

## RESEARCH ARTICLE

# Visual acuity in ray-finned fishes correlates with eye size and habitat

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## ABSTRACT

Visual acuity (the ability to resolve spatial detail) is highly variable across fishes. However, little is known about the evolutionary pressures underlying this variation. We reviewed published literature to create an acuity database for 159 species of ray-finned fishes (Actinopterygii). Within a subset of those species for which we had phylogenetic information and anatomically measured acuity data ( $n=81$ ), we examined relationships between acuity and both morphological (eye size and body size) and ecological (light level, water turbidity, habitat spatial complexity and diet) variables. Acuity was significantly correlated with eye size ( $P<0.001$ ); a weaker correlation with body size occurred via a correlation between eye and body size ( $P<0.001$ ). Acuity decreased as light level decreased and turbidity increased; however, these decreases resulted from fishes in dark or murky environments having smaller eyes and bodies than those in bright or clear environments. We also found significantly lower acuity in horizon-dominated habitats than in featureless or complex habitats. Higher acuity in featureless habitats is likely due to species having absolutely larger eyes and bodies in that environment, though eye size relative to body size is not significantly different from that in complex environments. Controlling for relative eye size, we found that species in complex environments have even higher acuity than predicted. We found no relationship between visual acuity and diet. Our results show that eye size is a primary factor underlying variation in fish acuity. We additionally show that habitat type is an important ecological factor that correlates with acuity in certain species.

**KEY WORDS:** Spatial resolution, Light level, Turbidity, Habitat complexity, Diet, Visual ecology

## INTRODUCTION

Visual acuity, the ability to resolve spatial detail, is critical for a wide range of vision-based tasks, including object detection and recognition, foraging and navigation (Cronin et al., 2014). Correspondingly, the variety of tasks requiring an organism to resolve spatial detail is vast, ranging from a male mayfly locating its dark, fast-moving mate against the bright sky, to a deep-sea dragonfish localizing a point source of bioluminescence against the black sea, to a tropical bird resolving the aposematic color patterns of a poison dart frog. Visual acuity is highly variable across species, varying over four orders of magnitude among animals that are considered to have image-forming eyes (Land and Nilsson, 2002).

Acuity is often reported in units of cycles per degree (cpd), which is the number of black and white stripe pairs an organism can discriminate within a single degree of visual angle. Some of the highest acuities known are found in birds of prey (140 cpd; Reymond, 1985) and in humans (70 cpd; Land and Nilsson, 2002), while the lowest acuity is found in small compound eyes such as those of *Drosophila* (0.01 cpd), and in simpler eyes, such as those in *Planaria* (0.01 cpd; Land, 1981). It is known that within an eye, acuity is locally adapted to the structure of the environment or specific tasks, as in foveae in camera eyes or acute zones in compound eyes (see Cronin et al., 2014). However, broad trends regarding the relationship between acuity and various aspects of the visual environment, from light level to physical structure, are relatively unknown, as few studies have examined the relationship between acuity, ecology and environment across a large number of species [but see Veilleux and Kirk (2014) for mammals and Land (1997) for insects].

One factor that dictates an eye's acuity is the angular width of the region that is viewed by each photoreceptor, which is equal to the diameter of the photoreceptor divided by the eye's focal length. Longer focal lengths result in smaller angular resolution and thus sharper acuity. However, photoreceptors with smaller angular resolutions collect light from a smaller angular area of the environment, reducing sensitivity (see Land and Nilsson, 2002). Increasing the size of the entire eye can increase either resolution or sensitivity without having to decrease the other. For example, a larger eye with a longer focal length can be more sensitive without losing acuity, or it can be more acute without losing sensitivity. However, one constraint on larger eyes is that they must still fit inside an animal's head: to double acuity, the volume of an eye must increase eightfold, all other things being equal. Additionally, larger eyes are associated with increased development and maintenance costs (Niven and Laughlin, 2008). Beyond eye size, increasing evidence suggests that visual acuity in vertebrates is driven by retinal ganglion cell (RGC) density or receptive field size, rather than photoreceptor density, as RGCs process visual information further in the processing pathway than do photoreceptors (Devries and Baylor, 1997; Enroth-Cugell and Robson, 1966; Lee and Stevens, 2007; Pettigrew et al., 1988).

Of course, not all animals have or require large eyes and/or high acuity. Species live in a variety of environments and thus have different visual requirements. These differences, combined with the trade-offs associated with greater acuity, suggest that relationships between acuity and aspects of an animal's ecology and environment exist. There are several aspects of an organism's lifestyle, ecology and environment that may be particularly relevant to spatial acuity. First, because of the trade-off between resolution and sensitivity described above, the light level in which an organism operates is likely to correlate with its spatial acuity. Light level is dictated by animal behavior, i.e. whether a species is diurnal, nocturnal or crepuscular, and, in aquatic environments, by both depth and

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turbidity. Turbidity also affects the perception of small details, because light scattering from suspended particles attenuates high spatial frequencies (Gazey, 1970; Wells, 1969). Habitat spatial complexity, or the amount of spatial information available in a given habitat, may also affect acuity. Aquatic organisms inhabiting more complex environments (e.g. coral reefs, mangroves, rocky shorelines) may need higher acuity for object recognition and navigation tasks than species in less complex habitats such as the pelagic realm (Hughes, 1977). Lastly, diet may affect spatial acuity, because higher acuity may be required for predatory species to detect and localize prey.

In this study, we examined correlations between acuity, morphology and ecology in ray-finned fishes (Actinopterygii). Fishes are an excellent system for the comparative study of acuity for several reasons. First, they are often highly visual and occupy an optically diverse range of habitats, from shallow, brightly lit coral reefs to pitch-dark depths of more than 8000 m (Lythgoe, 1979). Second, there is a long history of studying acuity in fishes, owing to previous work focusing on how acuity changes over ontogeny (Baburina et al., 1968; Baerends et al., 1960; Blaxter and Jones, 1967; Connell, 1963; Hairston et al., 1982; Hester, 1968; Johns and Easter, 1977; Lyall, 1957; Neave, 1984; Otten, 1981; Tamura, 1957; Yamanouchi, 1956). Third, previous studies on small numbers of fish species have found that acuity varies greatly (i.e. Collin and Pettigrew, 1988a,b; Douglas and Hawryshyn, 1990; Otten, 1981; Tamura, 1957; Tamura and Wisby, 1963). Among coral reef teleosts, for example, Collin and Pettigrew (1989) found acuities ranging from 4 to 27 cpd. Fourth, previous work using relatively small numbers of species has correlated acuity in fishes with various visually relevant ecological factors, including light level (Wagner et al., 1998; Warrant, 2000), habitat spatial complexity (Dobberfuhl et al., 2005) and diet type (Collin and Pettigrew, 1988a,b).

