

RESEARCH ARTICLE

Eye morphology contributes to the ecology and evolution of the aquatic avifauna

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Funding information

Katherine Ordway Chair of Ecosystem
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Handling Editor: Daniel Montoya

Abstract

1. Aquatic birds are notable among the global avifauna for living in environments exposed to large amounts of light. Despite growing evidence that visual adaptations to light underly the ecology and evolution of the avian tree of life, no comprehensive comparative analysis of visual acuity as approximated by eyes size exists for the global aquatic avifauna.
2. Here, I use Stanley Ritland's unpublished dataset of measurements for axial length collected from museum specimens to explore the ecology and evolution of eye size variation for half of the aquatic avifauna ($N=464$ species).
3. After correcting for body mass allometry and incorporating phylogenetic relationships, aquatic species had significantly smaller eyes compared to terrestrial species. Furthermore, species using hyperopic foraging manoeuvres, exhibiting carnivorous and insectivorous diets, and displaying nocturnal behaviour had larger eyes. Plunge-divers (e.g. boobies and tropic birds) and stalkers (e.g. herons) had the largest relative eye sizes, especially species identifying prey at higher altitudes or longer distances. Underwater pursuit-divers foraging at greater depths had larger eyes, likely due to the dramatic attenuation of light in the deep ocean. Overall, residual eye size was phylogenetically conserved ($I=0.94$), with phylogeny alone explaining 62% of residual eye size variation.
4. Collectively, these results suggest that the relatively bright environments found in aquatic ecosystems negate the adaptive benefits of costly metabolic investments associated with developing and maintaining larger eyes, while also reducing the potential occurrence of disability glare. Strong correlations between eye size and foraging ecology in different aquatic environments corroborate similar comparative studies of terrestrial birds and underscore the central role that vision has played in driving the ecology and evolution of the global avifauna.

KEYWORDS

aquatic, bird, ecology, evolution, eye, foraging, light, visual acuity

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1 | INTRODUCTION

Aquatic birds are notable among the global avifauna for the relative brightness of their optical environments—they generally persist in habitats exposed to large amounts of light (Machovsky-Capuska et al., 2012). With the exception of species inhabiting forested wetlands, groups such as shorebirds, seabirds, herons, and ducks live in environments with limited to no vegetation structure inhibiting solar illumination, meaning that the visual system of aquatic species has likely adapted to function under relatively bright conditions. Despite increasing interest in how morphology predicts ecology across the full avian tree of life (Pigot et al., 2020), little information exists on the functional traits employed by aquatic bird species when interpreting light intensity gradients, especially with regards to their foraging ecology.

Birds are highly visual organisms, relying on eyesight to forage, identify mates, and defend territories. As the one external anatomical trait adapted specifically to interpret light, the eye plays a central role in avian behaviour and survival (Lythgoe, 1979). While exquisite micro-anatomical adaptations in retinal cell ganglia and oil droplets are correlated with fine-scale foraging behaviour and colour recognition (e.g. Dolan & Fernandez-Juricic, 2010; Hart, 2001), the overall size of the eye provides information on the amount of light available for interpreting the surrounding environment (Martin, 1994). Briefly, larger eyes improve visual acuity and sensitivity by increasing the size of the pupil aperture, the number of light receptor cells, and the focal length (Caves et al., 2024; Martin, 1999). For this reason, nocturnal species and raptors that forage in extremely dark conditions or from great distances while rapidly pursuing prey have the largest eyes relative to body mass among the global avifauna (Hall & Ross, 2007; Potier et al., 2017). Across terrestrial birds, variation in eye size after correcting for body mass allometry has been linked to foraging behaviour, diet, and habitat, with larger-eyed species using far-sighted (hyperopic) foraging manoeuvres, eating invertebrate prey requiring enhanced capture recognition, and living in the dark forest understory (Ausprey, 2021; Garamszegi et al., 2002). Large eyes may also be maladaptive if birds experience disability glare (Fernandez-Juricic et al., 2012; Martin & Katzir, 2000), and species sensitive to habitat disturbance, especially in tropical forests, tend to have larger eyes (Ausprey et al., 2021; Jones et al., 2023; Martinez-Ortega et al., 2014). Furthermore, eyes require large metabolic investments to maintain, both due to their anatomy and interaction with the nervous system (Laughlin et al., 1998; Moran et al., 2015). Hence, eye size represents a trade-off between the adaptive benefits of enhanced visual acuity and the physiological costs of maintaining energetically expensive organs.

