gambusia* are present in the floodplain, we did not observe small fish that potentially prey on *Daphnia* in this pond at the time of sampling. We morphologically identified *Daphnia* in KNB using the key in Hebert (1995), having previously verified that ponds at Congaree contain *D. obtusa* but no morphologically similar congeners via allozyme electrophoresis.

Selection on eye size

We sampled *D. obtusa* from KNB on 31 May 2013, a time when sexual reproduction and males were rare. Sampling was performed according to procedures described in Dudycha (2004), generating a pooled sample drawn from throughout the pond. The sample was transported in a cooler with ice to the laboratory. We kept the sample of *Daphnia* at 4 °C to arrest embryonic development and the moult cycle until ready for processing. We counted clutch size and measured morphology on a total of 229 individuals.

We counted eggs from living *Daphnia* within 36 h of capture using a dissecting microscope. After counting, we preserved individuals in 100% ethanol and placed them into numbered wells on a 96-well plate for later imaging. The few females with resting eggs were excluded because an appropriate clutch size could not be determined. In addition, individuals carrying no eggs were excluded as this likely reflects a transition between reproductive modes. Exclusions accounted for < 2% of the population and thus have little effect on our analysis.

The compound eye of *Daphnia* is a composite of individual light-collecting units called ommatidia. The facet lens diameter within an individual ommatidium significantly influences an animal's visual capabilities (reviewed in Land, 1997). We have previously demonstrated that facet diameter and eye diameter have a strong positive correlation in *Daphnia* (Brandon & Dudycha, 2014). Beyond visual capabilities, total eye size potentially impacts *Daphnia* in terms of energy and predatory visibility (see Introduction); thus, we focused our study on total eye size. We used a Nikon 1500 SMZ dissecting scope to take lateral photographs of *Daphnia*, as illustrated in Brandon & Dudycha (2014). Photographs for body length were taken at 30×. Eyes were photographed at 112.5× magnification. We calibrated the dissecting scope with a stage micrometre to obtain pixel to length ratios, which we then used to obtain length measurements from the photographs. We measured *Daphnia* photographs using ImageJ freeware (Schneider *et al.*, 2012). We made body length measurements from the top of the head just above the eye to the base of the tail spine. Although *Daphnia* eyes are approximately spherical, most individuals deviate somewhat. We therefore measured eye diameter at the widest diameter.

We estimated selection on eye diameter and body length, following Lande & Arnold (1983) to account for correlations between the traits. To approximate a normal distribution, we transformed each trait to natural logarithms. We also standardized the fitness component by dividing an individual's clutch size by the mean clutch size, and then transformed relative fitness by the natural logarithm. We analysed the correlation between the transformed values of eye diameter and body length using Pearson's product–moment correlation test with the *Hmisc* package in R v3.0.2 (Harrell, 2015). We estimated the total effects of indirect and direct selection on both eye diameter and body length by calculating the selection differential as the covariance between relative fitness and each respective phenotype. We estimated the total effects of indirect and direct selection on both eye diameter and body length by calculating the selection differential (s) as the covariance between relative fitness and each respective phenotype. We also employed bootstrap replication with 1000 replications for estimations of s and used jackknife-after-bootstrap to generate estimates of standard error (Efron, 1992). We performed bootstrap statistics using the BOOTSTRAP package in R (Tibshirani & Leisch, 2015). We standardized the selection differential to phenotypic standard deviation units. To measure the direct effect of selection on a set of correlated multivariate traits, we calculated the selection gradient as the partial regression coefficient from a multiple least-squares regression analysis following Lande & Arnold (1983). We also calculated the standardized selection gradient as the partial regression coefficients from a multiple regression on standardized phenotypic trait values (Lande & Arnold, 1983). The significance of each partial regression coefficient was determined through a partial F-test. All statistical analyses were performed using R v3.0.2 (R Team, 2013).

Genetic variation of eye size

We obtained samples from the Congaree metapopulation of *D. obtusa* for a common garden analysis of genetic variation in eye size from a total of nine ponds in the floodplain. These ponds are linked by periodic flooding (Conrads *et al.*, 2008), which is the likely cause of relatively low levels of microsatellite differentiation among ponds (Sebastian & Dudycha, unpubl. data). Most ponds are similar in general characteristics, although one (POW) has a substantially more open canopy.

