

# Ecological and Morphological Correlates of Visual Acuity in Birds

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## Abstract

Birds use their visual systems for important tasks, such as foraging and predator detection, that require them to resolve an image. However, visual acuity (the ability to perceive spatial detail) varies by two orders of magnitude across birds. Prior studies indicate that eye size and aspects of a species' ecology may drive variation in acuity, but these studies have been restricted to small numbers of species. We used a literature review to gather data on acuity measured either behaviorally or anatomically for 94 species from 38 families. We then examined how acuity varies in relation to (1) eye size, (2) habitat spatial complexity, (3) habitat light level, (4) diet composition, (5) prey mobility, and (6) foraging mode. A phylogenetically-controlled model including all of the above factors as predictors indicated that eye size and foraging mode are significant predictors of acuity. Examining each ecological variable in turn revealed that acuity is higher in species whose diet comprises vertebrates or scavenged food and whose foraging modes require resolving prey from farther away. Additionally, species that live in spatially-complex, vegetative habitats have lower acuity than expected for their eye sizes. Together, our results suggest that the need to detect important objects from far away—such as predators for species that live in open habitats, and food items for species that forage on vertebrate and scavenged prey—has likely been a key driver of higher acuity in some species, helping to elucidate how visual capabilities may be adapted to an animal's visual needs.

**Keywords:** Spatial resolution, light level, habitat complexity, diet, visual ecology

## Introduction

Visual acuity, the ability to resolve static spatial detail, dictates what details can and cannot be resolved in a given scene. Acuity is therefore an important visual parameter in a wide range of visual tasks, such as object detection and recognition, foraging, navigation, and communication (Cronin et al., 2014). Acuity is also highly variable across species, varying over at least four orders of magnitude (Caves et al., 2018). Within an eye, areas of higher and lower acuity (such as foveae in camera eyes and acute zones in compound eyes) can be adapted to either the structure of the environment or to specific tasks (see (Cronin et al., 2014; Hughes, 1977; Land and Nilsson, 2002). Across species, however, few studies have investigated how acuity relates to a species' ecology or environment (but see (Veilleux and Kirk, 2014) for mammals, (Caves et al., 2017; Caves et al., 2023) for fish, and (Land, 1997) for insects). In this study, we examined correlations between acuity and several aspects of ecology in birds (Aves). Birds are an excellent study system for comparative work on acuity for a variety of reasons. First, they are highly visual animals: in the majority of extant bird species, vision is the primary sense (Martin, 2017). Second, birds occupy a diverse range of visual habitats and engage in a variety of visually-guided behaviors. Third, acuity varies thirty-fold among birds, and the highest known acuities in any species are found in raptorial birds (Caves et al., 2018; Land and Nilsson, 2002). Despite this, we have only a limited understanding of the evolutionary pressures that underlie variation in acuity in birds, or how acuity varies with avian species' morphology and ecology.

Based on the optical properties of eyes, the primary factor that correlates with variation in acuity is eye size. One aspect of an eye's morphology that dictates acuity is the angular width of the region that is viewed by each photoreceptor, which can be thought of as the sampling stations of the eye, and which mediate the first stage in the visual processing pathway. A photoreceptor's angular width is given by the diameter of the photoreceptor divided by the focal length of the eye; thus, longer focal lengths translate to smaller angular resolution, which imparts sharper vision (higher acuity) (McIlwain, 1996). Photoreceptors that collect light over a smaller area, however, suffer from reduced sensitivity (Land and Nilsson, 2002), leading to a fundamental tradeoff between acuity and sensitivity. One way to overcome this tradeoff, i.e. to increase either acuity or sensitivity without reducing the other, is to increase the eye's focal length, which can be accomplished by increasing the size of the eye. In line with this, acuity has been shown to positively correlate with eye size across highly diverse taxa with both camera-type and

compound eyes (Caves et al., 2018), as well as within specific groups, including fish (Caves et al., 2017), mammals (Veilleux and Kirk, 2014), and birds (Kiltie, 2000).

Beyond eye size, increasing evidence in vertebrates suggests that visual acuity is driven by the density or receptive field size of retinal ganglion cells (RGCs), rather than photoreceptor density. Although the photoreceptors (rods and cones) are the cells that detect light in vertebrates, and thus as the eye's sampling stations their density carries spatial information, retinal ganglion cells (RGCs) process visual information further along in the processing pathway than do photoreceptors. Thus, as an anatomical measure, the density of RGC's may provide more appropriate indicators of acuity than does photoreceptor density (Devries and Baylor, 1997; Enroth-Cugell and Robson, 1966; Lee and Stevens, 2007). Thus, many studies that map RGC densities across an eye use the highest density of RGC's present in the eye to calculate a species' acuity.

Of course, species live in a variety of different environments and have different ecologies, and thus face different perceptual challenges, some of which require higher acuity while others will not. One particularly relevant set of perceptual challenges when considering acuity are object detection and resolution. Acuity gives an indication of the distance from which an individual can resolve an object with enough visual information to make a behavioral decision (Kiltie, 2000), so object detection, in particular the need to detect items at large distances, is hypothesized to drive higher acuity (Fernández-Juricic, 2012; Martin, 2017). Support for this comes from insectivorous bats, in which acuity varies with foraging technique; specifically, gleaning species that use vision alone to detect prey have higher acuity than aerial-hawking species that combine vision with ultrasonic echolocation (Eklöf et al., 2014). In birds, some species' foraging methods require visual detection at great distances (for example, a wedge-tailed eagle *Aquila audax* searching for rodent prey while soaring high above the ground, (Billerman et al., 2022)), while others require visual detection at close range (like a house sparrow *Passer domesticus* scratching and pecking in the dirt (Billerman et al., 2022)), and still others rely more on other senses than on vision to forage (such as a brown kiwi *Apteryx australis* foraging in the leaf litter largely based on its olfactory senses (Billerman et al., 2022)). Here, we hypothesized that species that use foraging techniques that require localizing food from further away would have higher acuity than those that search for food from closer distances.

Another perceptual challenge that might relate to visual acuity is object localization. Different species forage for food items that vary in the visual demands required to localize them, from tiny seeds to larger fruits to large vertebrates and carrion, and from immobile (e.g., fruits and flowers) to highly mobile (e.g., invertebrates). Specializing on different food types has been shown to be correlated with acuity, for example in mammals (Veilleux and Kirk, 2014), reef fish (Collin and Pettigrew, 1988a; Collin and Pettigrew, 1988b), insects (Land, 1997), and elasmobranchs (Litherland and Collin, 2008), in which predatory species, which tend to forage on more mobile prey that is more difficult to localize, on average have higher acuity than non-predatory species. Thus, we hypothesized that species that forage for different types of food would have different acuities.

Several aspects of an organism's habitat can also relate to acuity. Because of the resolution-sensitivity trade-off described above, the light level in which a species operates is hypothesized to vary with its visual acuity. Specifically, for a given eye size, species that live in darker habitats or are active at lower light levels (e.g., are nocturnal) are hypothesized to have increased need for sensitivity, and thus lower acuity, than those that live in lighter habitats (Land, 1990). Habitat spatial complexity is also predicted to have an influence on visual acuity (as it does, for example, in ray-finned fishes (Caves et al., 2017)). In birds in particular, one hypothesis is that species in open habitats (such as an ostrich on a grassland or a shearwater soaring over the open ocean) should have higher acuities than species in denser, more vegetative habitats, given that important visual stimuli, for example aerial predators, are visible from greater distances in open habitats (Fernández-Juricic, 2012). Using eye size as a proxy for acuity, one study of 97 species found indirect support for this hypothesis, in that birds in open habitats had larger eyes than those in complex habitats (Møller and Erritzøe, 2010). However, a larger study of eye size in one third of terrestrial avian species found the opposite, that species in forested and understory habitats have larger eyes (Ausprey, 2021). Thus, support for this hypothesis is currently mixed. One reason for this may be that larger eyes do not necessarily confer higher acuity, as they can be an adaptation for increased sensitivity. Thus, studies that use direct measures of acuity, rather than eye size as a proxy for acuity, can aid our understanding of how acuity varies with habitat.

Here, we synthesized available literature on visual acuity in birds and then examined relationships between acuity and the factors that we discuss above. First, we calculated the relationship between acuity and eye size, represented by eye axial length, which are known to be

correlated (e.g. (Kiltie, 2000)), but here using the largest sample of birds to date. The purpose of re-examining a well-established relationship was to improve our understanding of how acuity and eye size scale in birds, which may facilitate future comparisons to groups such as mammals (Veilleux and Kirk, 2014) and fish (Caves et al., 2017), and to help researchers who lack behavioral or anatomical data on acuity in their study species, but who have eye size data, to easily extrapolate an acuity value. We then examined how acuity relates to five ecological variables relating to diet (specifically diet composition, prey mobility, and foraging mode), the light level in which a species primarily operates, and habitat.

## **Methods**

### *Comparative database of acuity*

We assembled a database of visual acuity in birds using published data; for each species, we recorded the highest reported acuity value, which in the vast majority of studies was the mean of the highest acuities measured across individuals. We then restricted the database to include only data measured using behavioral assays [optomotor assays, see (Caves et al., 2020) or conditioned responses] or anatomical methods (specifically studies that estimate acuity from the highest density of retinal ganglion cells, RGCs, and a measure or assumption of the eye's focal length). We did not include in our database acuity measurements collected using electrophysiological methods or lens optics.

Both anatomical and behavioral methods of measuring acuity have advantages and disadvantages. Unlike anatomical methods, behavioral methods are able to account for diffraction and other optical imperfections, spatial and temporal summation, and higher-order visual processing, and thus some have argued that behavioral measures are a better indicator of an eye's true acuity than those derived anatomically (Arrese et al., 1999). Additionally, behavioral experiments can be carried out at different light levels, to account for the fact that acuity varies with the ambient illumination, whereas RGC-based estimates refer only to resolution at high light levels. However, factors such as diffraction and lens aberrations, which can affect acuity, are not likely to vary significantly at least across diurnal bird species, since diurnal species tend to have similar eye shapes and also are not vision-limited by their sensitivity to ambient light (Fernández-Juricic, 2012). Behavioral measures can be confounded by factors

such as variation in motivation or acclimation to experimental environment. Additionally, in species with more than one area of specialization, as can occur in birds which have two foveas (e.g. (Fite and Rosenfield-Wessels, 1975)), behavioral assays may require an animal to fixate on a stimulus using an area of the visual field that does not correspond to the area of peak RGC density, resulting in an inaccurate estimate of acuity (see (Pettigrew et al., 1988)).

To determine whether it would be appropriate to combine acuity data derived from RGCs and behavioral assays for analyses, we performed two analyses. First, we compiled measures of acuity in 28 vertebrate species with camera eyes (the type of eye found in birds) in which acuity has been measured using both methods (Table S2). We found that behaviorally-derived and RGC-derived acuity measures from the same species are highly correlated ( $p < 0.0001$ ; Figure S1) in a phylogenetically-corrected model using a tree from timetree.org (Kumar et al., 2022). However, this analysis included only five species of birds; thus, to address this issue in a larger dataset of bird acuities, we created a PGLS regression in which acuity was the response variable and eye size and method of acuity measurement, and their interaction, were predictors. A phylogenetic ANCOVA (see below for details on the phylogenetic tree used) showed that, because the interaction term between eye size and method of measurement was not significant ( $p = 0.39$ ), the slope of the regression line between acuity and eye size is similar for both methods of measurement. Thus, we concluded that it was appropriate to include both RGC-derived and behaviorally-derived measures of acuity in our database for analyses.

For five species, the database included acuity estimates from both behavioral assays and RGC density (with the average difference between the behaviorally- and RGC-derived estimates being only 0.84 cpd). Given the very small differences in acuity from the two methods, and the analyses above regarding combining behavioral and RGC data together, we preferentially used estimates from RGC density in analyses if both behavioral and RGC-based measures of acuity existed. If multiple studies had used the same method to measure acuity in a given species, we used the acuity estimate from the most recent study. Species were only included in the database for analysis if we could locate both eye axial diameter and body mass data for that species (see below), resulting in a sample size of 94 species (Table S1).

Here, we refer to acuity throughout in units of cycles per degree (cpd), which is the number of pairs of black and white stripes an organism can discriminate within a single degree of visual angle. Higher values in cpd indicate ability to resolve finer spatial details, and thus higher

acuity. In some of the original literature we surveyed, acuity was reported in alternative units (such as minutes of arc or degrees); prior to inclusion in our database, we translated these values to cpd.

#### *Phylogenetic relatedness and Phylogenetic Signal ( $\lambda$ )*

To account for phylogenetic relatedness between species, we used a published phylogeny (Burleigh et al., 2015) of 6714 avian taxa which used a 29-locus supermatrix to build a phylogeny with branch lengths. The larger tree was trimmed to include only the 94 species in our acuity database, maintaining branch length information in our sub-tree. The degree of phylogenetic signal in acuity was estimated by calculating Pagel's  $\lambda$  (Freckleton et al., 2002; Pagel, 1999) using the “phylosig” function from the *phytools* package (Revell, 2012). Pagel's  $\lambda$  ranges from 0 (no covariance between trait and phylogenetic structure) and 1 (complete covariance between trait and phylogenetic structure). A likelihood ratio test was used to determine the significance of Pagel's  $\lambda$  against the null hypothesis that  $\lambda = 0$ .

#### *Eye size and body mass*

Where possible, we recorded eye axial length (hereafter ‘eye size’) in our database as reported in the original citation; this yielded data on eye size in 73 species. For the remainder, we located published eye size values from a variety of sources (see Table S1), to maximize the number of species for which we had analyzable data. It was uncommon for studies to report the body masses of the individuals used in acuity measurements; therefore, to obtain comparable body mass data for all of the species in our database, we used values from the CRC Handbook of Avian Body Masses (Dunning Jr, 2007).