Despite the wealth of available data, no study has yet combined this information into a comprehensive database, which is necessary for a broad comparative study of how acuity relates to morphological and ecological factors across species. Here, we synthesized available literature on visual acuity in adult ray-finned fishes and then examined the relationships between acuity and two aspects of morphology (eye size, represented by lens diameter, and body size, represented by total length), and four ecological factors (light level, turbidity, habitat spatial complexity and diet).

## MATERIALS AND METHODS

### Acuity across ray-finned fishes

#### Comparative database of fish acuity

We assembled a database of visual acuity in ray-finned fishes ( $n=159$  species) using published data. We restricted our database to include only acuity measured in adult individuals, because of the effects of ontogeny on acuity. Numerous methods have been used to estimate acuity, including behavior [using an optomotor or optokinetic response (Douglas and Hawryshyn, 1990)], anatomy (using photoreceptor density or peak RGC density) and optics (using the optical quality of the lens). Unfortunately, these different methods do not yield equivalent estimates even within the same species. For example, there is evidence in fishes, as well as other groups of animals, that the resolution of the optical system is much higher than that of the retina or behavior (e.g. Tamura, 1957; Charman and Tucker, 1973; Northmore and Dvorak, 1979; Otten, 1981; Hairston et al., 1982), potentially because a high-quality optical system may be for contrast enhancement and not increased acuity (Snyder et al., 1986).

Thus, a more accurate limit on an organism's acuity may be its retinal morphology. One potential measure of acuity is given by the angular density of the photoreceptors, which represents the sampling array of the eye. However, moving through the visual processing pathway, RGCs may be a more appropriate 'bottleneck' of spatial information than optics or photoreceptors, because each ganglion cell may connect to numerous bipolar cells, each of which in turn connects to many photoreceptors. Therefore, it has been suggested that peak RGC density is a more appropriate morphological measure of acuity (Pettigrew et al., 1988), despite the fact that acuity may more closely depend upon the size of the ganglion cell receptive field than it does on the density of ganglion cells (Devries and Baylor, 1997; Enroth-Cugell and Robson, 1966; Lee and Stevens, 2007).

Anatomical measures have the disadvantage that they cannot account for diffraction and optical imperfections, spatial and temporal summation, or other forms of higher-order neural processing of visual signals, all of which may limit the resolution of an eye. Thus, some have argued that behaviorally measured acuity is the most accurate representation of visual function (Arrese et al., 2000). Behavioral studies have shown that some fishes can distinguish striped gratings at periodicities near the theoretical limit imposed by photoreceptor densities (Browman et al., 1990; Haug et al., 2010; Miller et al., 1993; Northmore and Dvorak, 1979; Northmore et al., 2007), and evidence from birds and mammals suggests that acuity measured using anatomical and behavioral methods aligns fairly well (for example, see Pettigrew and Manger, 2008). However, other studies have found that behavioral methods yield much lower estimates of acuity than anatomical methods (Pettigrew et al., 1988). In general, because it is not practical or feasible to test large species using an optomotor or other behavioral apparatus, fewer studies have measured acuity behaviorally. For completeness, we compiled acuity data that had been measured using all of the methods outlined above into a comprehensive database of acuity across ray-finned fishes (Table S1).

#### Database of acuity for use in analyses

We restricted our analyses to only a subset of those species in the acuity database, to minimize the effects of measurement method on our results. We chose to examine only species for which acuity had been measured anatomically (using either photoreceptor density or peak RGC density), and for which phylogenetic relatedness was known ( $n=81$ ). To control for the effects of phylogenetic relatedness, we used a published species-level phylogeny of 7822 ray-finned fishes (Rabosky et al., 2013), and extracted the 81 species on the tree for use in analyses. To estimate phylogenetic signal, we calculated Pagel's  $\lambda$  (Freckleton et al., 2002; Pagel, 1999) using the caper package (Orme et al., 2013) in R version 3.2.5 (R Foundation for Statistical Computing, Vienna, Austria). Pagel's  $\lambda$  is a branch length transformation parameter that maximizes the likelihood of the observed data, assuming a Brownian model of evolution (Freckleton et al., 2002). It ranges from 0 (distribution of trait values independent of phylogeny) to 1 (direct covariance between trait values and phylogenetic structure). To test for significant phylogenetic signal, we used likelihood ratio tests against the null hypothesis that  $\lambda=0$ .

Throughout, we used phylogenetic generalized least squares (PGLS) regressions and multivariate models to control for phylogenetic relatedness. PGLS is a modification of generalized least squares, and uses a phylogeny to estimate an expected level of covariance between species in a dataset. The assumption is that species that are closely related will be more similar to one another in

the trait of interest, and thus will have more similar residuals from the least squares regression line. Thus, phylogenetic relatedness generates an expected covariance structure for the residuals, which can then be used to modify estimates of the slope and intercept of the regression line, correcting for phylogeny (for a recent review, see Symonds and Blomberg, 2014).

To avoid pseudoreplication in our database, we used only one measure of acuity for each species. However, some of these 81 species had their acuity measured either using multiple methods or in multiple studies (Fig. S1). In these cases, we used acuity measured by peak RGC density over acuity measured using photoreceptor density because RGC density may be a more accurate measure of acuity (Wagner, 1990).

A potential confounding factor was that our two anatomical measurements of acuity would not be comparable to one another, and thus not appropriate to combine for analyses. We examined this in two ways. First, we calculated separate PGLS regressions of acuity on eye size using datasets that comprised: (1) only photoreceptor density-derived acuity ( $n=54$ ), (2) only RGC density-derived acuity ( $n=27$ ) and (3) acuity from both methods combined ( $n=81$ ) (Table S2). We used ANCOVA to compare the photoreceptor density-derived and the RGC density-derived regression lines, and found that neither the slopes ( $P=0.45$ ) nor the intercepts ( $P=0.50$ ) differed significantly between the two regression lines (Table S2).