We initiated clonal lineages by placing single individuals collected from the field into individual beakers of filtered (1 μm) hypolimnetic lake water and allowed them to reproduce asexually. We maintained cultures in the laboratory at low density at 10 °C in environmental chambers on a 12-h:12-h light: dark photoperiod. We fed cultures a weekly diet of a vitamin-enriched green alga, *Ankistrodesmus falcatus* (Corda) Ralfs. To measure traits, we first separated animals from the laboratory stocks into new beakers kept at 20 °C and fed 20 000 cells mL^{-1} *A. falcatus* daily and allowed at least three generations to pass before measuring animals. Each generation was started when the previous generation was three weeks old, i.e. at or beyond their third clutch. We measured individuals from three size classes for each clone: small ($\leq$ 900 μm), medium (901–1399 μm) and adult ($\geq$ 1400 μm). These size classes reflect ontogenetic growth from juveniles to adults and were used to define a measure of eye size relative to body size for each clone. We measured 27–30 individuals (10 per size class) from each of 41 clonal lineages that had been isolated from the field during several trips in May of 2010, 2011 and 2013. For imaging, we haphazardly removed animals from culture media and killed them in a solution of 0.25 M KCl.

We estimated broad-sense heritability (H^2) as the ratio of genetic variance (V_G; the variance of mean relative eye size among clones) to phenotypic variance (V_P; the variance of relative eye size across all individuals) or $H^2 = \sigma_G/(\sigma_G + \sigma_E)$. To generate mean values of eye size relative to body size, we used residuals generated by an ordinary least-squares regression of eye diameter against body length for all individuals in all ontogenetic size classes (n = 1218) using the linear model function in R v3.0.2. Prior to the regression analysis, we transformed both eye diameter and body length by the natural logarithm to better approximate a normal distribution, but also to remain consistent with our measurements of selection. We used the residual values from the global regression analysis to then calculate the mean residual value for each clonal lineage and estimate H^2. Residual means were calculated using the PYSCH package in R v3.0.2. (Revelle, 2014). We tested the hypothesis that $H^2 \neq 0$ using a one-way ANOVA (Lynch & Walsh, 1998). We estimated H^2 and employed a bootstrap approach to estimate standard error of the H^2 ratio using the H2BOOT software package (Phillips, 2002), which uses ANOVA-based variance estimates. We performed 1000 bootstrap replicates for each trait heritability estimate.

Results and discussion

Body length, eye diameter and clutch size in adult female *D. obtusa* from Knobby Knees pond varied widely. Clutch sizes ranged from 2 to 13 and averaged 5.8 ± 0.14 SE eggs per clutch. Body length of adults ranged from 1080 to 1819 μm (mean = 1328.56 ± 8.22 SE). Absolute eye diameter had a mean of

138.79 ± 1.19 SE µm, ranging from 99 to 188 µm. This is at least a four-fold difference in light-collecting capacity. The sensitivity of the eye is defined as

$$S = 0.62D^2\Delta\rho^2 P_{abs}$$

where D is the diameter of the facet lens, $\Delta\rho$ is the sampling angle (which defines resolving ability), and P_{abs} is the proportion of photons absorbed (Land & Nilsson, 2012). An increase in D, with all the remaining components kept equal, will result in an increase in sensitivity that is proportional to the square. *Daphnia* facet lens diameter is positively and linearly correlated with changes in eye diameter (Brandon & Dudycha, 2014), such that a doubling in total eye diameter approximately equates to the same relative change in D.

Body size is known to be a significant driver of clutch size in *Daphnia* (Gliwicz & Boavida, 1996), and regression analysis on untransformed values confirms that clutch size increases with body length in *D. obtusa* ($\beta = 0.0069 \pm 0.001$ SE, $F_{(1,227)} = 48.2$, $P = 4.93 \times 10^{-11}$, adj. $R^2 = 0.175$), although it accounts for only 17% of the variation in clutch size. Unsurprisingly, eye diameter and body length have a strong positive correlation in *D. obtusa* (Pearson's $r = 0.588$, $t = 10.98$, d.f. = 227, $P < 2.2 \times 10^{-16}$); however, regression analysis reveals that nearly two-thirds of the variation ($\beta = 0.8383 \pm 0.0763$ SE, $F_{(1,227)} = 120.5$, $P < 2.0 \times 10^{-16}$, adj. $R^2 = 0.343$) in eye size is independent of body size. This is consistent with our previous work on phenotypic plasticity of eye size (Brandon & Dudycha, 2014) and allows for eye size to influence the fitness component independently of body size.