#### *Classifying Species According to Ecology*

We examined the relationship between visual acuity and several aspects of a species' ecology. Given that many bird species can inhabit a wide array of habitat types, or make use of a diversity of food sources, it can be complex to categorize birds by factors like diet and habitat; thus, our categories were relatively broad.

## Habitat

We examined how acuity relates to two aspects of habitat: spatial complexity and light level. To relate acuity to habitat spatial complexity, we used the Elton Traits database (Wilman et al., 2014), which details for all extant bird species the percentage of time spent foraging in eight different habitat types. First, we summed certain percentages to calculate the percent of time spent in spatially complex habitats (understory and mid-high vegetative habitats); open habitats (aerial and open water habitats); and horizon-dominated habitats (ground, water's surface, and at or just above the canopy). The distribution of these percentages revealed that species roughly broke into two broad classes: those that spent at least 70% of their time in one habitat type (complex, horizon-dominated, or open), and those that did not have any clear designation as to a primary habitat type. Therefore, we assigned any species that spends greater than 70% of its time in a given habitat class to that class; species that did not have a score greater than 70% for a given category were labelled as habitat generalists.

To relate habitat light level to acuity, we classified species using habitat descriptions provided on the Cornell Lab of Ornithology Birds of the World database (Billerman et al., 2022). Species were classed as operating in “low,” “medium,” or “high” light environments based upon their habitat and their activity pattern. Habitats with low light level included forest understories, mangroves, dense shrubland or heathland; species were also included in this category if it was noted that they favor dense habitats. High light level habitats included deserts, grasslands, savannah, farmland, steppe, meadow, pelagic oceans, open Antarctic islands, flat beaches or dunes, or mudflats. Medium light level habitats included forest edge, secondary forest, or scrub forest; species were also included in this category if they were noted as favoring “semi-open” habitats. Any species that was identified as primarily nocturnal in Wilman et al. (2014), or forages at pelagic depths great enough to be equivalent to nocturnal habitat (Martin, 2017), was classified as inhabiting “low” light habitat; this included all of the owls in our dataset, as well as the King penguin *Aptenodytes patagonicus* and Manx shearwater *Puffinus puffinus*.

## Diet and Foraging

To understand how acuity relates to diet, we first used the Elton traits database (Wilman et al., 2014), which assigns species to a “dominant” diet category based on the summed scores from ten constituent diet categories. These categories, which we related to acuity, were Plants



(including plants, seeds, fruits, and nectar), Invertebrates, and Vertebrates (including scavenging). Following the designations in the Elton traits database, any species which had a score of less than 50% for all of the prior categories was classified as an Omnivore. Species were also classified by whether their primary prey type was mobile or immobile prey. Mobile prey included vertebrates and invertebrates (outside of scavenging); immobile prey included plant matter of all kinds, such as fruits, seeds, nectar, flowers, and fruits, as well as scavenged prey.

Lastly, we classified species by foraging mode using information on the Cornell Lab of Ornithology Birds of the World database (Billerman et al., 2022). Specifically, species were classified as using foraging modes that involve resolving and targeting prey from a distance (far-sighted) versus from close up (near-sighted) foraging maneuvers. Following Ausprey (2021), distance maneuvers included, e.g., aerial chase, pursuit diving, scavenging, sallying, while close-up foraging maneuvers included, e.g., gleaning, pecking, dabbling, kicking/scratching, and probing.

### *Statistical Analyses*

To statistically analyze how acuity is related to the suite of ecological variables described above, we used a Phylogenetic Generalized Least Squares (PGLS) model run using the `gls` function from *ape* (Paradis and Schliep, 2019) and a variance-covariance structure based on a Brownian model of evolution. We first used the `pairs.panels` function of the *psych* package (Revelle, 2019) to examine whether any of our predictors—both continuous and categorical—were highly correlated with one another ( $\text{corr} > 0.7$ ) and thus should be dropped, but none were. We then built a series of PGLS models that included acuity as the response variable and every combination of eye size and all of the ecological variables we explored as predictors. We ranked models based on the Akaike Information Criterion [AIC (Akaike, 1974; Burnham and Anderson, 2002)], and then assigned  $\Delta\text{AIC}$  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),  $\Delta\text{AIC}$  values were used to calculate relative likelihoods for each model  $i$  within a set using the formula  $l_i = \exp[-(1/2) \Delta_i]$ . 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).

We then explored the results of the full model by examining each of the categorical ecological variables in turn. In addition to acuity, and following (Caves et al., 2017), we explored two additional metrics that give an idea of the importance of vision, and of spatial resolving power, for a given species. First, we calculated “relative eye size” by extracting the residuals from a PGLS model of body mass versus eye size, which can be interpreted as a single measure for each species of whether their eyes are larger or smaller than expected based on their body mass. Species with a positive “relative eye size” have larger eyes than expected for their body mass, whereas species with a negative value have smaller eyes than expected for their body mass. We then ran a PGLS regression on acuity versus relative eye size, and extracted the residuals from that relationship. These residuals, which we term “residual acuity” show whether a given species has even higher or lower acuity than would be expected based on its investment in eye size; in essence, these residuals represent the portion of variation in acuity that is unexplained by variation in relative eye size, and help us to examine acuity without the confounding effects of eye size.

We used *emmeans* (Lenth et al., 2019) to calculate estimated marginal mean acuity, relative eye size, and residual acuity in each ecological category. We then used phylogenetic ANOVA (*phytools*, (Revell, 2012) with post-hoc tests corrected for multiple testing (either  $n=2$ ,  $n=3$ , or  $n=4$  comparisons depending on the ecological category) using the Holm-Bonferroni correction (Holm, 1979) to examine whether differences between ecological categories were statistically significant when controlling for phylogeny.

All analyses were run using R version 4.0.3 (R Development Core Team, 2023). Prior to statistical analyses, acuity, eye size, and body mass were log-transformed to improve the normality of the residuals. Using Cook’s distance (Cook, 1977), three species (the wedge-tailed eagle *Aquila audax*, the Egyptian vulture *Neophron percnopterus*, and the barn owl *Tyto alba*) were found to be statistical outliers based on the relationship between acuity and eye size and so were excluded from further analyses. We ran all of the above analyses first only a complete dataset (including both behavioral and RGC-derived acuity), and secondarily on a dataset comprising only RGC data, though due to low sample sizes we lacked statistical power to run our analyses on a behavior-only dataset.

## Results

### *Acuity across birds*

Using the complete database of published acuity values from 94 species, acuity was highly variable across birds, with the lowest acuity (4.6 cpd in the Anna's Hummingbird *Calypte anna*) being two orders of magnitude lower than the highest acuity (143 cpd in the wedge-tailed eagle *Aquila audax*). Mean acuity ( $\pm$  standard deviation) was  $15.8 \pm 20.8$  cpd. Pagel's  $\lambda$  (the degree of phylogenetic signal) was estimated to be 0.99, which a likelihood ratio test showed was significantly different from  $\lambda = 0$  ( $p < 0.0001$ ). Thus, there was significant phylogenetic signal in acuity, indicating that shared phylogenetic history contributes strongly to trends in acuity across birds (Figure 1). After excluding statistical outliers, analyses were run on 91 species ( $n = 71$  species with RGC-derived acuity measures and  $n = 20$  with behaviorally-derived acuity measures) from 38 avian families and 17 avian orders.

### *Acuity, Eye Size, and Body Size*

As expected, PGLS regressions revealed significant, positive relationships between acuity and both eye size (coef.  $\pm$  s.e. =  $0.81 \pm 0.15$ ,  $t_{91} = 5.51$ ,  $R^2 = 0.56$ ,  $p < 0.0001$ ; Figure 2A) and body mass (coef.  $\pm$  s.e. =  $0.16 \pm 0.04$ ,  $t_{91} = 4.10$ ,  $R^2 = 0.46$ ,  $p = 0.0001$ ; Figure 2B). Thus, on average as eye size or body mass increases, acuity increases. However, extracting the residuals from the PGLS regression of acuity on eye size and examining the relationship between those residuals and body mass yielded no significant relationship (coef.  $\pm$  s.e. =  $-0.15 \pm 0.30$ ,  $t_{91} = -0.51$ ,  $p = 0.62$ ). Together these results show that eye size is a strong predictor of acuity, and that the observed correlation between acuity and body mass results from the correlation between eye size and body mass, which themselves are significantly correlated (coef.  $\pm$  s.e. =  $0.23 \pm 0.01$ ,  $t_{91} = 17.7$ ,  $R^2 = 0.93$ ,  $p < 0.0001$ ; Figure 2C). There was also a positive, significant relationship between relative eye size and acuity (coef.  $\pm$  s.e. =  $1.10 \pm 0.34$ ,  $t_{91} = 3.24$ ,  $R^2 = 0.42$ ,  $p = 0.002$ ; Figure 2D), indicating that species with higher relative eye size (larger eyes than expected based on their body size), on average exhibit higher acuity.

When considering acuity derived from RGC density and acuity derived from behavior separately, relationships between acuity and eye size, body size, and relative eye size were always in the same direction as for the complete dataset, but were only significant for the RGC-derived dataset (acuity and eye size: coef.  $\pm$  s.e. =  $0.63 \pm 0.09$ ,  $t_{71} = 7.08$ ,  $p < 0.0001$ ; acuity and

body mass: coef.  $\pm$  s.e.=  $0.14 \pm 0.02$ ,  $t_{71}=5.54$ ,  $p<0.0001$ ; acuity and relative eye size: coef.  $\pm$  s.e.=  $0.74 \pm 0.25$ ,  $t_{71}=2.93$ ,  $p=0.005$ ), and not the behavioral dataset (acuity and eye size: coef.  $\pm$  s.e.=  $0.93 \pm 0.60$ ,  $t_{20}=1.54$ ,  $p=0.14$ ; acuity and body mass: coef.  $\pm$  s.e.=  $0.15 \pm 0.16$ ,  $t_{20}=0.95$ ,  $p=0.35$ ; acuity and relative eye size: coef.  $\pm$  s.e.=  $1.42 \pm 1.15$ ,  $t_{20}=1.23$ ,  $p=0.24$ ). However, the lack of significance in the behavioral dataset is likely due to the low sample size ( $n=20$  species), since phylogenetic ANCOVAs showed no significant differences in the slope of the regression line between acuity and eye size ( $p=0.39$ ), acuity and body size ( $p=0.49$ ), or acuity and relative eye size ( $p=0.06$ ) for the behavioral versus RGC datasets. The relationship between eye and body size was significant for the behavior-only and RGC-only datasets (behavior only: coef.  $\pm$  s.e.=  $0.22 \pm 0.03$ ,  $t_{20}=6.71$ ,  $p<0.0001$ ; RGC only: coef.  $\pm$  s.e.=  $0.23 \pm 0.01$ ,  $t_{71}=17.07$ ,  $p<0.0001$ ).

### *Relationship between acuity and ecology*

To examine the effects of all of our ecological predictors and eye size on acuity together, we first constructed phylogenetically-corrected PGLS models that included all combinations of our ecological variables (habitat spatial complexity, light level, diet category, prey mobility, and foraging mode) and eye size as predictor variables and acuity as the response variable, and used AIC to rank the models based on fit. Then, to further examine acuity across ecological categories, and why only certain ecological factors significantly predicted acuity in the full model above, we used phylogenetic ANOVAs to examine how raw acuity, relative eye size, and residual acuity vary across ecological categories while controlling for species relatedness (Figure 3). We also performed the same analyses using a dataset comprising only acuity data measured using RGC density (Figure S2), though we lacked statistical power to perform the analyses on a dataset with only behavioral data.

Although the best fit model (model weight = 0.67) included only eye size, a model that also included foraging classification as a predictor had a  $\Delta$ AIC value of 1.81 relative to the best fit, and a model weight of 0.27, indicating it has substantial support. No other models had a  $\Delta$ AIC value of less than 6 relative to the best-fit model, or had a model weight higher than 0.03. When using a dataset comprising only acuity measured using RGC density, results were similar: the best-fit model still included only eye size, though two other models—one additionally including light level, and one additionally including foraging mode—had  $\Delta$ AIC values of less than 4 relative to the best fit model, and thus some support. When eye size was not included as a

predictor, the best-fit model included only foraging classification (model weight = 0.66), and no other parameters appeared in models with a  $\Delta\text{AIC}$  of less than 6 relative to the best-fit model. The same was found when using a dataset comprising only RGC data.

Raw acuity, eye size, and body mass across all ecological categories are detailed in Table 1; statistical results for pairwise comparisons within each ecological category are detailed in Table 2. We found that raw acuity (Figure 3A) was significantly higher in species whose diets consist of vertebrates and scavenged food than those who eat plant matter ( $p=0.05$ ). Acuity was also higher in species that forage via modes that involve resolving prey from far versus near ( $p=0.04$ ). There were no significant differences in raw acuity across different categories of habitat spatial complexity, habitat light level, or prey mobility (Table 2). The same results were found when considering only RGC data, except that additionally, acuity was significantly higher in species that eat vertebrates than those that eat either invertebrates ( $p=0.01$ ) or are omnivorous ( $p=0.01$ ) (Figure S2).

However, raw acuity does not account for variation in eye size, so we next examined how relative eye size varies across ecological categories (Figure 3B), since relative eye size shows how much larger or smaller a species' eyes are than expected based on their body mass. We found that species in low-light habitats had significantly higher eye investment than those in high-light habitats ( $p=0.009$ ); that species who eat vertebrates and scavenged food have higher eye investment than species that eat plants ( $p=0.02$ ); that species that eat mobile prey have higher relative eye size than those that eat immobile prey ( $p=0.007$ ); and that species who forage from a distance have higher relative eye sizes than those that forage close up ( $p=0.002$ ). There were no significant differences in relative eye size across habitats of different spatial complexity (Table 2). Again, results when examining only RGC-derived acuity were identical, except that additionally we found that species that eat vertebrates or scavenge have significantly higher relative eye size than omnivores ( $p=0.04$ ; Figure S2).