Second, we fit PGLS multivariate models that included acuity as the response variable and either body size or eye size a predictor variable. We then compared the fit of those models with models that included measurement method as a co-predictor, either using an additive or interaction term. We ranked models based on Akaike's information criterion (AIC; Akaike, 1974; Burnham and Anderson, 2002), and then assigned  $\Delta$ AIC values by calculating the difference between AIC value of a given model and the AIC value of the best-fit model (i.e. that with the lowest AIC value in that set). Following (Burnham et al., 2011),  $\Delta$ AIC values were used to calculate relative likelihoods for each model  $i$  within a set using the formula:

$$l_i = \exp[-(1/2)\Delta_i]. \quad (1)$$

We then calculated the probability that each model,  $w_i$ , within a set of models, is the best by dividing the likelihood of a given model  $l_i$  by the sum of the likelihoods of all models within that set (Burnham et al., 2011). PGLS bivariate regressions showed that adding method of measurement as a co-predictor to a regression of acuity on eye size did not improve model fit (Table S3). Thus, both the PGLS bivariate regressions and the PGLS multivariate models show that, in our dataset, the relationship between acuity and eye size is consistent regardless of whether acuity was measured using photoreceptor density or peak RGC density. This allows us to conclude that (1) it is appropriate to combine photoreceptor- and RGC-derived data for analyses, and (2) method of measurement can be discounted as a confounding factor in further analyses.

### Relationships between acuity, morphology and ecology

#### Eye size and body size

Where possible, for each species in our database for analyses, we recorded from the original citation the eye size and body size of the individual(s) used to measure acuity. It was more common for studies to report lens axial diameter than eye axial diameter. Thus, to maximize the number of species for which we had eye size data, we use lens diameter as a proxy for eye size, as the two measures are highly correlated (Fernald, 1991). Where provided, we noted the

body size of the individuals used in the acuity measurements. However, there are numerous established methods for measuring the body size of a fish, including total length, fork length and standard length [for definitions of each, see the FishBase website: [www.fishbase.org](http://www.fishbase.org); Froese and Pauly (2000)]. We used FishBase to transform reported measures of body size from the original citations into total length (a straight-line measure of length from the tip of the snout to the tip of the longer lobe of the caudal fin), using species-specific length–length relationships. When more than one length–length relationship was available for a species, we used the relationship based on the largest number of specimens. Thus, throughout the paper, the term ‘body size’ refers to total length.

#### Categorizing fishes according to ecology

We then classified each species in the analyses database according to four ecological variables: light level, turbidity, habitat spatial complexity and diet type. Each ecological variable was divided into three categories; for full descriptions of each category, see Table 1. The categories were defined using criteria that involved well-established definitions and measures that, though broad, were chosen so as to be repeatable by other studies. Light level categories are based on established relationships between water type, depth and available light (Mobley, 1994), and incorporate an organism's diel cycle. For example, nocturnal animals were placed in the ‘dim’ category, despite living at depths that would otherwise have daylight light levels. Turbidity categories were assigned using the parameter  $K$ , which is the diffuse attenuation coefficient of the water (Mobley, 1994). Habitats were divided into three broad spatial complexity categories: (1) featureless (pelagic habitats, or any species living in the dark), (2) horizon-dominated (benthic) and (3) complex (reefs, mangroves, kelp forests and rocky shorelines). Lastly, diet types were categorized as being composed primarily of sessile, motile benthic or pelagic prey.

To assign species to categories, we used FishBase to obtain data regarding each species' environment type (freshwater, brackish, marine or a combination), habitat preferences, minimum, maximum and common depth, diel activity pattern and diet (based on all recorded food items). All assignments were then confirmed by T.T.S.

#### Relationships between acuity and morphology

We used PGLS regressions to investigate the relationships between acuity and two morphological variables: eye size and body size. We investigated acuity versus both eye size and body size because, although tightly correlated, each gives different information about how a species may achieve higher acuity. Higher acuity can result from a longer focal length. In fishes, lens diameter and focal length are tightly correlated (described by Matthiessen's ratio; Matthiessen, 1882), and eyes with larger lenses also have longer focal lengths. Larger eyes relative to body size represent a greater investment in vision than smaller eyes; this thus gives some indication of the importance of vision for that species. Acuity, eye size and body size were log-transformed to meet the assumption of normality. PGLS analyses were performed using caper.

#### Relationships between acuity and ecology: PGLS multivariate models

We next examined the relationship between acuity and categorical measures of light level, turbidity, habitat spatial complexity and diet (Table 1). To assess the relative importance of the ecological variables on acuity, we fit PGLS multivariate models with acuity as the response variable.

Based on Burnham et al. (2011), we compared model fit between models that were selected to represent alternative hypotheses

**Table 1. Definitions of ecological categories used in analyses**

Category	Details
Light level	
Bright (full sun to 1% light level)	Top 200 m of offshore oceanic habitats ( $K \leq 0.02$ ) Top 25 m of oligotrophic freshwater and coastal habitats ( $K \leq 0.2$ ) Top 5 m of mesotrophic freshwater and coastal habitats ( $K \leq 0.8$ ) Top 2 m of eutrophic freshwater and coastal habitats ( $K \leq 2$ )
Dim (1% to limit of vision)	200–1000 m in offshore oceanic habitats 25–125 m in oligotrophic freshwater and coastal habitats 5–25 m in mesotrophic freshwater and coastal habitats 2–10 m of eutrophic freshwater and coastal habitats Nocturnal at 'bright' depths listed above
Dark (no light in freshwater, only bioluminescence available for vision in marine habitats)	>1000 m in offshore oceanic habitats >125 m in oligotrophic freshwater and coastal habitats >25 m in mesotrophic freshwater and coastal habitats >10 m of eutrophic freshwater and coastal habitats Nocturnal at 'dim' depths listed above Caves
Turbidity	
Murky	Eutrophic freshwater and coastal habitats ( $K > 1.0$ at all wavelengths)
Slightly murky	Mesotrophic and oligotrophic freshwater and coastal habitats ( $0.1 < K < 1.0$ )
Clear	Offshore oceanic habitats ( $K < 0.1$ )
Habitat spatial complexity	
Featureless	Pelagic, all eutrophic habitats, and all habitats not at 'dark' light levels
Horizon-dominated	Benthic (unless eutrophic or at light levels below 'dim')
Complex	Coral, sponge and worm reefs (unless eutrophic or at light levels below 'dim') Mangroves (unless eutrophic or at light levels below 'dim') Kelp forests, algal reefs (unless eutrophic or at light levels below 'dim') Rocky areas (unless eutrophic or at light levels below 'dim')
Diet type	
Sessile	Non-motile species such as: algae, detritus, coral, sponges, anemones
Motile benthic	Infaunal and errant benthic species: e.g. gastropods, asteroids, polychaetes, holothurians
Pelagic	Nekton (including benthic-associated species) Zooplankton

The parameter  $K$  is the diffuse attenuation coefficient.

regarding the factors that influence acuity. These alternative hypotheses were developed using primary literature and preliminary analyses. For example, our complete model could include acuity as the response variable, and eye size, body size, method of measurement, light level, turbidity, habitat complexity and diet type all as co-predictors. However, our morphological analyses showed that the weak correlation between acuity and body size arises only as a result of a stronger correlation between eye size and body size. Thus, we did not include body size in the models that included ecological variables. Additionally, several analyses showed that method of measurement does not have a significant impact on acuity in our dataset, so we excluded that from the complete model as well.