We observed that reproductive selection is acting on both body size and eye diameter independently of body size and that the strength of selection is stronger on eye diameter (Table 1, Fig. 1). Estimation of the selection differential, which accounts for all direct and indirect effects of selection, reveals that the standardized selection differential is ~20% higher on eye diameter ($s' = 0.183 \pm 0.011$) than body length ($s' = 0.15 \pm 0.013$). We also measured the direct effects of selection on each trait by measuring the selection gradient, and our analysis indicated that the direct effects of selection were stronger on eye diameter ($\beta' = 0.145 \pm 0.0247$, $F_{(1,226)} = 34.475$ $P = 1.53 \times 10^{-2}$) than body length ($\beta' = 0.066 \pm 0.0248$, $F_{(1,226)} = 7.18$, $P = 0.007913$). An increase in eye diameter of 19.9 µm – slightly more than one standard deviation – is associated with an increase in clutch size of one egg, or an increase of nearly 20% of the mean clutch size (Fig. 1).

We observed wide genetic variation of relative eye size in the metapopulation of *D. obtusa* at Congaree National Park ($H^2 = 0.19 \pm 0.04$ SE, $F_{(40,1177)} = 8.466$ $P < 2.2 \times 10^{-16}$). We also observed a wide range of mean values across clones (Fig. 2). Broad-sense heritability measures are important in *Daphnia* because they undergo several generations of asexual reproduction in each population cycle, during which clonal selection can substantially alter the genetic composition of the population (Pfrender & Lynch, 2000; Haag & Ebert, 2007; Vanoverbeke & De Meester, 2010). Additionally, clones that are more successful asexually, and hence more frequent when the population switches to sexual reproduction, can contribute more sexual offspring. Our measure of broad-sense heritability may be biased downward because maternal effects were not specifically controlled for in the experimental design (Lynch & Walsh, 1998). Instead, because multiple mothers

Table 1 Standardized selection differentials (s') and standardized selection gradients (β') for the correlated phenotypic traits, body length and eye diameter. Relative fitness and both variance-standardized phenotypic traits have been transformed to natural logarithms.

Trait	$s' \pm$ SE	$\beta' \pm$ SE (P value)
Body length	0.151 ± 0.013	0.066 ± 0.024 (P = 0.0079)
Eye diameter	0.183 ± 0.011	0.145 ± 0.024 (P < 0.0001)

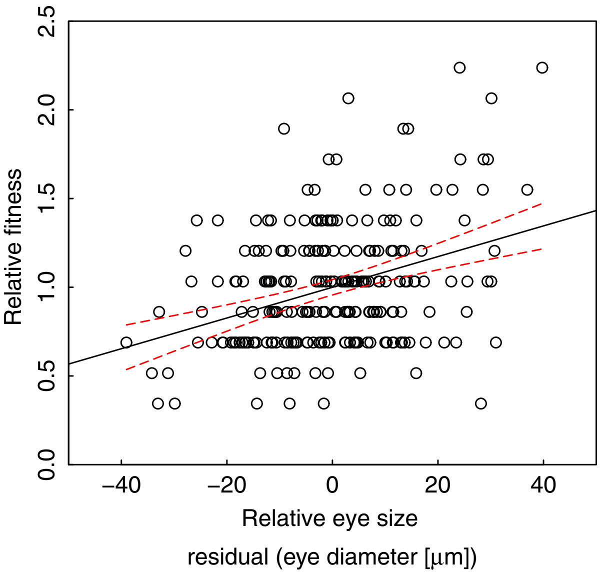

Fig. 1 Relative fitness (individual clutch size/mean clutch size) as a function of relative eye size in the Knobby Knees pond population of *Daphnia obtusa* ($n = 229$, $\beta = 0.0087 \pm 0.0015$ SE, adj. $R^2 = 0.119$, $P = 5.4 \times 10^{-8}$). For simpler presentation, we illustrate how the univariate trait, relative eye size, relates to relative fitness as opposed to illustrating the multivariate space. Solid line shows the least-squares regression, and red dashed lines show 95% confidence interval. Clutch size was counted as number of eggs in the brood chamber of *D. obtusa*. Relative eye size is defined as the vertical residual value from a regression of *D. obtusa* eye diameter on body length for each individual.

were used for each clone, variation due to maternal effects is incorporated in the error variance (hence inflating our estimate of V_E). However, we raised *Daphnia* in controlled experimental conditions for several generations before measurements, thus limiting maternal effects' variation.