Examining relative eye size as above can give an indication of how important vision is for a species in a given ecological category, but larger eyes than expected could contribute to increased sensitivity to light, rather than acuity. Therefore, to relate relative eye size directly to acuity, we calculated residual acuity for each species by extracting the residuals from a regression between relative eye size and acuity (Figure 3C). There were no significant differences in residual acuity across light level, diet category, prey mobility, or foraging mode

categories (Table 2). We did, however, find that species inhabiting complex environments had lower residual acuity than those in horizon-dominated habitats ( $p=0.04$ ) or aerial and open-water habitats ( $p=0.05$ ). Species inhabiting complex environments also had lower residual acuity than did habitat generalists ( $p=0.04$ ), but not when using an RGC-only dataset ( $p=0.27$ ) (Figure S2).

## Discussion

This is the largest examination to date of how acuity relates to morphology and ecology in birds. Acuity varies over two orders of magnitude within birds, resulting in interspecific differences in which spatial details can be resolved in a given scene (Figure 4). As expected based on previous work, we found a strong, positive correlation between acuity and eye size. This finding is in line with predictions based on the optics of camera-type eyes: in camera-type eyes, the angle between photoreceptors, the inter-receptor angle, can be estimated by dividing the distance between photoreceptors by the focal length of the eye (the distance from the point in the lens through which light pass without being bent, to the image on the retina). Thus, larger eyes, which have longer focal lengths, also have smaller inter-receptor angles, translating to higher acuity. The  $R^2$  value for the phylogenetically-corrected relationship between acuity and eye size, was 0.56, implying that eye size alone explains more than half of the variation in acuity; however, we also found evidence that several aspects of a species' ecology also relate to acuity.

### *Acuity and habitat*

We found that raw acuity did not differ across either habitat spatial complexity or light level categories, though residual acuity was significantly higher in species inhabiting aerial and open-water and horizon-dominated habitats, as well as habitat generalists, than those in complex habitats. How can we explain the presence of significant differences in only residual, but not raw, acuity between different habitat types? The fact that relative eye size also did not differ significantly across habitats shows that species in all three habitat types have eye sizes that are, on average, in line with allometric predictions based on their body masses. However, our residual acuity results suggest that species inhabiting complex environments have even lower acuity than one would expect based on their eye investment.

The spatial complexity of the physical environment has previously been shown to have an impact on differences in acuity across species. For example, habitat complexity is correlated

with acuity in fishes (Caves et al., 2017), including in reef fishes (Collin and Pettigrew, 1988a; Collin and Pettigrew, 1988b), cichlids (Dobberfuhl et al., 2005), and elasmobranchs (Litherland and Collin, 2008). Interestingly, however, in fishes increased habitat spatial complexity is associated with higher acuity, which is opposite of what is seen here in birds, with species living in the most spatially complex (vegetative) habitats having the lowest acuity. These differences may be explained by the fact that in aquatic environments, sighting distance is constrained by the optics of the medium (water) long before it is constrained by acuity (Johnsen, 2012), whereas in terrestrial environments, acuity can be a primary factor influencing the distance at which objects, such as predators, are detected (Tisdale and Fernández-Juricic, 2009). For species that forage in vegetative habitats, predators may only be visible from relatively short distances. By contrast, species that forage on the ground (which here we term “horizon-dominated”) might be predicted to have higher acuity, in order to resolve predators approaching at a distance.

Regarding light level, we found no significant differences in either raw or residual acuity across levels. Although we saw that species in low-light habitats have significantly higher relative eye size than those in high-light habitats, the fact that residual acuity did not differ suggests that any increased investment in eye size likely doesn't serve to increase the eye's acuity. A recent study of eye size across more than 2700 species of birds found that species that live in dark understory and forest habitats (which here were classified as closed environments) had larger eyes than species that lived in more open habitats (Ausprey, 2021); however, larger eye size does not necessarily translate to higher acuity. Our results, which use direct measures of acuity rather than eye size as a proxy, suggest that particularly in relatively dark environments like forests, larger eyes may be specialized for increased sensitivity to light, rather than for higher acuity.

Another factor besides that dictates the light level in which a species operates is activity time, i.e. whether a species is nocturnal, diurnal, or crepuscular. Species that are nocturnal are predicted to maximize sensitivity over acuity, and thus to have lower acuity than diurnal birds with similarly-sized eyes. In our dataset, the only nocturnal species for which we also had acuity data were seven species of owls, meaning we lacked statistical power to compare acuity in nocturnal versus diurnal birds. An informal comparison, however, showed that average acuity is lower in owls (21.9cpd) than diurnal orders with similar eye sizes and foraging styles (i.e. visually from a distance), including hawks and eagles (Accipitriformes; 24.9cpd) and falcons

(Falconiformes; 47.4 cpd), lending support to the hypothesis that activity time may also shape acuity through trade-offs with sensitivity.

### *Acuity and Diet*

We found higher raw acuity in species that eat vertebrates and which scavenge, compared to those that eat plant matter. We also found that relative eye size was higher in species that eat vertebrates and scavenge compared to those that eat plants. Species that eat vertebrates, or which scavenge for prey, thus have higher acuity, and also larger eyes than expected for their body sizes, but beyond that they do not have higher acuity than predicted based on the size of their relatively large eyes alone. Raw acuity was also higher in species whose foraging maneuvers involve resolving prey from a distance (as species that scavenge and perhaps those who eat vertebrates likely do) than those whose foraging strategies involve resolving prey from close up. Although the most familiar example of this might be the raptorial birds who search for vertebrate prey from far above the ground, and whose acuities are some of the highest ever measured in animals, this pattern also held among smaller species. For example, the black phoebe *Sayornis nigricans* (8.9cpd) and least flycatcher *Empidonax minimus* (8.9 cpd), both of whom “sally” or leap from branches to catch flying insects at a distance, have higher acuity than sparrows with similarly-sized eyes that scratch and peck the ground to find food (e.g., White-throated sparrow *Zonotrichia albicollis* 7.7cpd; White-crowned sparrow *Zonotrichia leucophrys* 5.9cpd, House sparrow *Passer domesticus* 4.9cpd; and House finch *Carpodacus mexicanus* 4.7cpd).

Higher acuity in predatory versus non-predatory species has been shown previously in other groups, including reef fish (Collin and Pettigrew, 1988a; Collin and Pettigrew, 1988b), mammals (Veilleux and Kirk, 2014), insects (Land, 1997), and elasmobranchs (Litherland and Collin, 2008), although across a large sample of ray-finned fishes, (Caves et al., 2017) did not find any association between acuity and diet. In birds, our results together suggest that for species that eat vertebrates or scavenged prey, the need to resolve prey objects may be a powerful force shaping visual function, specifically higher acuity, but that rather than being driven by the mobility of prey items, the more important factor may be the need to detect them from a distance (Tyrrell and Fernández-Juricic, 2017). This is supported by previous work on passerine birds that forage on the ground, which has suggested that species consuming food close to their bills may not require higher acuity (Dolan and Fernández-Juricic, 2010).



### *Other factors shaping eyes and acuity*

In our dataset, relative eye size differed across numerous ecological categories, including light level, diet, prey mobility, and foraging mode. Thus, how large or small eyes are relative to bodies varies with many aspects of ecology, underscoring the fact that eyes are of course shaped by a number of selection pressures beyond visual acuity, including to the developmental and energetic costs associated with eyes (Niven and Laughlin, 2008), and their numerous functions beyond resolving an image. For example, species with the highest relative eye sizes were all owls, suggesting that large eyes relative to body size may be most important in nocturnal species that require highly sensitive vision. Some of the lowest relative eye investment was found in the flamingos *Phoenicopterus chilensis* and *P. ruber*, filter feeders which may not need to invest in large eyes given their ability to often forage non-visually (Martin, 2012).

Residual acuity, or how much higher acuity is than expected based on relative eye size, was highest in the brown falcon *Falco berigora*, but the highest residual acuity outside of falcons was found in the corvids. Although we didn't classify corvids as foraging visually from a distance, given that many forage primarily on the ground using a variety of techniques, it is possible that some are indeed relying on distance vision, since they do occasionally soar when foraging (although at lower altitudes than raptors like eagles), highlighting the complexities of assigning species as flexible as corvids to categories. Additionally, they are highly intelligent birds that use vision in social and cognitive tasks. For example, tool use has been shown to shape aspects of the visual system in New Caledonian crows (Troscianko et al., 2012), implying that the perceptual demands of cognitive tasks may potentially represent other, underexplored, drivers of visual acuity.

Eyes must also, among other things, resolve motion, and although visual acuity is no doubt an important component of motion perception, motion detection may not vary in a clear-cut manner with acuity across species. This idea is supported by our finding that whether or not prey are mobile does not seem to be the key factor underlying the higher acuity seen in species that eat vertebrates, since we found no significant differences in raw or residual acuity between species that eat mobile versus immobile prey. This could arise from the fact that detection of mobile prey may be largely a factor of motion perception, rather than visual acuity. Motion perception and visual acuity arise as a result of different retinal processes. While acuity arises from RGC receptive fields, motion vision is attributed to the photoreceptor type known as double

cones (e.g. (Goldsmith and Butler, 2005; von Campenhausen and Kirschfeld, 1998), which send information through to RGCs and trigger a pattern of activity across the optic tectum, resulting in the perception of object motion. Additionally, the visual processes by which individuals locate mobile versus immobile prey may be different. Searching for mobile prey items may rely on visual tracking, whereby attention is focused on an object for a longer period of time, as opposed to visual search, where individuals scan their surroundings using fast saccadic eye or head movements to locate immobile food items like seeds (see (Fernández-Juricic, 2012) for a discussion), though some species likely use both visual tracking and visual search techniques, depending on prey, as in hawks and eagles which search for both live prey and carcasses.

### *Limitations of the study*

One limitation of this study is that acuity can be measured in several ways, each of which has advantages and disadvantages (as discussed in the introduction). Here, however, we attempted to ensure that using acuity data derived in different ways would have minimal impacts on our results by demonstrating that, in species with camera eyes that have had acuity measured using both behavioral and anatomical methods, the two measures are highly correlated.

Another limitation arises from the need to use acuity values as reported in the literature for large, comparative studies such as this one. The majority of studies on acuity report only a single value as representative of a species' acuity, usually the peak acuity measured at any point in the eye. In reality, however, the density of both photoreceptors and ganglion cells, and thus acuity, varies across the retina (e.g. (Querubin et al., 2009), with some species possessing two foveas (e.g. (Fite and Rosenfield-Wessels, 1975), meaning that different portions of the visual field are viewed with different acuities. Additionally, in some species, the topography of photoreceptors and RGCs can differ between the right and left eyes, as occurs in some parrot species (e.g. (Coimbra et al., 2014; Hart et al., 2000; Mitkus et al., 2014), implying that acuity may be lateralized, and differ between eyes. In our literature search, we found only a handful of studies that reported any information about variation in acuity either between eyes or within a single eye. Future studies—especially those which utilize retinal ganglion cell maps, and thus have access to data about variation across the visual field—should report how acuity might vary across the eye.

Lastly, although we include data on more than 90 species in this study, this still represents only a tiny fraction of the total diversity of birds. Thus, studies should continue to measure visual acuity in new species, and analyses such as those conducted here should be revisited, to continue adding to our understanding of the morphological and ecological factors underlying variation in acuity across birds.

## **Conclusions**

A great deal of work on the function of ganglion cell distribution patterns in birds has identified two primary drivers: foraging, specifically the detection of food items, and predator detection (Martin, 2017). Selection on adaptations to increase the efficiency of foraging may be especially strong in birds, since birds are particularly constrained by the need to have both high power output and low body weight (King and King, 1980). To increase foraging efficiency, higher acuity may be favored especially in species that forage on prey that may be far away. Similarly, early detection of predators—spotting them while they are still at a distance—is key to increasing the likelihood of avoiding a predation attempt (Fernández-Juricic, 2012), so selection on vision to achieve this aim is likely strong. Overall, our findings support these ideas, specifically that a key factor influencing visual acuity in birds is the need to detect objects at a distance: our results support the hypothesis that higher acuity will be selected for in species in open habitats, perhaps for predator detection, and species that forage on vertebrates and scavenge, perhaps to detect their prey from a distance.

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## **Data Availability**

All data, codes, phylogenetic trees, and other files necessary to reproduce the analyses in this paper have been uploaded to the Dryad data repository: <https://doi.org/10.5061/dryad.bzkh189g3>

## Literature Cited

- Akaike, H.** (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**, 716–723.
- Arrese, C., Dunlop, S. a, Harman, a M., Braekevelt, C. R., Ross, W. M., Shand, J. and Beazley, L. D.** (1999). Retinal structure and visual acuity in a polyprotodont marsupial, the fat-tailed dunnart (*Sminthopsis crassicaudata*). *Brain, behavior and evolution* **53**, 111–26.
- Ausprey, I. J.** (2021). Adaptations to light contribute to the ecological niches and evolution of the terrestrial avifauna. *Proceedings of the Royal Society B: Biological Sciences* **288**, 20210853.
- Billerman, S., Keeney, B., Rodewald, P. and Schulenberg, T.** (2022). *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA: <https://birdsoftheworld.org/bow/home>.
- Burleigh, J. G., Kimball, R. T. and Braun, E. L.** (2015). Building the avian tree of life using a large-scale, sparse supermatrix. *Molecular Phylogenetics and Evolution* **84**, 53–63.
- Burnham, K. P. and Anderson, D. R.** (2002). *Model selection and multimodel interference: a practical information-theoretic approach*. New York: Springer.
- Burnham, K. P., Anderson, D. R. and Huyvaert, K. P.** (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* **65**, 23–35.
- Caves, E. M. and Johnsen, S.** (2017). AcuityView: An R package for portraying the effects of visual acuity on scenes observed by an animal. *Methods in Ecology and Evolution* **9**, 793–797.
- Caves, E. M., Sutton, T. T. and Johnsen, S.** (2017). Visual acuity in ray-finned fishes correlates with eye size and habitat. *The Journal of Experimental Biology* **220**, 1586–1596.
- Caves, E. M., Brandley, N. C. and Johnsen, S.** (2018). Visual acuity and the evolution of signals. *Trends in Ecology & Evolution* **33**, 358–372.
- Caves, E. M., Troscianko, J. and Kelley, L. A.** (2020). A customizable, low-cost optomotor apparatus: A powerful tool for behaviourally measuring visual capability. *Methods in Ecology and Evolution* **11**, 1319–1324.
- Caves, E. M., Sutton, T. T., Warrant, E. J. and Johnsen, S.** (2023). Measures and models of visual acuity in epipelagic and mesopelagic teleosts and elasmobranchs. *Journal of Comparative Physiology A* 1–20.