Therefore, we examined a model set where acuity was the response variable, and co-predictors included eye size, as well as all possible additive combinations of our four ecological categories, which we felt represented reasonable biological hypotheses. As above, for each model, we also calculated the likelihood and probability for each model in the set. As a separate method of confirming the results of our modeling approach, we also performed a stepwise AIC model selection using the stepAIC function of the mass package (Venables and Ripley, 2002). The results of the stepwise model selection approach (Table S4) yielded the same best-fit model as our hypothesis-based approach.

#### Raw acuity, relative eye investment and residual acuity

To further investigate how acuity varies across ecological categories, we examined 'raw acuity' across ecological categories. However, raw acuity is uncorrected for eye size, body size or

phylogenetic relationships. To calculate the predicted relationship between eye size and body size [which are not linearly related (Howland et al., 2004; Hughes and Crescitelli, 1977)], we calculated a PGLS regression between eye size and body size. However, there are both positive and negative residuals around this allometric relationship. These residuals can be interpreted as a single measure for each species of whether eyes are smaller or larger than is expected based on body size, which we term 'relative eye investment'. Species with positive relative eye investment have larger eyes relative to their body size than expected based on allometry, and species with negative relative eye investment have smaller eyes relative to their body size than expected.

Similarly, plotting acuity versus relative eye investment shows that each species has a predicted acuity based on its relative eye investment. However, there are also residuals present around that line, showing that certain species have higher than predicted acuity, even after accounting for the fact that they have higher relative eye size than expected. To examine acuity without the confounding effects of eye size, one thus needs to examine the residuals from the regression of acuity on relative eye investment.

As a more familiar illustration of this logic, think of playing the piano. The ability to quickly play notes that are far apart (large intervals) on the piano depends on hand size, which has a positive relationship with body size. Of course, residuals exist around this relationship, so that some people have larger or smaller hands than expected based on their body size. However, some people exhibit higher skill levels on the piano than their relative hand size would predict. For example, the Russian pianist Vladimir Ashkenazy has famously small hands, and yet still manages difficult piano music.

Thus, if one were to perform a regression of body versus hand size to yield ‘relative hand investment’, Ashkenazy would represent a point with a negative residual, because he has smaller than expected hands for his body. If one were to then regress ‘relative hand investment’ versus ‘skill at playing large intervals’, the relationship would be positive, as people with larger relative hands are on average more skilled at playing large intervals. Ashkenazy, however, would have a positive residual on this regression, because his skill at intervals is far above that predicted by his relative hand size.

Returning to acuity, some fish species have even higher acuity than can be explained by relative eye investment alone. To disentangle acuity from eye size, we performed a PGLS regression of acuity on relative eye investment, and extracted the residuals. In this case, the model residuals for each species, which we term residual acuity (after Veilleux and Kirk, 2014), represent the portion of variation in acuity that is unexplained by variation in relative eye size. In essence, residual acuity quantifies whether a species has higher or lower acuity than expected given its relative eye investment, while accounting for phylogenetic relatedness.

Because our data met the assumptions of normality and equal variances, we used pairwise Student’s *t*-tests to test for differences in acuity between categories. We corrected for multiple testing (in our case,  $n=3$  pairwise comparisons) using the Bonferroni correction (Dunn, 1961). Sample sizes of species in each category were highly variable; in some cases, we performed power analyses to determine whether the sample sizes we had were sufficient to yield any significant result. Power analyses were performed using the pwr package (<http://CRAN.R-project.org/package=pwr>).

## RESULTS

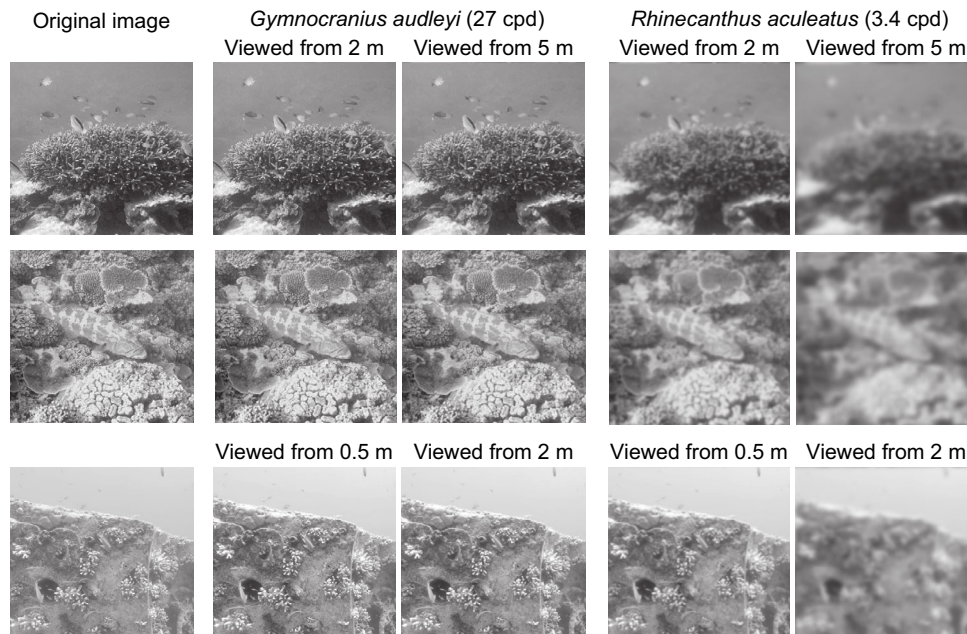
### Acuity across ray-finned fishes

We found that acuity is highly variable across ray-finned fishes. Within the 81 species used in our analyses, the highest acuity (40 cpd; rock bass *Ambloplites rupestris*) was approximately 45 times higher than the lowest acuity (0.87 cpd; zebrafish *Danio rerio*). To illustrate the differences in spatial information available to fish of differing acuities, we modified photographs of coral reef scenes by removing all spatial detail below the acuity limit found in the two reef-associated species with the highest and lowest anatomically measured acuity (Fig. 1).