We found clear evidence that small changes in eye morphology are under selection in a wild population of *D. obtusa*, observing a strong positive correlation between eye size and reproduction. The size of an eye is an important determinant of its optical capability, such that increases in eye size can lead to enhancements in an eye's ability to resolve images, and/or capture more photons (Land, 1997; Land & Nilsson, 2012). Across broad taxonomic scales, there are many general examples where animals that perform tasks for which excellent visual capabilities are needed have larger eyes relative to species which do not perform such tasks (Garamszegi *et al.*, 2002; Møller & Erritzøe, 2010). A similar pattern exists in animals that inhabit dim light environments, which have larger eyes relative to those that inhabit bright environments (Bauer *et al.*, 1998; Thomas *et al.*, 2006; Hall, 2008; Somanathan *et al.*, 2009; Schmitz & Wainwright, 2011; Veilleux & Lewis, 2011). Eye size differences have also been documented between populations that may have different visual needs (Protas *et al.*, 2008; Glazier & Deptola, 2011), although these examples are far fewer than the differences documented across species. Although eye size is not the only component that determines an animal's visual capabilities (Land & Nilsson, 2012), it is certainly an important trait which figures prominently into our understanding of how larger environmental differences and behavioural tasks affect variation of visual structures at macroevolutionary scales.

We use clutch size as an indicator of reproductive fitness in this study. Although reproduction provides an incomplete picture of fitness, clutch size drives short-term birth rates in *Daphnia* and hence is a significant determinant of *r*, the intrinsic rate of population growth (Dudycha, 2001). For any iteroparous organism, the residual reproductive value is more strongly influenced by near-term reproduction than reproduction farther in the future (Stearns, 1992). Because *Daphnia* mature rapidly relative to their interclutch interval, only the first few clutches make substantial contributions to *r* (Dudycha & Tessier, 1999) and the current reproductive investment is the most critical component of overall fitness in our population. At Congaree, *D. obtusa* inhabit shallow forest ponds that vary haphazardly with respect to their population demography and the time in which they are filled with water. *D. obtusa* populations generally persist through clonal reproduction for weeks to months (~3–7 generations at field temperatures) before shifting into sexual, dormancy-based reproductive modes.

We demonstrate that selection on eye size in our population has strong potential for evolutionary consequences, because there is substantial genetic variation of relative eye size within the metapopulation. When we returned to Knobby Knees in 2014, we were unable to determine whether there had been a response to selection, or whether the pattern of selection continued. This was because mosquitofish, *Gambusia* sp., had