- Coimbra, J. P., Collin, S. P. and Hart, N. S.** (2014). Topographic specializations in the retinal ganglion cell layer correlate with lateralized visual behavior, ecology, and evolution in cockatoos. *Journal of Comparative Neurology* **522**, 3363–3385.
- Collin, S. P. and Pettigrew, J. D.** (1988a). Retinal topography in reef teleosts. I. Some species with well-developed areae but poorly-developed streaks. *Brain, Behavior and Evolution* **31**, 269–282.
- Collin, S. P. and Pettigrew, J. D.** (1988b). Retinal topography in reef teleosts II. Some species with prominent horizontal streaks and high-density areae. *Brain, Behavior and Evolution* **31**, 283–295.
- Cook, R. D.** (1977). Detection of influential observation in linear regression. *Technometrics* **19**, 15–18.
- Cronin, T. W., Johnsen, S., Marshall, N. J. and Warrant, E. J.** (2014). *Visual Ecology*. Princeton, NJ: Princeton University Press.
- Devries, S. H. and Baylor, D. a** (1997). Mosaic arrangement of ganglion cell receptive fields in rabbit retina. *Journal of Neurophysiology* **78**, 2048–2060.
- Dobberfuhr, A. P., Ullmann, J. F. P. and Shumway, C. A.** (2005). Visual acuity, environmental complexity, and social organization in African cichlid fishes. *Behavioral Neuroscience* **119**, 1648–1655.
- Dolan, T. and Fernández-Juricic, E.** (2010). Retinal ganglion cell topography of five species of ground-foraging birds. *Brain, Behavior and Evolution* **75**, 111–121.
- Dunning Jr, J. B.** (2007). *CRC handbook of avian body masses*. CRC press.
- Eklöf, J., Šuba, J., Petersons, G. and Rydell, J.** (2014). Visual acuity and eye size in five European bat species in relation to foraging and migration strategies. *Environ Exp Biol* **12**, 01–06.
- Enroth-Cugell, C. and Robson, J. G.** (1966). The contrast sensitivity of retinal ganglion cells of the cat. *Journal of Physiology* **187**, 517–552.
- Fernández-Juricic, E.** (2012). Sensory basis of vigilance behavior in birds: synthesis and future prospects. *Behavioural Processes* **89**, 143–152.
- Fite, K. V. and Rosenfield-Wessels, S.** (1975). A comparative study of deep avian foveas. *Brain, Behavior and Evolution* **12**, 97–115.
- Freckleton, R. P., Harvey, P. H. and Pagel, M.** (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist* **160**, 712–726.

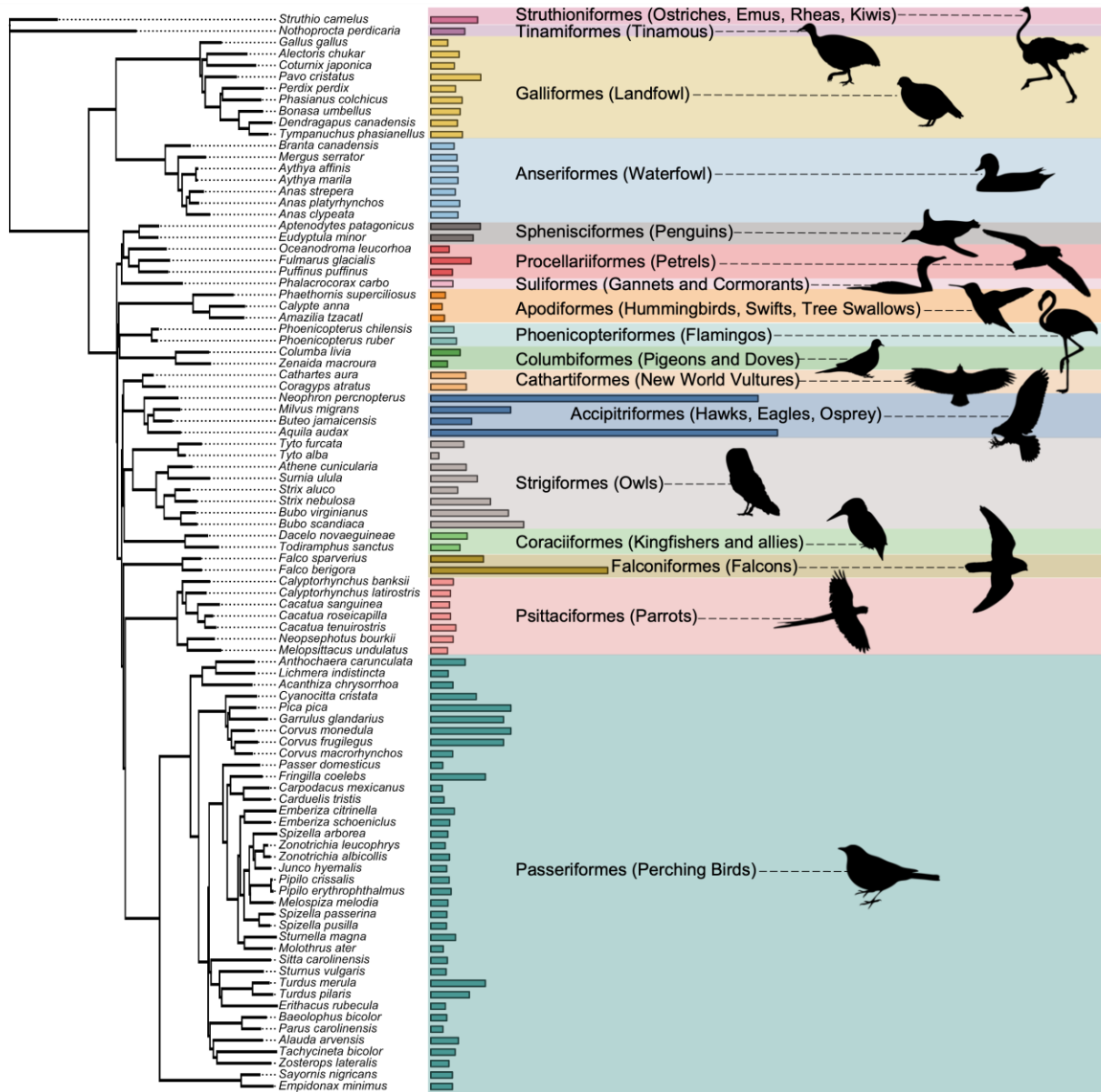
- Goldsmith, T. H. and Butler, B. K.** (2005). Color vision of the budgerigar (*Melopsittacus undulatus*): hue matches, tetrachromacy, and intensity discrimination. *Journal of Comparative Physiology A* **191**, 933–951.
- Hart, N., Partridge, J. and Cuthill, I.** (2000). Retinal asymmetry in birds. *Current Biology* **10**, 115–117.
- Holm, S.** (1979). A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics* 65–70.
- Hughes, A.** (1977). The topography of vision in mammals of contrasting lifestyle: comparative optics and retinal organisation. In *Handbook of Sensory Physiology, Vol. 7* (ed. Crescitelli, F.), pp. 613–756. Berlin: Springer-Verlag.
- Johnsen, S.** (2012). *The Optics of Life*. Princeton, NJ: Princeton University Press.
- Kiltie, R. A.** (2000). Scaling of visual acuity with body size in mammals and birds. *Functional Ecology* **14**, 226–234.
- King, A. and King, D.** (1980). Avian morphology: general principles. In *Form and function in birds*, pp. 10–89. London: Academic Press.
- Kumar, S., Suleski, M., Craig, J. M., Kasprowicz, A. E., Sanderford, M., Li, M., Stecher, G. and Hedges, S. B.** (2022). TimeTree 5: an expanded resource for species divergence times. *Molecular Biology and Evolution* **39**, msac174.
- Land, M. F.** (1990). Optics of the eyes of marine animals. In *Light and life in the sea* (ed. Herring, P. J.), Campbell, A. K.), Whitfield, M.), and Maddock, L.), pp. 149–166. Cambridge, UK: Cambridge University Press.
- Land, M. F.** (1997). Visual acuity in insects. *Annual review of entomology* **42**, 147–177.
- Land, M. F. and Nilsson, D.-E.** (2002). *Animal Eyes*. Oxford, UK: Oxford University Press.
- Lee, S. and Stevens, C. F.** (2007). General design principle for scalable neural circuits in a vertebrate retina. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 12931–12935.
- Lenth, R., Singmann, H., Love, J., Buerkner, P. and Herve, M.** (2019). Package ‘emmeans.’ *The American Statistician* **34**, 216–221.
- Litherland, L. and Collin, S. P.** (2008). Comparative visual function in elasmobranchs: spatial arrangement and ecological correlates of photoreceptor and ganglion cell distributions. *Visual neuroscience* **25**, 549–561.

- Martin, G. R.** (2012). Through birds' eyes: insights into avian sensory ecology. *Journal of Ornithology* **153**, 23–48.
- Martin, G. R.** (2017). *The sensory ecology of birds*. Oxford University Press.
- McIlwain, J. T.** (1996). *An introduction to the biology of vision*. Cambridge University Press.
- Mitkus, M., Chaib, S., Lind, O. and Kelber, A.** (2014). Retinal ganglion cell topography and spatial resolution of two parrot species: Budgerigar (*Melopsittacus undulatus*) and Bourke's parrot (*Neopsephotus bourkii*). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* **200**, 371–384.
- Møller, A. P. and Erritzøe, J.** (2010). Flight distance and eye size in birds. *Ethology* **116**, 458–465.
- Niven, J. E. and Laughlin, S. B.** (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *The Journal of Experimental Biology* **211**, 1792–1804.
- Pagel, M.** (1999). Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884.
- Paradis, E. and Schliep, K.** (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528.
- Pettigrew, J. D., Dreher, B., Hopkins, C. S., McCall, M. J. and Brown, M.** (1988). Peak density and distribution of ganglion cells in the retinae of Microchiropteran bats: implications for visual acuity. *Brain, Behavior, and Evolution* **32**, 39–56.
- Querubin, A., Lee, H. R., Provis, J. M. and O'Brien, K. M. B.** (2009). Photoreceptor and ganglion cell topographies correlate with information convergence and high acuity regions in the adult pigeon (*Columba livia*) retina. *Journal of Comparative Neurology* **517**, 711–722.
- R Development Core Team** (2023). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Revell, L. J.** (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217–223.
- Revelle, W.** (2019). An introduction to the psych package: Part I: data entry and data description. *Northwestern University*.
- Tisdale, V. and Fernández-Juricic, E.** (2009). Vigilance and predator detection vary between avian species with different visual acuity and coverage. *Behavioral Ecology* **20**, 936–945.
- Troscianko, J., Von Bayern, A. M., Chappell, J., Rutz, C. and Martin, G. R.** (2012). Extreme binocular vision and a straight bill facilitate tool use in New Caledonian crows. *Nature communications* **3**, 1110.

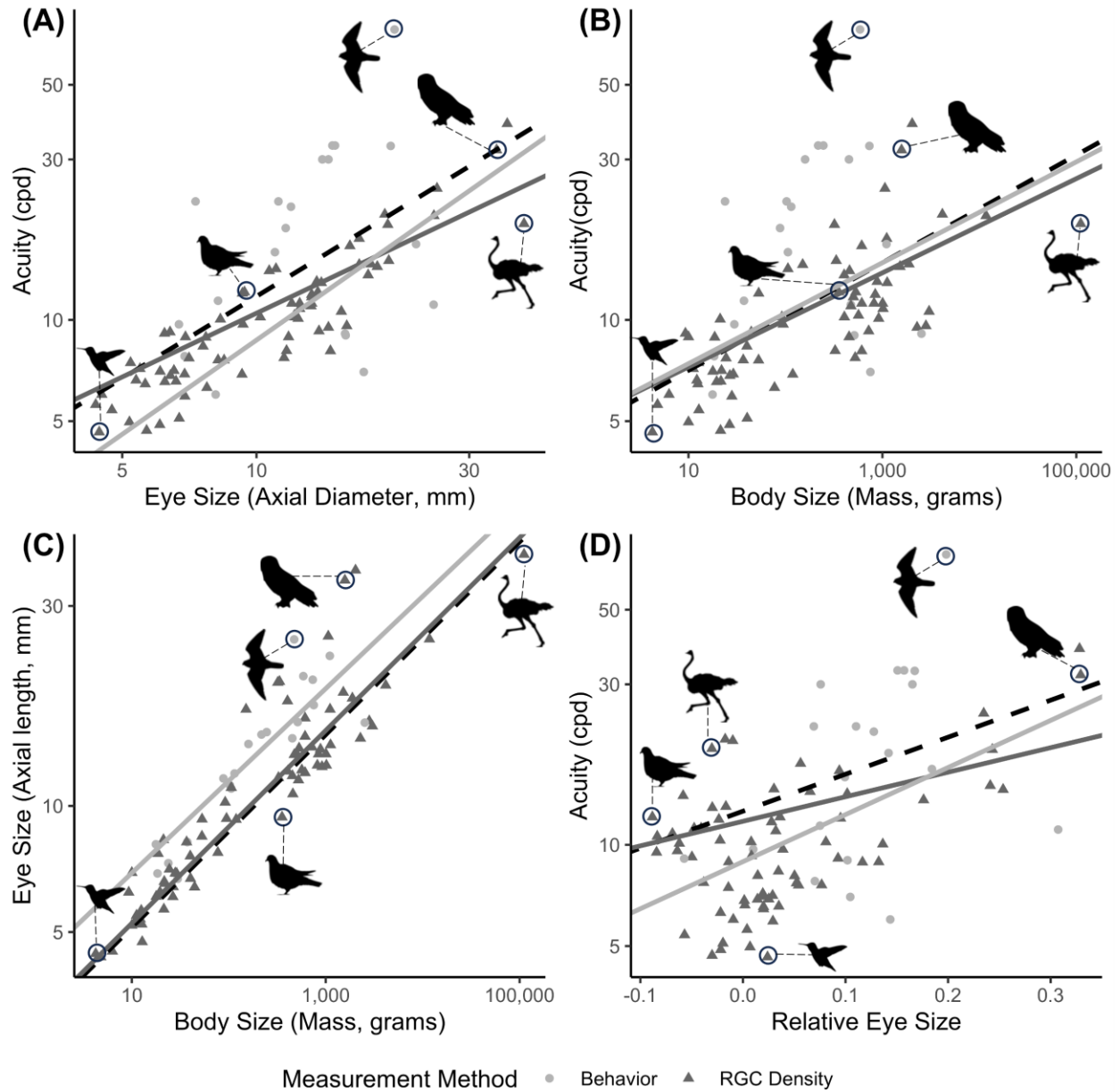
- Tyrrell, L. P. and Fernández-Juricic, E.** (2017). The hawk-eyed songbird: retinal morphology, eye shape, and visual fields of an aerial insectivore. *The American Naturalist* **189**, 709–717.
- Veilleux, C. C. and Kirk, E. C.** (2014). Visual acuity in mammals: Effects of eye size and ecology. *Brain, Behavior and Evolution* **83**, 43–53.
- von Campenhausen, M. and Kirschfeld, K.** (1998). Spectral sensitivity of the accessory optic system of the pigeon. *Journal of Comparative Physiology A* **183**, 1–6.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M. and Jetz, W.** (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological Archives E095-178. *Ecology* **95**, 2027–2027.