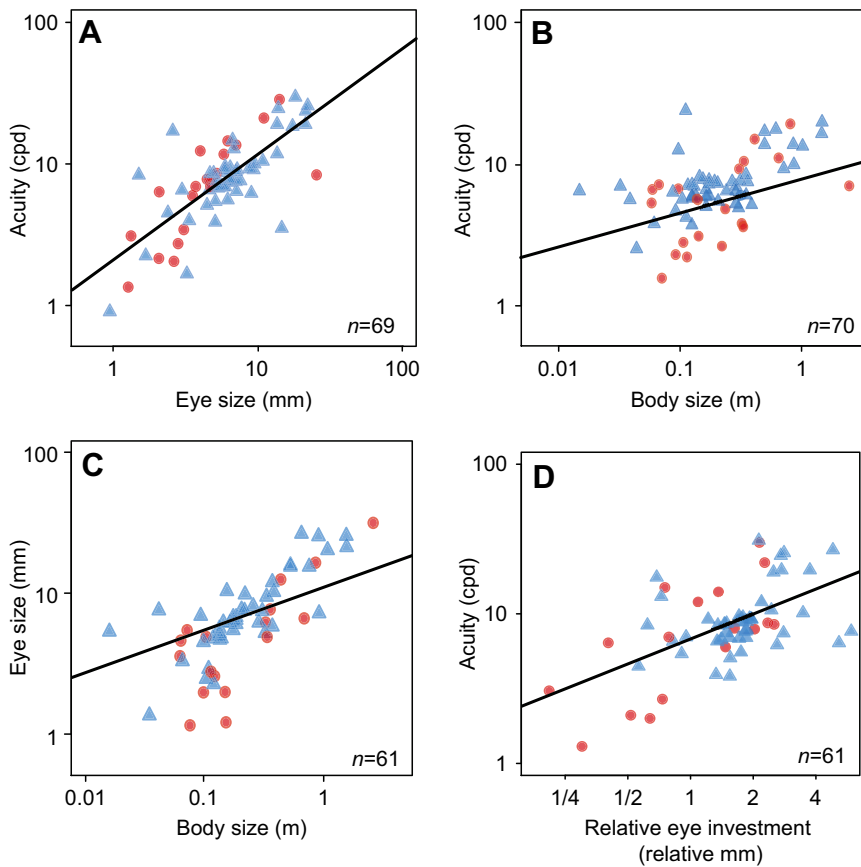
We found significant phylogenetic signal in acuity ( $P<0.0001$ ,  $\lambda=0.71$ , 95% CI=0.34–0.86; Fig. S2), eye size ( $P<0.001$ ,  $\lambda=0.87$ , 95% CI=0.66–0.96) and body size ( $P<0.001$ ,  $\lambda=0.76$ , 95% CI=0.39–0.93). Thus, shared phylogenetic history contributes to trends in acuity across fishes, likely driven by the impact of phylogeny on eye size and body size.

### Acuity, eye size and body size

PGLS regressions revealed significant, positive relationships between acuity and both eye size ( $F_{1,67}=84.4$ ,  $R^2=0.55$ ,  $P<0.001$ ,  $n=69$ ) and body size ( $F_{1,68}=18.2$ ,  $R^2=0.20$ ,  $P<0.001$ ,  $n=70$ ; Fig. 2A, B), though the relationship with eye size was stronger. Thus, as eye size or body size increases, on average acuity increases. Extracting the residuals from a PGLS regression of acuity on lens diameter, and then examining the relationship between those residuals and body size showed no significant relationship ( $n=61$ ,  $F_{1,59}=1.04$ ,  $R^2=0.02$ ,  $P=0.31$ ). This implies that eye size is a strong predictor of acuity, while the weaker correlation between acuity and body size in turn results from the correlation between eye size and body size.



**Fig. 1. Accounting for fish spatial acuity in perception of coral reef scenes.** These coral reef scenes have been modeled to remove spatial information below the acuities the reef-associated fish with the highest retinal ganglion cell (RGC) density-derived acuity (*Gymnocranius audleyi*, 27 cpd; Collin and Pettigrew, 1988b) and the lowest acuity (*Rhinecanthus aculeatus*, 3.4 cpd; Champ et al., 2014) in our database. Comparing the photographs from two different viewing distances illustrates the effects that distance has on acuity and how a given scene may be perceived. Images were assumed to be either 1 m (top two rows) or 0.5 m (bottom row) across in absolute size. To create these images, we used Fourier methods (following Caves et al., 2016). We began with square (1024×1024 pixel) color images and extracted the green color channel, as acuity is achromatic. We then multiplied the Fourier transform of that image by a Gaussian modulation transfer function whose value at the maximum resolvable spatial frequency was equal to 2% (Douglas and Hawryshyn, 1990). We then applied an inverse Fourier transform to recover the image; in the recovered image, all spatial information spanning angles less than the spatial resolution of the organism had been removed.



**Fig. 2. Relationships between acuity, eye size, body size and relative eye investment, and between eye and body size in ray-finned fishes.** Panels show PGLS bivariate regressions of (A) acuity versus eye size, (B) acuity versus body size, (C) eye size versus body size and (D) acuity versus relative eye investment. Relative eye investment was calculated using the residuals from the regression in C. Symbols represent the method used to measure acuity (circles, peak retinal ganglion cell density; triangles, photoreceptor density). In D, the x-axis has been translated from log space into relative eye investment (mm), meaning that a relative eye investment of two indicates a species that has an eye twice as large as the mean of species with the same body size. For statistics, see Results.

We also found a significant, positive relationship between eye size and body size ( $F_{1,59}=45.0$ ,  $R^2=0.43$ ,  $P<0.001$ ,  $n=61$ ), so it is expected that both would, in turn, be correlated with acuity (Fig. 2C). Extracting the residuals from the regression of eye size on body size yielded a measure for each species of relative eye investment. As expected, we found a significant, positive relationship between relative eye investment and acuity ( $F_{1,59}=27.4$ ,  $R^2=0.31$ ,  $P<0.001$ ,  $n=61$ ). Thus, species with higher relative eye investment (larger eyes than expected based on body size) on average exhibit increased acuity (Fig. 2D).