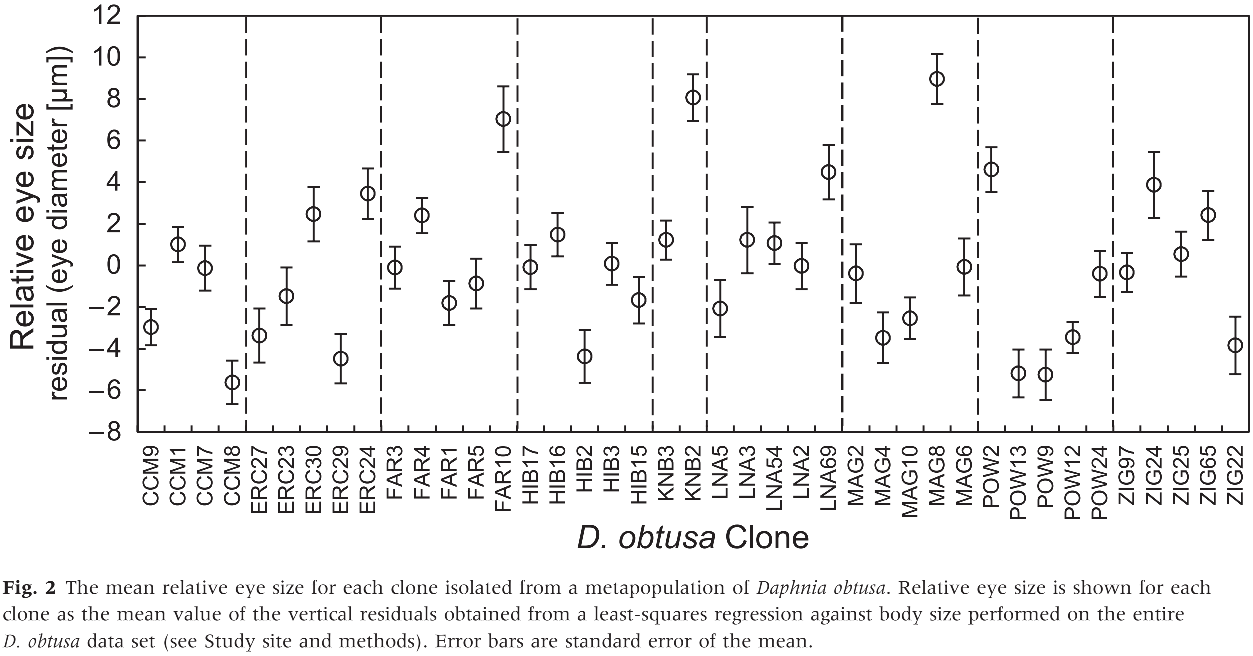

Fig. 2 The mean relative eye size for each clone isolated from a metapopulation of *Daphnia obtusa*. Relative eye size is shown for each clone as the mean value of the vertical residuals obtained from a least-squares regression against body size performed on the entire *D. obtusa* data set (see Study site and methods). Error bars are standard error of the mean.

invaded the pond (presumably during a flood event), and the population of *D. obtusa* had been replaced by *D. ambigua* Scourfield, a species with smaller bodies and smaller eyes.

Our results clearly demonstrate that variation in eye size is associated with variation in a fitness component; hence, selection is operating, directly or indirectly, on eye size variation. Indeed, our measurement of the selection gradient of eye size is consistent with measurements typical of morphological traits (Kingsolver & Diamond, 2011). However, we caution that although our study demonstrates selection on eye size that is independent of body size, it does not demonstrate that selection acts directly on eye size. We have no data to identify a mechanism by which larger relative eye size causes improved fitness. Yet, this point could be raised for a large number of selection studies that imply causality for measured traits simply because it seems likely. Nevertheless, a difference in eye size necessarily causes a difference in visual capability, but precisely how these differences may affect ecological function and ultimately affect fitness is unclear. One possibility is that improved vision conferred by larger eyes may allow for better predator avoidance or escape, particularly in dim environments. This is more likely to play a role in survival-related fitness components than reproductive fitness components, but it may also influence resource acquisition through altered foraging behaviour. A second possibility is that improved vision directly improves foraging, by allowing better identification of optimal micropatches where resources are either denser or higher quality. Such improved foraging would be expected to lead to increased resources available to allocate to reproduction and hence higher current clutch sizes.

In general, eyes seem well-tuned to their specific animal's environment and behavioural needs. Given that the structure and physiology of eyes allow researchers to measure how and what an animal can see, inferences can be made about what use an eye may provide to an animal in a given ecological context. What is much less known is the amount of variation that exists in visual structures on a population level and how that variation may influence ecological performance and thus fitness. Our study demonstrates that selection can act on eye size independently of body size and that there can be significant reproductive consequences associated with incremental variation of eye size. Future studies that demonstrate the causal link between variation in visual structures and ecological performance may yield great insight into microevolutionary patterns of eye evolution.

Acknowledgments

We would like to thank Sally Woodin, Tammi Richardson, Sean Place, Todd Oakley, Matthew Hall, Michael Jennions and an anonymous reviewer for helpful comments and suggestions on this project. We thank Congaree National Park for field site access. This work was supported by a US Department of Education GAANN fellowship and a National Science Foundation S-STEM fellowship awarded to CSB, and as part of a University of South Carolina – Morris College Mentoring Program to TJ. Files containing eye and body size measurements of all individuals are available through Dryad at doi:10.5061/dryad.27kk4.

References

Bauer, T., Desender, K., Morwinsky, T. & Betz, O. 1998. Eye morphology reflects habitat demands in three closely related ground beetle species (Coleoptera: Carabidae). *J. Zool.* **245**: 467–472.

Baylor, E.R. & Smith, F.E. 1953. The orientation of cladocera to polarized light. *Am. Nat.* **87**: 97–101.