# Figures and Tables

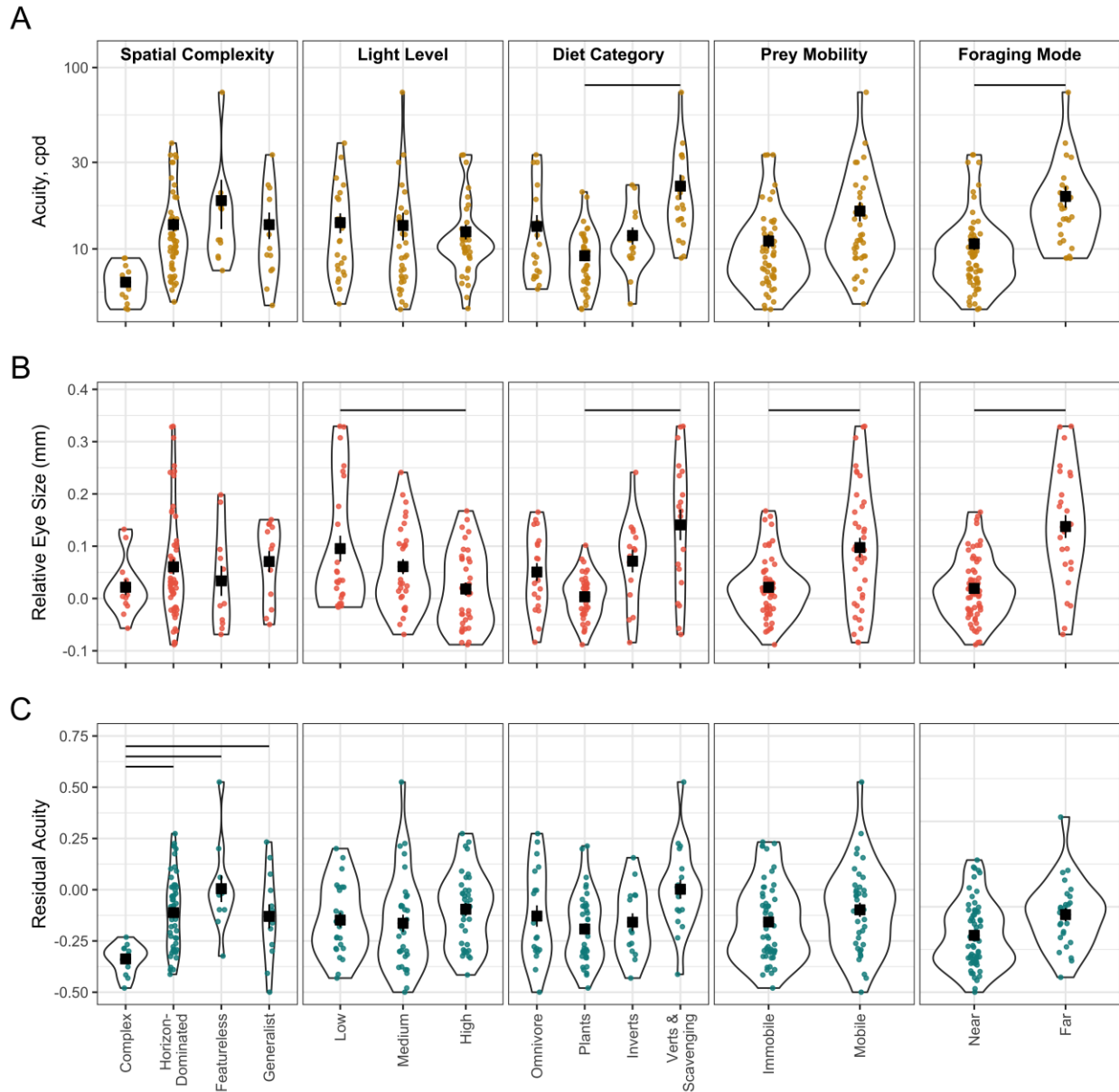


**Fig. 1.** The phylogenetic distribution of visual acuity in 94 species of birds. Bars represent acuity in cycles per degree. Icons (from phylopic.org) show a representative member of each order. Tree pruned from a 6714-taxon tree built by (Burleigh et al., 2015).

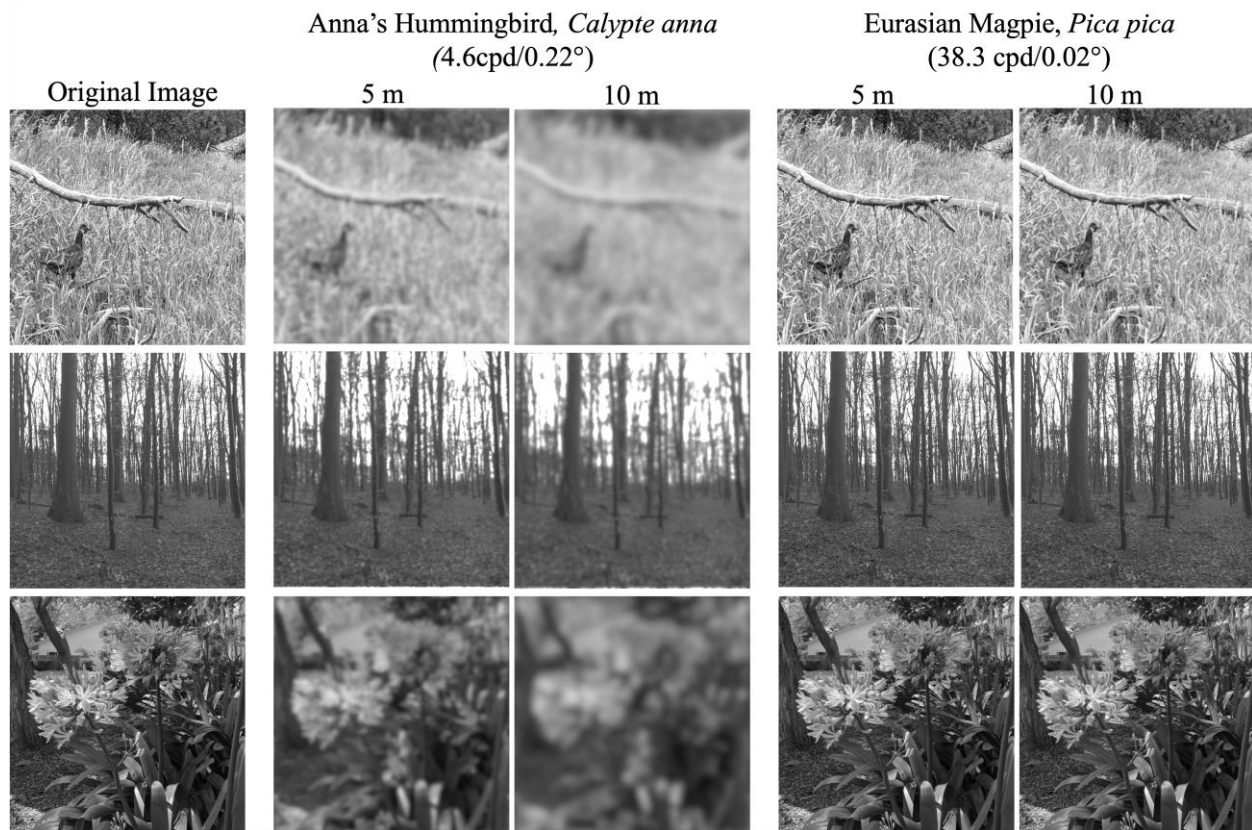


**Fig. 2.** Phylogenetically-corrected relationships between acuity, eye size, body mass, and relative eye size in birds ( $n=91$  species), for a behavior-only dataset (light gray, circles), an RGC-only dataset (dark gray, triangles), and a combined dataset (dashed black line). Panels show PGLS regressions of (A) acuity versus eye size, (B) acuity versus body mass, (C) eye size versus body mass, and (D) acuity versus relative eye size. Relative eye size in (D) was calculated using the residuals from the regression line in (C). Icons show, from left to right in panel A: Anna's

hummingbird *Calypte anna* (lowest acuity and lowest body mass), rock dove *Columba livia* (lowest relative eye size), Brown falcon *Falco berigora* (highest acuity), Great horned owl *Bubo virginianus* (highest relative eye size), and common ostrich *Struthio camelus* (largest eye size and highest body mass).



**Fig. 3.** (A) Acuity, (B) relative eye size, and (C) residual acuity across ecological categories in birds ( $n=91$  species). Points show raw data for individual species; black squares show mean and vertical black bars show standard error. Horizontal black bars connect categorizations that differed significantly (statistical results in main text). Statistics from a phylogenetic ANOVA.



**Fig. 4.** Portraying avian visual acuity in perception of natural scenes, including (top) a bird in a grassy field, (2) a forest, and (3) flowers, chosen to represent natural scenes and objects at a variety of spatial scales, from viewing distances of 5 and 10m. These scenes have been modified using the R package *AcuityView* (Caves and Johnsen, 2017), which uses Fourier methods to delete spatial frequencies from an image that are below the acuity of a given viewer from a given viewing distance. Here, we have portrayed scenes based on the lowest measured acuity in birds (Anna's hummingbird, *Calypte anna*) and the highest non-raptorial acuity (Eurasian magpie, *Pica pica*). Although raptors have the highest known acuity in birds, *AcuityView* can only portray scenes based on acuity lower than that of humans. The labels show species common and latin name (top) and visual acuity in cycles per degree (cpd) and minimum resolvable angle in degrees (bottom). The labels above each image show the assumed viewing distance. Images shown are the green color channel extracted from a full color image, since acuity is achromatic. Photo credits: EM Caves.

**Table 1.** Raw acuity, eye size, and body mass across habitat and diet categories.

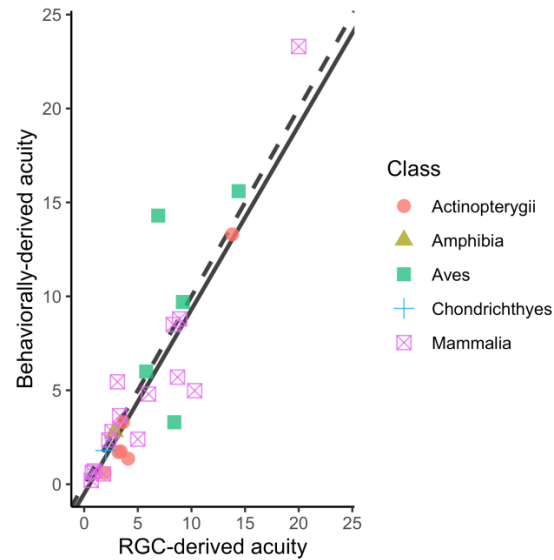
<b>Category</b>		<b>Raw Acuity (cpd)</b>			<b>Eye Size(mm)</b>		<b>Body Mass (g)</b>	
		N	Mean	s.e.	Mean	s.e.	Mean	s.e.
<b>Spatial Complexity</b>	Aerial and Open-water	11	18.6	2.84	15.9	1.98	1909	3557
	Horizon-Dominated	54	13.6	1.28	13.8	0.86	2681	1605
	Complex	13	6.55	2.61	6.30	1.74	59.4	3272
	Generalist	13	13.6	2.61	9.92	1.74	156.9	3272
<b>Light Level</b>	Low	22	13.9	2.10	14.4	1.23	493	2487
	Medium	31	13.5	1.77	11.4	1.23	422	2095
	High	38	12.5	1.60	12.2	1.11	3807	1892
<b>Diet Category</b>	Vertebrates & Scavenge	19	22.2	1.97	20.5	1.28	1553	2701
	Invertebrates	15	11.9	2.22	10.0	1.48	314	3040
	Plant Matter	38	9.16	1.39	10.2	0.90	3336	1910
	Omnivore	19	13.3	1.92	11.0	1.28	401	2701
<b>Prey Mobility</b>	Mobile	38	16.2	1.54	14.6	1.08	906	1896
	Immobile	53	11.1	1.30	10.9	0.92	2531	1606
<b>Foraging Mode</b>	Far	26	19.5	1.76	17.6	1.19	1152	2296
	Near	65	10.7	1.11	10.4	0.75	2133	1452

**Table 2.** Pairwise contrasts between estimated marginal mean acuity, relative eye size, and residual acuity across ecological categories, and t-statistics and p-values for pairwise comparisons from a phylogenetic ANOVA. Categories and levels are: Spatial Complexity (C=Complex, H=Horizon-Dominated, A=Aerial/Open Water, G=Generalist); Light Level (L=Low, M=Medium, H=High), Diet Category (Om=omnivore, P=plant material, I=invertebrates, VS=Vertebrates and Scavenged prey); Prey Mobility (M=mobile, Im=Immobile); Foraging mode (N=Near, F=Far).