### The relationship between acuity and ecology PGLS multivariate models

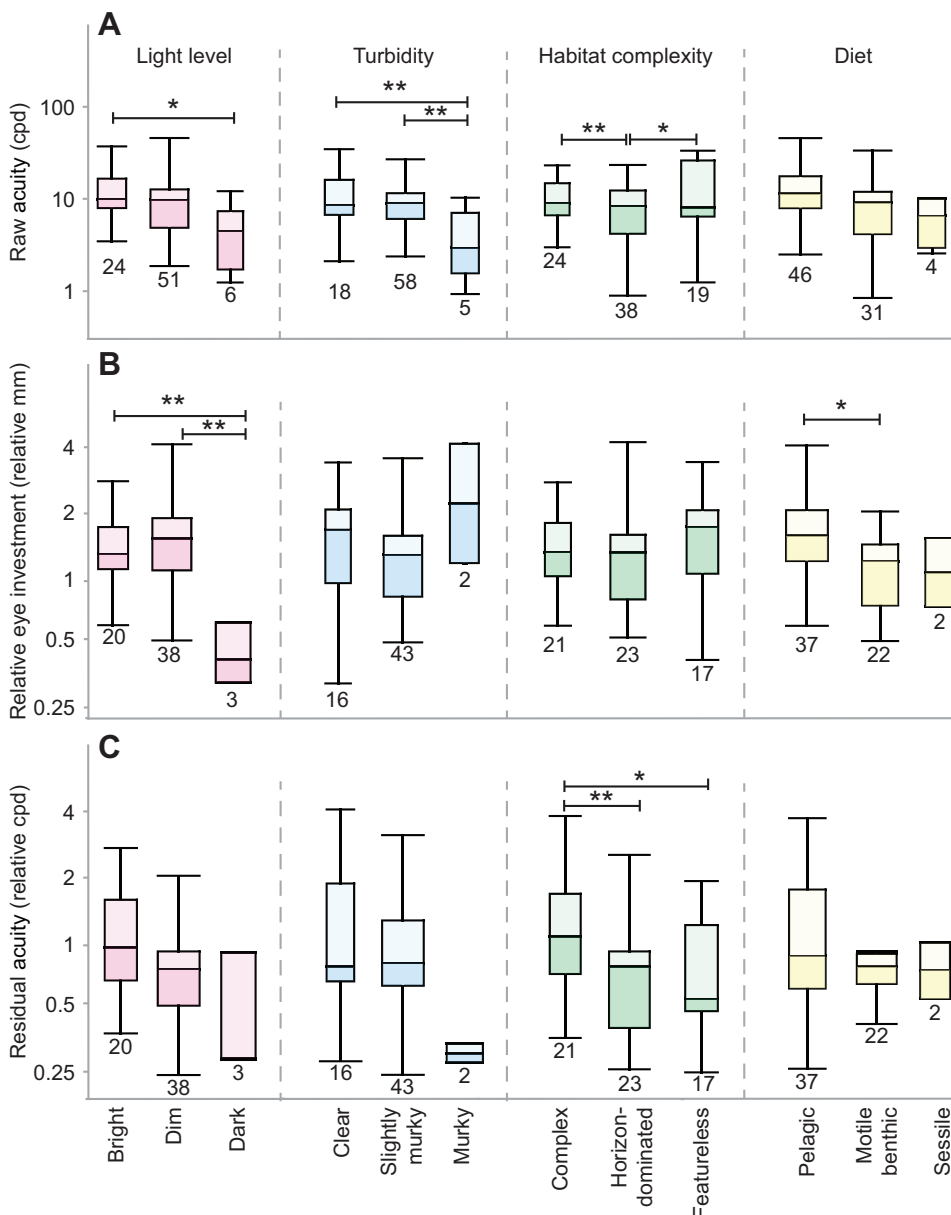
To assess the relative importance of various ecological factors on acuity, we fit PGLS models with acuity as the response variable.

The model that best fit the data included both eye size and habitat complexity as co-predictors (Table 2). Only one other model – which included eye size, habitat complexity and turbidity – had  $\Delta\text{AIC}<2$  relative to the best-fit model. Thus, adding turbidity to the best-fit model does not improve the model's explanatory power, but also does not weaken it. Two additional models, including light level, or both light level and turbidity, had  $\Delta\text{AIC}<3$  relative to the best-fit model. However, support for the best ( $w_i=0.3$ ) and the second best models ( $w_i=0.28$ ) were roughly equivalent, and were approximately four times as strong as the support for the next two most likely models ( $w_i=0.08$  and  $0.07$ ). Expanding to consider models with  $\Delta\text{AIC}<4$ , which are still considered to have some support (Burnham et al., 2011), we see very low model probability ( $w_i=0.05$ – $0.06$ ), indicating that the probability of the hypotheses represented by these models is low

**Table 2. Raw acuity, eye size and body size values across light level, turbidity, habitat complexity and diet categories**

Category		Raw acuity (cpd)			Eye size (cm)			Body size (cm)		
		<i>n</i>	Mean	s.d.	<i>n</i>	Mean	s.d.	<i>n</i>	Mean	s.d.
Light level	Dark	13	5.7	2.9	4	0.24	0.07	4	16	9.9
	Dim	51	9.2	7.9	45	0.57	0.40	45	34	46
	Bright	25	10	6.2	24	0.64	0.45	21	38	36
Turbidity	Murky	5	3.5	3.2	3	0.27	0.18	3	10	8.5
	Slightly murky	60	9.2	6.8	51	0.55	0.33	51	29	24
	Clear	27	9.7	8.0	26	0.58	0.55	16	53	74
Habitat	Featureless	28	10	8.7	27	0.60	0.55	17	55	72
	Horizon-dominated	39	7.0	6.3	29	0.45	0.23	32	22	16
	Complex	25	11	5.5	24	0.60	0.38	21	34	29
Diet	Sessile	4	5.1	2.3	3	0.45	0.70	4	26	9.6
	Motile benthic	33	8.1	7.3	31	0.42	0.24	24	19	10
	Pelagic	55	9.9	7.1	47	0.64	0.48	42	43	52

cpd, cycles per degree.



**Fig. 3. Acuity and eye investment across ecological categories in ray-finned fishes.** (A) Raw acuity (uncorrected for morphology or phylogeny), (B) relative eye investment and (C) residual acuity across light level (pink), turbidity (blue), habitat spatial complexity (green) and diet (yellow) categories. Sample sizes are presented below each box. Statistics are from pairwise Student's *t*-tests ( $0.02 > P > 0.01$ ;  $**P < 0.01$ ). Only comparisons with  $P \leq 0.02$  are shown, which is the Bonferroni-corrected significance level for three pairwise comparisons. In B and C, the *y*-axis has been translated from log space into either relative eye investment (mm) or relative acuity (cpd). This means that, for example, a residual acuity of two in C indicates a species that has acuity twice as high as the mean of species with the same relative eye investment. For a figure that includes *P*-values for each pairwise comparison, see Fig. S3.

compared with the probability of the hypothesis represented by the best-fit model.

Because the top two models had roughly equal support, but the model without turbidity was simpler, the data suggest that the hypothesis that both eye size and habitat complexity predict acuity is both the most parsimonious and the most supported.

#### Raw acuity, relative eye investment and residual acuity

To further examine acuity across ecological categories, and why the best-fit model included only habitat complexity and eye size, we looked at how raw acuity, relative eye investment and residual acuity vary across ecological categories (Fig. 3). Raw acuity, eye size and body size across all four ecological variables are detailed in Table 3.