Boersma, M., Spaak, P. & De Meester, L. 1998. Predator-mediated plasticity in morphology, life history, and behavior of *Daphnia*: the uncoupling of responses. *Am. Nat.* **152**: 237–248.

Brandon, C.S. & Dudycha, J.L. 2014. Ecological constraints on sensory systems: compound eye size in *Daphnia* is reduced by resource limitation. *J. Comp. Physiol. A* **200**: 749–758.

Branstrator, D.K. & Holl, C.M. 2000. Planktivory by bluegill (*Lepomis macrochirus*) on *Leptodora kindti* in a small North American lake. *Hydrobiologia* **437**: 101–106.

Conrads, P.A., Feaster, T.D. & Harrelson, L.G. 2008. The effects of the Saluda Dam on the surface-water and ground-water hydrology of the Congaree National Park Flood Plain, South Carolina. U. S. Geological Survey Scientific Investigations Report 2008-5170.

Dudycha, J.L. 2001. The senescence of *Daphnia* from risky and safe habitats. *Ecol. Lett.* **4**: 102–105.

Dudycha, J.L. 2004. Mortality dynamics of *Daphnia* in contrasting habitats and their role in ecological divergence. *Freshwater Biol.* **49**: 505–514.

Dudycha, J.L. & Tessier, A.J. 1999. Natural genetic variation of life span, reproduction and juvenile growth in *Daphnia*. *Evolution* **53**: 1744–1756.

Efron, B. 1992. Jackknife-after-bootstrap standard errors and influence functions. *J. R. Stat. Soc. Ser. B Stat.* **54**: 83–127.

Garamszegi, L.Z., Møller, A.P. & Erritzøe, J. 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proc. R. Soc. Lond. B Biol.* **269**: 961–967.

Glazier, D.S. & Deptola, T.J. 2011. The amphipod *Gammarus minus* has larger eyes in freshwater springs with numerous fish predators. *Invertebr. Biol.* **130**: 60–67.

Gliwicz, Z.M. & Boavida, M.J. 1996. Clutch size and body size at first reproduction in *Daphnia pulicaria* at different levels of food and predation. *J. Plankton Res.* **18**: 863–880.

Haag, C.R. & Ebert, D. 2007. Genotypic selection in *Daphnia* populations consisting of inbred sibships. *J. Evol. Biol.* **20**: 881–891.

Hall, M.I. 2008. Comparative analysis of the size and shape of the lizard eye. *Zoology* **111**: 62–75.

Hamza, W. & Ruggiu, D. 2000. Swimming behaviour of *Daphnia galeata x hyalina* as a response to algal substances and to opaque colours. *Int. Rev. Hydriobiol.* **85**: 157–166.

Harrell, F.E. 2015. *Hmisc* (available at http://biostat.mc.vanderbilt.edu/wiki/Main/Hmisc)

Hebert, P.D.N. 1995. The *Daphnia* of North America. (CD-ROM, beta version, UGuelph, Guelph, Ontario).

Hiller-Adams, P. & Case, J.F.J. 1988. Eye size of pelagic crustaceans as a function of habitat depth and possession of photophores. *Vision Res.* **28**: 667–680.

Kingsolver, J.G. & Diamond, S.E. 2011. Phenotypic selection in natural populations: what limits directional selection? *Am. Nat.* **177**: 346–357.

Land, M.F. 1997. Visual acuity in insects. *Annu. Rev. Entomol.* **42**: 147–177.

Land, M.F. & Nilsson, D.-E. 2012. *Animal Eyes*, 2nd edn. Oxford University Press Inc, New York, NY.

Lande, R. & Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.

Laughlin, S.B., de Ruyter van Steveninck, R.R. & Anderson, J.C. 1998. The metabolic cost of neural information. *Nat. Neurosci.* **1**: 36–41.

Lisney, T.J. & Collin, S.P. 2007. Relative eye size in elasmobranchs. *Brain Behav. Evol.* **69**: 266–279.

Lynch, M. & Walsh, B. 1998. *Genetics and Analysis of Quantitative Traits*. Sinauer Associates Inc, Publishers, Sunderland, Massachusetts.

Møller, A.P. & Erritzøe, J. 2010. Flight distance and eye size in birds. *Ethology* **116**: 458–465.