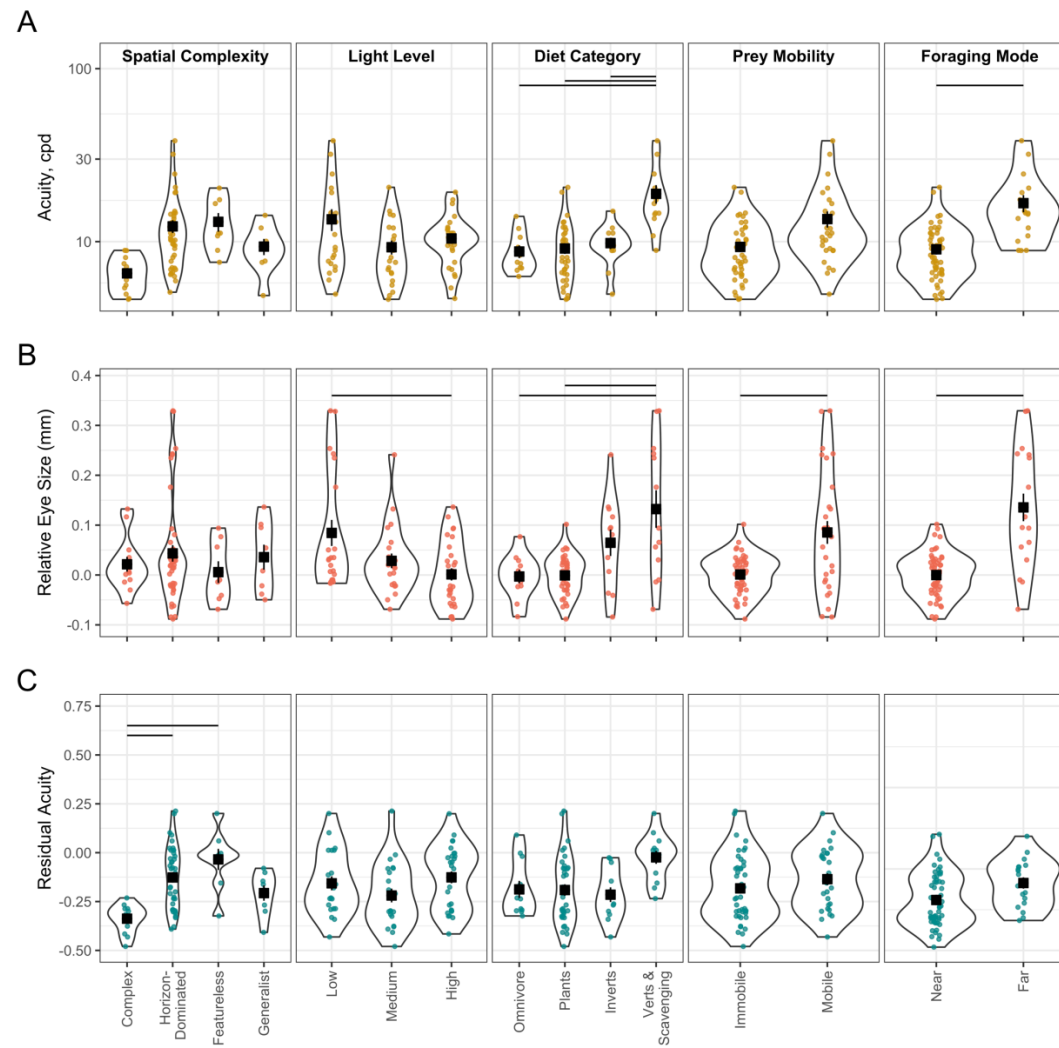
Contrast	Raw Acuity			Relative Eye Size			Residual Acuity		
	coef. $\pm$ s.e.	t	p	coef. $\pm$ s.e.	t	p	coef. $\pm$ s.e.	t	p
Habitat Spatial Complexity									
C-H	-7.05 $\pm$ 2.91	-2.43	0.50	-0.04 $\pm$ 0.03	-1.33	1	-0.23 $\pm$ 0.06	-3.69	0.05
C-A	-11.9 $\pm$ 3.86	-3.09	0.46	0.01 $\pm$ 0.04	-0.32	1	-0.34 $\pm$ 0.10	-3.10	0.03
C-G	-7.05 $\pm$ 3.69	-1.91	0.46	-0.05 $\pm$ 0.04	-1.32	1	-0.21 $\pm$ 0.07	-2.85	0.03
H-A	-4.85 $\pm$ 3.11	-1.56	0.94	0.03 $\pm$ 0.03	0.85	1	-0.12 $\pm$ 0.06	-0.50	0.59
H-G	0.003 $\pm$ 2.91	0.001	1.00	-0.01 $\pm$ 0.03	-0.35	1	0.01 $\pm$ 0.06	0.12	0.82
A-G	4.86 $\pm$ 3.86	1.26	0.98	-0.04 $\pm$ 0.04	-0.95	1	0.14 $\pm$ 0.07	0.50	0.63
Habitat Light Level									
L-M	0.43 $\pm$ 2.75	0.16	1	0.04 $\pm$ 0.03	1.78	0.14	0.00 $\pm$ 0.06	0.01	0.99
L-H	-1.35 $\pm$ 2.64	0.51	1	0.09 $\pm$ 0.02	3.72	0.006	-0.07 $\pm$ 0.05	-1.39	0.59
M-H	0.92 $\pm$ 2.39	0.38	1	0.04 $\pm$ 0.02	2.06	0.14	-0.07 $\pm$ 0.05	-1.55	0.52
Diet Category									
Om-P	4.14 $\pm$ 2.41	1.71	0.83	0.05 $\pm$ 0.02	2.09	0.40	0.06 $\pm$ 0.05	1.18	1
Om-I	1.45 $\pm$ 2.97	0.49	0.94	-0.02 $\pm$ 0.03	-0.75	0.47	0.03 $\pm$ 0.07	0.45	1

Om-VS	-8.88± 2.79	-3.19	0.49	-0.09± 0.03	-3.46	0.40	-0.13± 0.06	-2.12	1
P-I	-2.68± 2.62	-1.02	0.94	-0.07± 0.02	-2.78	0.19	-0.03± 0.06	-0.58	1
P-VS	-13.0± 2.41	-5.39	0.04	-0.14± 0.02	-6.09	0.02	-0.19± 0.05	-3.64	0.40
I-VS	-10.3± 2.97	-3.48	0.15	-0.07± 0.03	-2.50	0.40	-0.16± 0.07	-2.45	0.08
Prey Mobility									
Im-M	-5.11± 2.02	-2.53	0.11	-0.08± 0.02	-4.09	0.007	-0.06± 0.04	-1.40	0.40
Foraging Mode									
N-F	-8.80± 2.08	-4.22	0.04	-0.12± 0.02	-6.51	0.002	0.12± 0.05	-2.70	0.19





**Fig. S1.** Correlation between behaviorally- and RGC-derived acuity in 28 vertebrate species. The solid line indicates the predicted relationship if behaviorally- and RGC-derived acuity align perfectly (slope of 1) and the dashed line is the best-fit line from a phylogenetically-corrected (PGLS) regression. Acuity in cycles per degree on both axes.



**Fig. S2.** (A) Acuity, (B) relative eye size, and (C) residual acuity across ecological categories in birds, using only acuity data measured using the density of retinal ganglion cells. Points show raw data for individual species; black squares show mean and vertical black bars show standard error. Horizontal black bars connect categorizations that differed significantly.

**Table S1.** Complete database for analysis of acuity across 93 species of birds, listed in the taxonomic order given by the IOC World Bird List, version 13.2 [1]. Columns are: Common name, scientific name (again given by IOC World Bird List), synonyms (listed if they are used either by BirdTree.org, from which the phylogenetic tree used here was generated, or in the original acuity publication), acuity in cycles per degree (cpd), method of acuity measurement, eye axial length (EL, mm), body mass (BM, g), and categorizations for ecological variables [Spatial Complexity (Complex=C, HD=Horizon-Dominated, AO=Aerial/Open Water, G=Generalist); Light Level (L=Low, M=Medium, H=High), Diet Category (Om=Omnivore, P=Plant Material, I=Invertebrates, VS=Vertebrates and Scavenged prey); Prey Mobility (M=Mobile, Im=Immobile); Foraging mode (N=Near, F=Far)]. (\*) indicates updated taxonomic name, i.e. the name reported in the original publication is different from that presented here.

Common Name	Scientific Name	Synonym	Acuity (cpd)	Method	ED (mm)	BM (g)	Foraging Mode	Prey Mobility	Diet Type	Habitat Light Level	Spatial Complexity	Citation (acuity, eye size)
<b>Struthioniformes</b>												
Common Ostrich	<i>Struthio camelus</i>		19.3	RGC	39.8	111000	N	Im	P	H	HD	[2],[2]
<b>Tinamiformes</b>												
Chilean Tinamou	<i>Nothoprocta perdicaria</i>		14	RGC	10.7	458	N	Im	Om	H	HD	[3],[3]
<b>Anseriformes</b>												
Canada Goose	<i>Branta canadensis</i>		9.6	RGC	15.9	2812	N	Im	P	H	HD	[4],[4]
Northern Shoveler	<i>Spatula clypeata</i>	<i>Anas clypeata</i>	11.2	RGC	12	613	N	M	I	H	HD	[5],[5]
Gadwall	<i>Mareca strepera</i>	<i>Anas strepera</i>	10.1	RGC	12.4	916	N	Im	P	H	HD	[5],[5]
Mallard	<i>Anas platyrhynchos</i>		11.9	RGC	13.3	843	N	M	Om	H	HD	[5],[5]

Greater Scaup	<i>Aythya marila</i>		11.2	RGC	13.3	1005	N	M	I	H	AO	[5],[5]
Lesser Scaup	<i>Aythya affinis</i>		11.2	RGC	12.5	819	N	Im	P	H	AO	[5],[5]
Red-breasted Merganser	<i>Mergus serrator</i>		10.8	RGC	12.5	1015	F	M	VS	M	AO	[5],[5]
<b>Galliformes</b>												
Ruffed Grouse	<i>Bonasa umbellus</i>		12.1	RGC	13.7	531	N	Im	P	M	HD	[6],[6]
Sharp-tailed Grouse	<i>Tympanuchus phasianellus</i>		13	RGC	13.7	882	N	Im	P	L	HD	[6],[6]
Spruce Grouse	<i>Canachites canadensis</i>	<i>Dendragapus canadensis</i>	11	RGC	13.2	474	N	Im	P	L	HD	[6],[6]
Grey Partridge	<i>Perdix perdix</i>		10.2	RGC	12.1	405	N	Im	P	H	HD	[6],[6]
Common Pheasant	<i>Phasianus colchicus</i>		12.9	RGC	13.9	1120	N	Im	P	H	HD	[6],[6]
Indian Peafowl	<i>Pavo cristatus</i>		20.6	RGC	19.4	4155	N	Im	P	M	HD	[7],[6]
Red Junglefowl	<i>Gallus gallus</i>		7	B	17.4	7512	N	Im	Om	M	HD	[6],[6]
Japanese Quail	<i>Coturnix japonica</i>		9.7	RGC	9.33	95	N	Im	P	H	HD	[6],[6]
Chukar Partridge	<i>Alectoris chukar</i>		11.7	RGC	13.3	502	N	Im	P	H	HD	[6],[6]
<b>Apodiformes</b>												
Long-tailed Hermit	<i>Phaethornis superciliosus</i>		6	RGC	4.5	6	N	Im	P	L	C	[8],[8]
Anna's Hummingbird	<i>Calypte anna</i>		4.64	RGC	4.44	4	N	Im	P	M	C	[9],[9]

Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	5.6	RGC	4.36	5	N	Im	P	M	C	[8],[8]	
<b>Columbiformes</b>												
Rock Dove	<i>Columba livia</i>	12.1	RGC	9.4	354	N	Im	P	H	HD	[7],[10]	
Mourning Dove	<i>Zenaida macroura</i>	6.89	RGC	9.28	119	N	Im	P	M	HD	[11],[10]	
<b>Phoenicopteriformes</b>												
American Flamingo	<i>Phoenicopus ruber</i>	10.6	RGC	15.5	3032	N	M	Om	H	HD	[12],[12]	
Chilean Flamingo	<i>Phoenicopus chilensis</i>	9.5	RGC	14.5	2277	N	M	I	H	HD	[12],[12]	
<b>Sphenisciformes</b>												
King Penguin	<i>Aptenodytes patagonicus</i>	20.4	RGC	25	11731	F	M	VS	H	AO	[13],[13]	
Little Penguin	<i>Endyptula minor</i>	17.46	RGC	17	1108	F	M	VS	H	AO	[13],[13]	
<b>Procellariiformes</b>												
Leach's Storm Petrel	<i>Hydrobates leucorhous</i>	<i>Oceanodroma leucorhoa</i>	7.6	RGC	8.2	37	N	M	Om	H	AO	[14],[14]
Northern Fulmar	<i>Fulmarus glacialis</i>		16.6	RGC	16.2	612	F	M	VS	H	AO	[14],[14]
Manx Shearwater	<i>Puffinus puffinus</i>		8.9	RGC	11.8	453	F	M	VS	H	AO	[14],[15,16]
<b>Suliformes</b>												
Great Cormorant	<i>Phalacrocorax carbo</i>		9.1	B	15.8	2529	F	M	VS	H	AO	[17],[18]
<b>Cathartiformes</b>												