Examining raw acuity across categories (Fig. 3A), we found that acuity in bright habitats was significantly higher than acuity in dark habitats ( $P=0.02$ ); acuity in clear habitats was significantly higher than in either slightly murky ( $P=0.003$ ) or murky habitats ( $P=0.004$ ); acuity in horizon-dominated (benthic) habitats was significantly higher than in either complex ( $P=0.003$ ) or featureless

( $P=0.02$ ) habitats; and that the highest acuity was found in species with pelagic diets as compared with those with motile benthic ( $P=0.11$ ) or sessile ( $P=0.15$ ) diets, though differences between diet categories were not significant.

However, raw acuity does not control for eye size when examining acuity across species. Therefore, we examined how relative eye investment varies across ecological categories (Fig. 3B). We found that relative eye investment was significantly lower in species that live in dark habitats, as compared with species that live in either dim ( $P=0.001$ ) or bright ( $P=0.001$ ) habitats. Additionally, relative eye investment was significantly higher in species with pelagic diets compared with those that have motile benthic diets ( $P=0.01$ ). We did not find any significant differences in relative eye investment across turbidity or habitat complexity categories.

Relative eye investment offers an indication of the importance of vision for species in different ecological categories. To relate that measure directly to acuity, we extracted the residuals from a regression of acuity on relative eye investment and examined those residuals (residual acuity) across categories (Fig. 3C). We did not find any

**Table 3. Summary of predictor combinations of ecological variables fitted to PGLS multivariate models of acuity**

Model	$\Delta$ AIC	$l_i$	$w_i$
ES+HC	0.00	1.0	0.30
ES+HC+T	0.14	0.93	0.28
ES+HC+LL	2.6	0.28	0.08
ES +HC+LL+T	2.8	0.24	0.07
ES+HC+T+D	3.1	0.22	0.06
ES+HC+D	3.4	0.19	0.05
ES	3.8	0.15	0.05
ES+HC+LL+T+D	4.9	0.09	0.03
ES+HC+LL+D	5.3	0.07	0.02
ES+LL	5.5	0.06	0.02
ES+T	6.1	0.05	0.01
ES+D	6.8	0.03	0.01
ES+LL+D	7.4	0.02	0.01
ES+LL+T	8.0	0.02	0.01
ES+T+D	8.4	0.01	0.00
ES+LL+T+D	9.4	0.01	0.00

All models control for eye size.  $\Delta$ AIC values were calculated relative to the best-fit model.  $l_i$  is relative model likelihood, and  $w_i$  is model probability. ES, eye size; HC, habitat complexity; LL, light level; T, turbidity; D, diet.

significant differences in residual acuity across light level, turbidity or diet categories. Residual acuity was, however, significantly higher in complex environments than in either horizon-dominated ( $P=0.009$ ) or featureless environments ( $P=0.013$ ). This shows that species in complex habitats tend to have even higher acuity than is expected based on their relative eye investment.

Overall, species in complex habitats on average have larger eyes relative to their body size than those in featureless habitats, but these differences are in line with allometric predictions. Residual acuity shows, however, that species in complex habitats exhibit even higher acuity than their larger eyes relative to body size would predict.

## DISCUSSION

### Acuity, light level and turbidity

This is the largest examination to date of how acuity relates to morphology, environment and ecology across ray-finned fish species. We found a positive correlation between acuity and eye size, indicating that as eye size increases, acuity tends to increase. This finding is in line with predictions based on the optics of camera-type eyes, namely, that larger lenses have longer focal lengths and thus smaller inter-receptor angles, leading to increased acuity (Kirschfeld, 1976; Land and Nilsson, 2002; Walls, 1942). Here, we found a weaker, but significant, positive relationship between acuity and body size, which agrees with previous findings relating body size to acuity in birds (Kiltie, 2000) and mammals (Kiltie, 2000; Veilleux and Kirk, 2014); importantly, however, the correlation between acuity and body size in our dataset clearly arises via the correlation between body size and eye size.

Although morphological features explained greater than 50% of the variation we found in acuity, it is likely that factors relating to a species' ecology or environment also play an important role (Hughes, 1977; Land and Nilsson, 2002; Walls, 1942). We found support for the hypothesis that habitat type correlates with acuity, but not with light level, turbidity or diet type. How can we explain the significant differences we found in raw acuity across light level and turbidity categories, but not in residual acuity? Examining Table 3 shows that trends in body and eye size across both light level and turbidity categories exactly mirror those in raw acuity; this implies that the significantly lower raw acuity seen in the darkest and

murkiest environments is due to species having significantly smaller eyes and bodies in those environments. Indeed, this conclusion is supported by the fact that species in dark environments had the lowest relative eye investment of any light level category. For turbidity, we saw a downward trend in relative eye investment from clear to murky habitats; the higher relative eye investment in murky habitats is likely due to extremely small sample sizes in that category, which gave that comparison very low power.

The smaller body sizes we found in both turbid and dark habitats are likely due to real differences between habitats, rather than a sampling bias among acuity studies. First, studies of fish communities in lakes have found that water turbidity is a significant predictor of fish community structure, with larger piscivorous fishes tending to inhabit clear waters and smaller fishes inhabiting turbid waters (e.g. Rodríguez and Lewis, 1997). Second, there is evidence that fish size decreases with increases in depth (Rex et al., 2006; Thiel, 1975), although these trends may differ among different functional groups (Collins et al., 2005).

With regard to light level, it has been hypothesized that as ambient light decreases, there may be an adaptive advantage to favoring sensitivity over acuity (Land, 1990). We did indeed see a decrease in raw acuity with decreases in light level, though whether this indicates that species were increasing sensitivity in favor of acuity cannot be concluded from our dataset. Interestingly, our results contrast with those of a previous study of acuity across a depth gradient in fishes, which found higher acuity as depth increased, and the sharpest acuity below 1000 m (Warrant, 2000). We believe that the differences between that study and ours are attributable to both (1) having a larger number of species, particularly mesopelagic species, sampled for this study and (2) differences in classifying species as to whether they live above or below the 1000 m depth mark. Depth records for fishes can be extremely broad, sometimes spanning several thousand meters, and thus for most species, categorizing them as living in dark or dim regions can be problematic. In reality, many deep-sea species migrate over a range of depths.

Overall, however, our results for both light level and turbidity imply that future work on acuity should ensure that observed differences are not simply the result of differences in eye and body size.