Nilsson, D.-E. 2009. The evolution of eyes and visually guided behaviour. *Philos. Trans. R. Soc. B* **364**: 2833–2847.

Nilsson, D.-E. & Pelger, S. 1994. A pessimistic estimate of the time required for an eye to evolve. *Proc. R. Soc. Lond. B Biol.* **256**: 53–58.

Niven, J.E. & Laughlin, S.B. 2008. Energy limitation as a selective pressure on the evolution of sensory systems. *J. Exp. Biol.* **211**: 1792–1804.

Novales Flamarique, I. & Browman, H.I. 2000. Wavelength-dependent polarization orientation in *Daphnia*. *J. Comp. Physiol. A* **186**: 1073–1087.

Pfrender, M.E. & Lynch, M. 2000. Quantitative genetic variation in *Daphnia*: temporal changes in genetic architecture. *Evolution* **54**: 1502–1509.

Phillips, P.C. 2002. *H2boot*: Bootstrap estimates and tests of quantitative genetic data. (available at http://darkwing.uoregon.edu/~pphil/software.html)

Protas, M., Tabansky, I., Conrad, M., Gross, J.B., Vidal, O., Tabin, C.J. *et al.* 2008. Multi-trait evolution in a cave fish, *Astyanax mexicanus*. *Evol. Dev.* **10**: 196–209.

R Team. 2013. *R*: A language and environment for statistical computing. (available at http://www.r-project.org/).

Revelle, W. 2014. *psych*: Procedures for Personality and Psychological Research. (available at http://CRAN.R-project.org/package=psych)

Ringelberg, J., Flik, B. & Buis, R. 1974. Contrast orientation in *Daphnia magna* and its significance for vertical plane orientation in the pelagic biotope in general. *Neth. J. Zool.* **25**: 454–475.

Ross, C.F. & Kirk, E.C. 2007. Evolution of eye size and shape in primates. *J. Hum. Evol.* **52**: 294–313.

Salvini-Plawen, L. & Mayr, E. 1977. On the evolution of photoreceptors and eyes. *Evol. Biol.* **10**: 207–263.

Schmitz, L. & Wainwright, P.C. 2011. Nocturnality constrains morphological and functional diversity in the eyes of reef fishes. *BMC Evol. Biol.* **11**: 338.

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**: 671–675.

Schwind, R. 1999. Daphnia pulex swims towards the most strongly polarized light - a response that leads to “shore flight”. *J. Exp. Biol.* **202**: 3631–3635.

Smith, F.E. & Baylor, E.R. 1953. Color responses in the cladocera and their ecological significance. *Am. Nat.* **87**: 49–55.

Somanathan, H., Kelber, A., Borges, R.M., Wallén, R. & Warrant, E.J. 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.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.

Thomas, R.J., Szekely, T., Cuthill, I.C., Harper, D.G.C., Newson, S.E., Frayling, T.D. *et al.* 2002. Eye size in birds and the timing of song at dawn. *Proc. R. Soc. Lond. B Biol.* **269**: 831–837.

Thomas, R.J., Szekely, T., Powell, R.F. & Cuthill, I.C. 2006. Eye size, foraging methods and the timing of foraging in shorebirds. *Funct. Ecol.* **20**: 157–165.

Tibshirani, R. & Leisch, F. 2015. *bootstrap*. (available at http://cran.r-project.org/web/packages/bootstrap)

Vanni, M.J. & Lampert, W. 1992. Food quality effects on life history traits and fitness in the generalist herbivore *Daphnia*. *Oecologia* **92**: 48–57.

Vanoverbeke, J. & De Meester, L. 2010. Clonal selection and genetic drift in cyclical parthenogens – the interplay between neutral and selective processes. *J. Evol. Biol.* **23**: 997–1012.

Veilleux, C.C. & Lewis, R.J. 2011. Effects of habitat light intensity on mammalian eye shape. *Anat. Rec.* **294**: 905–914.

Young, S., Taylor, V. & Watts, E. 1984. Visual factors in *Daphnia* feeding. *Limnol. Oceanogr.* **29**: 1300–1308.

Zaret, T. & Kerfoot, W. 1975. Fish predation on *Bosmina longirostris*: body-size selection vs. visibility selection. *Ecology* **56**: 232–237.

Data deposited at Dryad: doi: 10.5061/dryad.27kk4

Received 12 January 2015; revised 9 July 2015; accepted 29 July 2015