Black Vulture	<i>Coragyps atratus</i>	14.65	RGC	18.1	1882	F	Im	VS	L	HD	[19], [19]	
Turkey Vulture	<i>Cathartes aura</i>	14.4	RGC	18.7	1518	F	Im	VS	M	HD	[19], [19]	
<b>Accipitriformes</b>												
Egyptian Vulture	<i>Neophron percnopterus</i>	135	B	22.1	2082	F	Im	VS	H	HD	[20], [18]	
Wedge-tailed Eagle	<i>Aquila audax</i>	143	B	36.0	3449	F	M	VS	M	HD	[21], [16,21]	
Black Kite	<i>Milvus migrans</i>	32.9	B	20.0	734	F	Im	VS	H	HD	[22], [18]	
Red-tailed Hawk	<i>Buteo jamaicensis</i>	16.8	B	22.8	1101	F	M	VS	M	AO	[23], [10]	
<b>Strigiformes</b>												
Western Barn Owl	<i>Tyto alba</i>	3.3	RGC	17.5	403	F	M	VS	L	HD	[24,25], [43]	
American Barn Owl	<i>Tyto furcata*</i>	13.6	RGC	17.8	403	F	M	VS	L	HD	[26], [18]	
Burrowing Owl	<i>Athene cunicularia</i>	14.6	RGC	17.0	151	F	M	VS	L	HD	[26], [26]	
Northern Hawk-Owl	<i>Surnia ulula</i>	19.2	RGC	19.7	320	F	M	VS	L	HD	[26], [26]	
Snowy Owl	<i>Bubo scandiacus</i>	<i>Bubo scandiaca</i>	38.3	RGC	36.5	2029	F	M	VS	L	HD	[26], [26]
Great Horned Owl	<i>Bubo virginianus</i>	32	RGC	34.6	1576	F	M	VS	L	HD	[26],[10]	
Tawny Owl	<i>Strix aluco</i>	11.1	B	24.9	472	F	M	VS	L	HD	[27], [18]	
Great Grey Owl	<i>Strix nebulosa</i>	24.6	RGC	25.4	1062	F	M	VS	L	HD	[26], [26]	
<b>Coraciiformes</b>												

Laughing Kookaburra	<i>Dacelo novaeguineae</i>		15	RGC	19.8	334	F	M	I	M	HD	[28], [18]
Sacred Kingfisher	<i>Todiramphus sanctus</i>		12	RGC	9.30	53	F	M	I	M	G	[28], [18]
<b>Falconiformes</b>												
American Kestrel	<i>Falco sparverius</i>		21.7	B	11.9	115	F	M	I	H	G	[23],[1 0]
Brown Falcon	<i>Falco berigora</i>		73	B	20.4	587	F	M	VS	M	G	[29],[1 0]
<b>Psittaciformes</b>												
Red-tailed Black Cockatoo	<i>Calyptorhynchus banksii</i>		9.27	RGC	13.8	722	N	Im	Om	L	G	[30], [30]
Carnaby's Black Cockatoo	<i>Zanda latirostris</i>	<i>Calypto- rhyncbus latirostris</i>	8.09	RGC	14.7	612	N	Im	P	L	C	[30], [30]
Galah	<i>Eolophusroseic apilla</i>	<i>Cacatua roseicapilla</i>	8.1	RGC	11.7	325	N	Im	P	M	HD	[30], [30]
Long-billed Corella	<i>Cacatua tenuirostris</i>		10.32	RGC	12.2	567	N	Im	P	M	HD	[30], [30]
Little Corella	<i>Cacatua sanguinea</i>		7.72	RGC	11.5	524	N	Im	P	M	G	[30], [30]
Bourke's Parrot	<i>Neopsephotus bourkii</i>		9.2	RGC	6.4	44	N	Im	P	M	G	[31], [18]
Budgerigar	<i>Melopsittacus undulatus</i>		6.9	RGC	6.9	29	N	Im	P	H	HD	[31], [18]
<b>Passeriformes</b>												
Black Phoebe	<i>Sayornis nigricans</i>		8.88	RGC	7.7	19	F	M	I	H	C	[32], [18]
Least Flycatcher	<i>Empidonax minimus</i>		8.9	RGC	6.93	10	F	M	I	M	C	[33], [33]

Brown Honeyeater	<i>Lichmera indistincta</i>		7.16	RGC	5.48	11	N	Im	P	L	C	[34], [34]
Red Wattlebird	<i>Anthochaera carunculata</i>		14.19	RGC	11.1	106	N	Im	P	M	G	[34], [34]
Yellow-rumped Thornbill	<i>Acanthiza chrysorrhoa</i>		9.12	RGC	6.22	9	N	M	I	H	HD	[34], [34]
Blue Jay	<i>Cyanocitta cristata</i>		18.75	B	11.6	88	F	Im	Om	L	G	[35], [36]
Eurasian Jay	<i>Garrulus glandarius</i>		30	B	14.1	159	N	M	Om	M	HD	[37], [36]
Eurasian magpie	<i>Pica pica</i>		33	B	14.8	217	N	Im	VS	M	HD	[37], [36]
Western Jackdaw	<i>Coloens monedula</i>		33	B	15.0	246	N	Im	Om	H	G	[37], [38]
Rook	<i>Corvus frugilegus</i>		30	B	14.5	452	N	M	Om	H	HD	[37], [39]
Large-billed Crow	<i>Corvus macrorhynchos</i>		9	B	15.9	513	N	Im	Om	M	HD	[40], [36]
Tufted Titmouse	<i>Baeolophus bicolor</i>		6.57	RGC	6.60	22	N	M	I	L	C	[41], [41]
Carolina Chickadee	<i>Poecile carolinensis</i>	<i>Parus carolinensis</i>	4.97	RGC	5.19	10	N	M	I	L	C	[41], [41]
Eurasian Skylark	<i>Alauda arvensis</i>		11.4	B	8.20	37	N	Im	P	H	HD	[42], [42]
Tree Swallow	<i>Tachycineta bicolor</i>		10.05	RGC	8.30	21	F	M	I	H	G	[33], [33]
Silvereye	<i>Zosterops lateralis</i>		7.46	RGC	5.22	13	N	Im	Om	L	C	[34], [34]
White-breasted Nuthatch	<i>Sitta carolinensis</i>		6.83	RGC	6.41	27	N	M	Om	L	C	[41], [41]
Common Starling	<i>Sturnus vulgaris</i>		6.29	RGC	7.74	77	N	Im	Om	H	HD	[11], [11]



Common Blackbird	<i>Turdus merula</i>		22.5	B	11.2	103	N	Im	Om	M	HD	[42], [42]
Fieldfare	<i>Turdus pilaris</i>		15.9	B	11.0	106	N	M	I	M	HD	[42], [42]
European robin	<i>Erithacus rubecula</i>		6	B	8.10	18	N	M	Om	M	G	[42], [42]
House Sparrow	<i>Passer domesticus</i>		4.88	RGC	6.07	27	N	Im	P	M	G	[11], [11]
Eurasian Chaffinch	<i>Fringilla coelebs</i>		22.5	B	7.30	24	F	M	I	L	G	[42], [42]
House Finch	<i>Haemorhous mexicanus</i>	<i>Carpodacus mexicanus</i>	4.69	RGC	5.67	21	N	Im	P	H	C	[11], [11]
American Goldfinch	<i>Spinus tristis</i>	<i>Carduelis tristis</i>	5.4	RGC	4.74	13	N	Im	P	H	C	[43], [43]
Yellowhammer	<i>Emberiza citrinella</i>		9.7	B	6.70	30	N	Im	P	H	HD	[42], [42]
Common Reed Bunting	<i>Emberiza schoeniclus</i>		7.8	B	6.90	18	N	Im	P	H	HD	[42], [42]
Chipping Sparrow	<i>Spizella passerina</i>		6.62	RGC	5.37	12	N	Im	P	M	HD	[44], [44]
Field Sparrow	<i>Spizella pusilla</i>		6.45	RGC	5.63	13	N	Im	P	H	HD	[44], [44]
American Tree Sparrow	<i>Spizelloides arborea</i>	<i>Spizella arborea</i>	7.03	RGC	6.08	18	N	M	Om	H	HD	[44], [44]
Dark-eyed Junco	<i>Junco hyemalis</i>		6.55	RGC	6.23	20	N	Im	P	M	HD	[44], [44]
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>		5.93	RGC	6.91	28	N	Im	P	M	HD	[45], [45]
White-throated Sparrow	<i>Zonotrichia albicollis</i>		7.7	RGC	7.06	24	N	Im	P	L	HD	[44], [44]

Song Sparrow	<i>Melospiza melodia</i>		7.07	RGC	6.53	22	N	Im	Om	M	HD	[44], [44]
California Towhee	<i>Melospiza crissalis</i>	<i>Pipilo crissalis</i>	7.59	RGC	8.46	53	N	Im	P	M	G	[45], [45]
Eastern Towhee	<i>Pipilo erythrophthalmus</i>		8.35	RGC	7.59	40	N	Im	Om	L	HD	[44], [44]
Eastern Meadowlark	<i>Sturnella magna</i>		10.2	RGC	10.2	92	N	M	I	H	HD	[46], [46]
Brown-headed Cowbird	<i>Molothrus ater</i>		5.1	RGC	6.71	40	N	Im	P	M	HD	[11], [11]

**Table S2.** 28 vertebrate species with camera eyes in which acuity has been measured both behaviorally and using peak retinal ganglion cell density. A (\*) indicates a species name that was different in the original publication and has been updated to reflect current taxonomic designations.

Class	Scientific Name	Common Name	Acuity from Behavior (cpd)	Acuity from RGC density (cpd)	Behavior Citation	RGC citation
<b>Actinopterygii</b>	<i>Danio rerio</i>	Zebrafish	0.59	1.89	[47]	[48]
	<i>Pomacentrus amboinensis</i>	Ambon damelfish	1.36	4.1	[49]	[49]
	<i>Pseudochromis fuscus</i>	Yellow dottedback	1.71	3.2	[49]	[49]
	<i>Rhinecanthus aculeatus</i>	Triggerfish	1.75	3.41	[50]	[50]
	<i>Toxotes chatareus</i>	Largescale archerfish	3.3	3.62	[51]	[51]
	<i>Toxotes jaculatrix</i>	Archerfish	13.3	13.8	[52]	[52]
<b>Amphibia</b>	<i>Lithobates pipiens</i> *	Northern leopard frog	2.8	2.82	[53]	[53]
<b>Aves</b>	<i>Tyto alba</i>	Barn owl	3.3	8.4	[25]	[54]
	<i>Calypte anna</i>	Anna's Hummingbird	6	5.78	[9]	[9]
	<i>Neopsephotus bourkii</i>	Bourke's parrot	9.7	9.2	[55]	[31]
	<i>Melopsittacus undulatus</i>	Budgerigar	14.3	6.9	[55]	[55]
	<i>Columba livia</i>	Pigeon	15.6	14.4	[56]	[56]
	<b>Chondrichthyes</b>	<i>Chiloscyllium punctatum</i>	Brown-banded bamboo shark	1.8	2.02	[57]
<b>Mammalia</b>	<i>Myotis daubentonii</i>	Daubenton's bat	0.2	0.66	[59]	[60]
	<i>Mesocricetus auratus</i>	Golden hamster	0.55	1.8	[61]	[62]
	<i>Tarsipes rostratus</i>	honey possum	0.63	0.75	[63]	[64]
	<i>Carollia perspicillata</i>	Seba's short-tailed bat	0.71	0.94	[65]	[66]
	<i>Tursiops truncatus</i>	Bottlenose dolphin	3.65	3.3	[67]	[68]
	<i>Sminthopsis crassicaudata</i>	Fat-Tailed Dunnart	2.36	2.3	[69]	[69]
	<i>Tupaia belangeri</i>	Northern tree shrew	2.4	5	[70]	[70]

<i>Dasyurus maculatus</i> *	Northern native cat	2.8	2.6	[71]	[71]
<i>Notamacropus eugenii</i> *	Tamar wallaby	4.8	6	[72]	[72]
<i>Bos taurus</i>	Cow	4.98	10.3	[73]	[74]
<i>Orcinus orca</i>	Killer whale (water)	5.45	3.1	[75]	[76]
<i>Phoca vitulina</i>	Harbor seal	5.7	8.7	[77]	[77]
<i>Canis familiaris</i>	Domestic dog	6.2	8.3	[78]	[79]
<i>Aotus azarai</i>	Azara's owl monkey	8.5	8.3	[80]	[81]
<i>Felis catus</i>	Domestic cat	8.8	8.9	[82]	[79]
<i>Equus caballus</i>	Horse	23.3	20	[83]	[83]