### Acuity and diet

One surprising result was that neither raw nor residual acuity differed significantly across diet categories. Previous research has shown that predatory species on average have finer acuity than non-predators, in taxa as diverse as reef fish (Collin and Pettigrew, 1988a,b), mammals (Veilleux and Kirk, 2014), insects (Land, 1997) and elasmobranchs (Litherland and Collin, 2008); why then did we find no such trend across ray-finned fishes? First, it may be that the diet categories we defined for this study were either too broad to detect functional differences, or not actually a good match for real fish diets, which can consist of a variety of types of food items. Additionally, it could be that higher acuity is not adaptively beneficial to predatory fish species. Because of attenuation in a medium such as water, a prey item moving away from a predator would likely fade away before it became too small to see (Johnsen, 2012). Thus, increased sensitivity may be more beneficial than increased acuity to predators, especially in the pelagic. Previous studies have compared only predatory versus non-predatory species within a single habitat, such as a coral reef, and our results have shown that habitat has a marked impact on acuity. Lastly, it should be noted that power analyses (Champely, 2015) show that our sample sizes of species that have sessile diets for which we also had



data on eye size ( $n=3$ ) or body size ( $n=4$ ) were too low to achieve statistical significance (Cohen, 1988).

### Acuity and habitat

Overall, our results point to habitat as the most significant predictor of acuity among our ecological variables. Although in this study we categorize habitats in terms of spatial complexity, there are likely other differences between habitats that may underlie these differences in acuity. For example, we saw significantly higher raw acuity in complex and featureless habitats as compared with horizon-dominated habitats. However, nearly all of the species in our featureless category live in the pelagic realm, while the majority of those in complex habitats are from coral reefs. Therefore, differences in acuity that we observed may be due to the fact that different communities and ecologies, as well as different spatial complexities, exist on coral reefs as compared with the pelagic zone.

Measures of eye size and body size in each habitat category showed that the increased acuity in featureless environments is likely attributable to eyes and bodies in that habitat being larger in an absolute sense, while species in complex habitats had smaller bodies (Table 3), even though relative eye investment did not differ significantly across categories. This is in line with previous studies which have found that, in general, small fish species are particularly abundant on coral reefs as compared with other habitats (Barlow, 1981; Choat and Bellwood, 1991). However, despite the fish in complex habitats being smaller than those in featureless habitats, we observed increased residual acuity in complex habitats, indicating that fish in complex habitats have higher acuity than would be expected even on top of their slightly larger eyes relative to body size.

If spatial complexity is the most salient habitat feature for acuity, our results could lend support to the ‘terrain theory’ (Hughes, 1977), which states that species inhabiting more spatially complex habitats require higher acuity to perform complex navigation or object recognition tasks. Several previous studies have also found sharper acuity in organisms that live in more complex habitats, for example, among reef fishes (Collin and Pettigrew, 1988a,b), cichlids (Dobberfuhl et al., 2005) and elasmobranchs (Litherland and Collin, 2008). Alternatively, there may be other differences in ecology between habitats that drive variation in acuity. For example, the higher number and density of species on coral reefs may lead to greater selection for the ability to identify members of the same species using color patterns, which may require higher acuity. Evidence for the importance of color patterns in species recognition has been found in communities of closely related, sympatric cichlids (Couldridge and Alexander, 2002). Overall, our results underscore the influence of habitat on acuity. Future comparative studies of carefully selected groups of species could help illuminate which aspects of an organism’s habitat are the most relevant to differences in acuity.

### Methods used to study acuity

One limitation of this study is that acuity is measured in several, not necessarily equivalent, ways. Here, we attempted to avoid the potentially confounding effects of measurement method by using data derived using either photoreceptor density or peak RGC density, and by showing that in our dataset, the relationship between acuity and eye size is statistically the same, regardless of whether photoreceptor density or RGC density was used to estimate acuity.

Lastly, acuity is not static, and can change over short time spans via spatial summation, in which multiple photoreceptors or RGCs pool together to collect light over a larger area (Warrant, 1999). Spatial summation is particularly common in dim environments, where organisms have a greater need for sensitivity to light (Cronin

et al., 2014). This results in eyes that are more sensitive, but also lowers acuity. The inability of these methods to account for spatial summation that may occur past RGCs in the visual processing pathway, as well as diffraction, aberration, optical imperfections and higher-order visual processing, means that both of these anatomical methods likely overestimate acuity compared with a behavioral measure. Conversely, behavioral measures likely underestimate acuity, as the strength of the optomotor response falls off right at the limit of an animal’s acuity. Continued study may allow us to construct relationships that could roughly translate how measurements taken using different methods equate to one another.

### Conclusions

It has been hypothesized that one factor influencing the evolution of increased eye size is selection for greater acuity. Support for this hypothesis has previously been found in animals that move quickly; in particular, Leuckert’s law states that animals capable of achieving high angular speeds (i.e. optic flow) require high visual acuity and thus large eyes to avoid collisions. Support for Leuckert’s law has been found in birds (Brooke et al., 1999; Hall and Heesy, 2011; Walls, 1942) and mammals (Heard-Booth and Kirk, 2012). Additionally, among mammals, several nocturnal taxa have been suggested to possess large eyes in order to improve sensitivity, without sacrificing acuity [e.g. nocturnal haplorhine primates (Kay and Christopher Kirk, 2000)]. In fishes, the large eyes of the blue marlin, *Makaira nigricans*, and the rock bass, *Ambloplites rupestris*, may be adapted for increased sensitivity, presumably without sacrificing resolving power (Fritsches et al., 2003; Williamson and Keast, 1988).

Larger eyes can, in the simplest terms, result in either higher acuity or higher sensitivity for an organism. Here, we found that larger eye size is associated with higher visual acuity, though variation in this relationship could be due to the fact that some species increase their eye size to obtain higher sensitivity, rather than higher acuity. Additionally, we found that, on average, species in more spatially complex habitats have higher acuity than species in other habitats, even after controlling for larger relative eye size. This supports the prediction that species in certain environments require higher resolving power than do species in less spatially complex habitats.

Overall, this study shows that acuity in fishes is affected by eye size and the habitat in which a given species lives. Additionally, visual acuity is highly variable across species, even within ray-finned fishes, and thus may represent an aspect of visual physiology that is flexible and adaptable to visual environments and visually guided behaviors.

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### Competing interests

The authors declare no competing or financial interests.

### Author contributions

E.M.C. performed the literature review, analyzed the data, and wrote the manuscript. S.J. provided intellectual input, devised categories for ecological analyses, provided images that modeled visual perception by reef fish, and revised the manuscript. T.T.S. confirmed category designations for all species of fish in this study and revised the manuscript. All authors reviewed and corrected the manuscript.

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## Supplementary information

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