## Literature Cited

1. Gill, F. *et al.* (2021) *IOC world bird list*, IOC
2. Boire, D. *et al.* (2001) Quantitative analysis of the retinal ganglion cell layer in the ostrich, *Struthio camelus*. *Brain, Behavior, and Evolution* 58, 343–355
3. Krabichler, Q. *et al.* (2015) The visual system of a Palaeognathous bird: Visual field, retinal topography and retino-central connections in the Chilean Tinamou (*Nothoprocta perdicaria*). *Journal of Comparative Neurology* 523, 226–250
4. Fernández-Juricic, E. *et al.* (2011) Testing the terrain hypothesis: Canada geese see their world laterally and obliquely. *Brain, Behavior and Evolution* 77, 147–158
5. Lisney, T.J. *et al.* (2013) Ecomorphology of eye shape and retinal topography in waterfowl (Aves: Anseriformes: Anatidae) with different foraging modes. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 199, 385–402
6. Lisney, T.J. *et al.* (2012) Interspecific variation in eye shape and retinal topography in seven species of galliform bird (Aves: Galliformes: Phasianidae). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 198, 717–731
7. Hart, N.S. (2002) Vision in the peafowl (Aves: *Pavo cristatus*). *The Journal of experimental biology* 205, 3925–3935
8. Lisney, T.J. *et al.* (2015) Eye Morphology and Retinal Topography in Hummingbirds (Trochilidae: Aves). *Brain, Behavior and Evolution* 86, 176–190
9. Goller, B. *et al.* (2019) Spatial and temporal resolution of the visual system of the Anna's hummingbird (*Calypte anna*) relative to other birds. *Physiological and biochemical zoology* 92, 481–495
10. Hall, M.I. and Ross, C.F. (2007) Eye shape and activity pattern in birds. *Journal of Zoology* 271, 437–444
11. Dolan, T. and Fernández-Juricic, E. (2010) Retinal ganglion cell topography of five species of ground-foraging birds. *Brain, Behavior and Evolution* 75, 111–121
12. Lisney, T.J. *et al.* (2020) Retinal topography in two species of flamingo (Phoenicopteriformes: Phoenicopteridae). *Journal of Comparative Neurology* 528, 2848–2863
13. Coimbra, J.P. *et al.* (2012) Retinal ganglion cell topography and spatial resolving power in penguins. *Brain, Behavior and Evolution* 80, 254–268
14. Mitkus, M. *et al.* (2016) Vision on the high seas: spatial resolution and optical sensitivity in two procellariiform seabirds with different foraging strategies. *Journal of Experimental Biology* 219, 3329–3338
15. Martin, G.R. (2017) *The sensory ecology of birds*, Oxford University Press
16. Brooke, M.D.L. *et al.* (1999) The scaling of eye size with body mass in birds. *Proceedings of the Royal Society B: Biological Sciences* 266, 405
17. Strod, T. *et al.* (2004) Cormorants keep their power: Visual resolution in a pursuit-diving bird under amphibious and turbid conditions. *Current Biology* 14, 376–377

18. Ritland, S.M. (1982) *The allometry of the vertebrate eye*, The University of Chicago
19. Lisney, T.J. *et al.* (2013) Comparison of eye morphology and retinal topography in two species of new world vultures (Aves: Cathartidae). *Anatomical Record* 296, 1954–1970
20. Fischer, A.B. (1968) Laboruntersuchungen und freilandbeobachtungen zum sehvermögen und verhalten von altweltgeiern. PhD Thesis
21. Reymond, L. (1985) Spatial visual acuity of the eagle *Aquila audax*: A behavioural, optical and anatomical investigation. *Vision Research* 25, 1477–1491
22. Potier, S. *et al.* (2016) Visual abilities in two raptors with different ecology. *The Journal of Experimental Biology* 219, 2639–2649
23. Mcisaac, H.P. (2001) Raptor acuity and wind turbine blade conspicuity. In *National Avian - Wind Power Planning Meeting IV*, pp. 59–87
24. Harmening, W.M. *et al.* (2009) Spatial contrast sensitivity and grating acuity of barn owls. *Journal of Vision* 9, 1–12
25. Orłowski, J. *et al.* (2012) Night vision in barn owls: visual acuity and contrast sensitivity under dark adaptation. *Journal of vision* 12, 4–4
26. Lisney, T.J. *et al.* (2012) Eye shape and retinal topography in owls (Aves: Strigiformes). *Brain, Behavior and Evolution* 79, 218–236
27. Martin, G.R. and Gordon, I.E. (1974) Increment-threshold spectral sensitivity in the tawny owl (*Strix aluco*). *Vision Research* 14, 615–621
28. Moroney, M.K. and Pettigrew, J.D. (1987) Some observations on the visual optics of kingfishers (Aves, Coraciiformes, Alcedinidae). *Journal of Comparative Physiology A* 160, 137–149
29. Reymond, L. (1987) Spatial visual acuity of the falcon, *Falco berigora*: A behavioural, optical and anatomical investigation. *Vision Research* 27, 1859–1874
30. Coimbra, J.P. *et al.* (2014) Topographic specializations in the retinal ganglion cell layer correlate with lateralized visual behavior, ecology, and evolution in cockatoos. *Journal of Comparative Neurology* 522, 3363–3385
31. Mitkus, M. *et al.* (2014) Retinal ganglion cell topography and spatial resolution of two parrot species: Budgerigar (*Melopsittacus undulatus*) and Bourke’s parrot (*Neopsephotus bourkii*). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 200, 371–384
32. Gall, M.D. and Fernández-Juricic, E. (2010) Visual fields, eye movements, and scanning behavior of a sit-and-wait predator, the black phoebe (*Sayornis nigricans*). *Journal of Comparative Physiology A* 196, 15–22
33. Tyrrell, L.P. and Fernández-Juricic, E. (2017) The hawk-eyed songbird: retinal morphology, eye shape, and visual fields of an aerial insectivore. *The American Naturalist* 189, 709–717
34. Coimbra, J.P. *et al.* (2014) Topographic specializations in the retinal ganglion cell layer of Australian passerines. *Journal of Comparative Neurology* 522, 3609–3628

35. Fite, K.V. and Rosenfield-Wessels, S. (1975) A comparative study of deep avian foveas. *Brain, Behavior and Evolution* 12, 97–115
36. Ausprey, I.J. (2021) Adaptations to light contribute to the ecological niches and evolution of the terrestrial avifauna. *Proceedings of the Royal Society B: Biological Sciences* 288, 20210853
37. Dabrowska, B. (1975) Investigations on visual acuity of some corvine species. *Folia Biologica* 23, 311–332
38. Howland, H.C. *et al.* (2004) The allometry and scaling of the size of vertebrate eyes. *Vision Research* 44, 2043–2065
39. Browne, R.G. *et al.* (2007) The schematic eye of the rook, *Corvus frugilegus*. *Folia Zoologica* 56, 399–404
40. Yamamoto, K. *et al.* (2001) Near-field visual acuity in Japanese jungle crows (*Corvus macrorhynchos*). *Physiology and Behavior* 72, 283–286
41. Moore, B.A. *et al.* (2013) Interspecific differences in the visual system and scanning behavior of three forest passerines that form heterospecific flocks. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 199, 263–277
42. Donner, K. (1951) The visual acuity of some passerine birds. *Acta zoologica Fennica* 66
43. Baumhardt, P.E. *et al.* (2014) Do American goldfinches see their world like passive prey foragers? A study on visual fields, retinal topography, and sensitivity of photoreceptors. *Brain, Behavior and Evolution* 83, 181–198
44. Moore, B.A. *et al.* (2015) Vision in avian emberizid foragers: maximizing both binocular vision and fronto-lateral visual acuity. *Journal of Experimental Biology* 218, 1347–1358
45. Fernández-Juricic, E. *et al.* (2011) Visual systems and vigilance behaviour of two ground-foraging avian prey species: White-crowned sparrows and California towhees. *Animal Behaviour* 81, 705–713
46. Tyrrell, L.P. *et al.* (2013) Looking above the prairie: localized and upward acute vision in a native grassland bird. *Scientific Reports* 3, 3231
47. Tappeiner, C. *et al.* (2012) Visual acuity and contrast sensitivity of adult zebrafish. *Frontiers in zoology* 9, 10
48. Pita, D. *et al.* (2015) Vision in two cyprinid fish: Implications for collective behavior. *PeerJ* DOI: 10.7717/peerj.1113
49. Parker, A.N. *et al.* (2017) Comparison of functional and anatomical estimations of visual acuity in two species of coral reef fish. *The Journal of Experimental Biology* 220, 2387–2396
50. Champ, C. *et al.* (2014) Visual acuity in a species of coral reef fish: *Rhinecanthus aculeatus*. *Brain, Behavior and Evolution* 83, 31–42
51. Temple, S.E. *et al.* (2013) A comparison of behavioural (Landolt C) and anatomical estimates of visual acuity in archerfish (*Toxotes chatareus*). *Vision Research* 83, 1–8
52. Ben-Simon, A. *et al.* (2012) Visual acuity in the archerfish: behavior, anatomy, and neurophysiology. *Journal of vision* 12, 18–18
53. Aho, A.-C. (1997) The visual acuity of the frog (*Rana pipiens*). *Journal of Comparative Physiology A* 180, 19–24
54. Wathey, J.C. and Pettigrew, J.D. (1989) Quantitative analysis of the retinal ganglion cell layer and optic nerve of the barn owl *Tyto alba*. *Brain, Behavior, and Evolution* 33, 279–292

55. Lind, O. *et al.* (2012) Luminance-dependence of spatial vision in budgerigars (*Melopsittacus undulatus*) and Bourke's parrots (*Neopsephotus bourkii*). *Journal of Comparative Physiology A* 198, 69–77
56. Hodos, W. *et al.* (1991) Age-Dependent Retinal Changes in Visual Acuity Morphology in Pigeons. *Vision research* 31, 669–677
57. Ryan, L.A. *et al.* (2016) Visual resolution and contrast sensitivity in two benthic sharks. *The Journal of Experimental Biology* 219, 3971–3980
58. Lisney, T.J. and Collin, S.P. (2008) Retinal ganglion cell distribution and spatial resolving power in elasmobranchs. *Brain, Behavior and Evolution* 72, 59–77
59. Eklöf, J. (2003) Vision in echolocating bats. Göteborg University, Göteborg, Sweden
60. Cechetto, C. *et al.* (2020) Retinal ganglion cell topography and spatial resolving power in echolocating and non-echolocating bats. *Brain, Behavior and Evolution* 95, 58–68
61. Emerson, V.F. (1980) Grating acuity of the golden hamster. *Experimental Brain Research* 38, 43–52
62. Y-C, T. and Blakemore, C. (1976) Regional specialization in the golden hamster's retina. *Journal of Comparative Neurology* 168, 439–457
63. Arrese, C. *et al.* (2002) Visual capabilities in a crepuscular marsupial, the honey possum (*Tarsipes rostratus*): a visual approach to ecology. *Journal of Zoology* 256, 151–158
64. Dunlop, S.A. *et al.* (1994) The retinal ganglion cell layer and optic nerve in a marsupial, the honey possum (*Tarsipes rostratus*). *Brain, behavior and evolution* 44, 307–323
65. Suthers, R. (1966) Optomotor responses by echolocating bats. *Science* 152, 1102–1104
66. Heffner, R.S. *et al.* (2007) Sound-localization acuity and its relation to vision in large and small fruit-eating bats: I. Echolocating species, *Phyllostomus hastatus* and *Carollia perspicillata*. *Hearing Research* 234, 1–9
67. Herman, L.M. *et al.* (1975) Bottle-nosed dolphin: double-slit pupil yields equivalent aerial and underwater diurnal acuity. *Science* 189, 650–652
68. Mass, A.M. and Supin, A.Y. (1995) Ganglion cell topography of the retina in the bottlenosed dolphin, *Tursiops truncatus*. *Brain, Behavior and Evolution* 45, 257–265
69. Arrese, C. *et al.* (1999) Retinal structure and visual acuity in a polyprotodont marsupial, the fat-tailed dunnart (*Sminthopsis crassicaudata*). *Brain, behavior and evolution* 53, 111–26
70. Petry, H.M. *et al.* (1984) Spatial contrast sensitivity of the tree shrew. *Vision research* 24, 1037–1042
71. Harman, A.M. *et al.* (1986) Visual acuity of the northern native cat (*Dasyurus hallucatus*) - Behavioural and anatomical estimates. *Behavioural Brain Research* 22, 211–216
72. Hemmi, J.M. and Mark, R.F. (1998) Visual acuity, contrast sensitivity and retinal magnification in a marsupial, the tammar wallaby (*Macropus eugenii*). *Journal of Comparative Physiology - A Sensory, Neural, and Behavioral Physiology* 183, 379–387
73. Entsu, S. *et al.* (1992) Visual acuity of cattle determined by the method of discrimination learning. *Applied Animal Behaviour Science* 34, 1–10



74. Hebel, R. (1976) Distribution of retinal ganglion cells in five mammalian species (pig, sheep, ox, horse, dog). *Anatomy and Embryology* 150, 45–51
75. White, D. *et al.* (1971) Visual acuity of the killer whale (*Orcinus orca*). *Experimental Neurology* 32, 230–236
76. Mass, A.M. *et al.* (2013) Ocular anatomy, ganglion cell distribution and retinal resolution of a killer whale (*Orcinus orca*). *Brain, Behavior and Evolution* 81, 1–11
77. Hanke, F.D. *et al.* (2009) Retinal ganglion cell topography in juvenile harbor seals (*Phoca vitulina*). *Brain, Behavior and Evolution* 74, 102–109
78. Neuhaus, W. and Regenfuss, E. (1967) The visual acuity of the dog under different brightness. *Zeitschrift für vergleichende Physiologie* 57, 137–146
79. Heffner, R.S. and Heffner, H.E. (1992) Visual factors in sound localization in mammals. *Journal of Comparative Neurology* 317, 219–232
80. Ordy, J. and Samorajski, T. (1968) Visual acuity and ERG-CFF in relation to the morphologic organization of the retina among diurnal and nocturnal primates. *Vision research* 8, 1205–1225
81. Yamada, E.S. *et al.* (2001) M and P retinal ganglion cells of the owl monkey: morphology, size and photoreceptor convergence. *Vision Research* 41, 119–131
82. Hall, S. and Mitchell, D. (1991) Grating acuity of cats measured with detection and discrimination tasks. *Behavioural brain research* 44, 1–9
83. Timney, B. and Keil, K. (1992) Visual acuity in the horse. *Vision Research* 32, 2289–2293