Aquatic birds exhibit a diversity of behavioural traits mediated by light that likely have co-evolved with visual adaptations that maximise foraging success. Some families largely forage on the surface of water (Anatidae: ducks), probe or peck on the shoreline (Scolopacidae: shorebirds) or sweep through the upper water column (Recurvirostridae: avocets). Many of these species rely more on tactile cues (storks, shorebirds) to identify food or are largely

herbivorous (coots, ducks). Other families rely on active hunting strategies that require long-distance prey recognition, such as chasing prey (Charadriidae: Plovers), stalking (Ardeidae: Herons), plunge diving (Sulidae: boobies), or underwater pursuit (Alcidae: auks). While extensive research exists into how visual fields and binocular vision guide the foraging behaviour of species occupying different aquatic environments (Cantlay et al., 2023; Martin, 1999, 2007), no comprehensive study exists on how visual acuity as approximated by eye size correlates with the ecology and evolution of the aquatic avifauna.

Here, I use Stanley Ritland's unpublished dataset of eye size measurements collected from museum specimens to explore the ecology and evolution of eye size variation for half of the aquatic avifauna (Ritland, 1982). While I recognise that other facets of the avian visual system contribute to a species' ecology, such as colour recognition, topology of retinal ganglia, orientation of visual fields or ocular adaptations to water immersion (Cronin, 2012; Dolan & Fernandez-Juricic, 2010; Hart, 2001; Martin, 2007), no datasets that span the avian tree of life exist for these traits, and for this reason I focus on eye size. Specifically, I test the following hypotheses:

1. Eye size varies with environmental brightness, with the prediction that aquatic species have smaller eyes than terrestrial species due to relatively brighter conditions. Furthermore, species that live in forested wetlands should have larger eyes that improve visual acuity in relatively darker conditions.
2. Eye size varies with foraging behaviour, with the prediction that species employing hyperopic manoeuvres requiring long-distance prey recognition have larger eyes that improve visual acuity.
3. Eye size varies with nocturnality, with the prediction that species specialising in nocturnal activity have larger eyes.
4. Eye size varies with diet, with the prediction that species foraging more frequently on animals and invertebrates have larger eyes given their need to visualise and capture distant prey.
5. Eye size varies with the distance that birds visualise prey and the quality of light, with the following predictions:
 - a. For species that forage while standing, walking or running, taller species will have larger eyes given that they visualise prey at a greater distance.
 - b. For species that forage by plunging into the water to catch prey, species that dive from greater heights will have larger eyes given that they identify prey at a greater distance.
 - c. For species that pursue prey underwater, species that dive to deeper depths will have larger eyes due to the paucity of light.

2 | METHODS

2.1 | Species

For the purposes of this study, I defined an 'aquatic' species as being in one of two groups (taxonomy follows Jetz et al. (2012)). The first group consisted of 'seabirds' largely associated with

marine environments and included all species in the following families: Alcidae, Chionidae, Fregatidae, Phaethontidae, Procellariidae, Spheniscidae, Stercorariidae, and Sulidae. The second group included all species in families defined as 'aquatic' by the Wetlands International Species Assessment: Anatidae, Anhimidae, Anhingidae, Anseranatidae, Aramidae, Ardeidae, Balaenicipitidae, Burhinidae, Charadriidae, Ciconiidae, Dromadidae, Eurypygidae, Gaviidae, Glareolidae, Gruidae, Haematopodidae, Heliornithidae, Hydrobatidae, Ibidorhynchidae, Jacanidae, Laridae, Pedionomidae, Pelecanidae, Pelecanoididae, Phalacrocoracidae, Phoenicopteridae, Podicipedidae, Rallidae, Recurvirostridae, Rostratulidae, Scolopacidae, Scopidae, Thinocoridae and Threskionithidae. This excluded two families that live in non-wetland terrestrial environments but forage in water (Cinclidae (dippers) and Alcedinidae (kingfishers)), as well as species from largely terrestrial families that specialise in water, such as *Seiurus noveboracensis* (Northern Waterthrush) or *Phaeothlypis fulvicauda* (Buff-rumped Warbler). The ecological correlates of eye size for these families and species have been treated in previous analyses (Ausprey, 2021).

2.2 | Eye morphology

I extracted eye measurements from Stanley Ritland's unpublished dissertation, excluding measurements for juveniles or embryos (Ausprey & Ritland, 2024; Ritland, 1982). Briefly, SR extracted whole eyes from specimens preserved in formaldehyde or alcohol and measured the transverse width and axial length using 0.1mm Vernier callipers. For this manuscript I used axial length, which is considered a proxy for visual acuity, especially for species that hunt prey at large distances (Hall & Ross, 2007; Martin, 1994). In total I extracted all eye data collected by SR, which included $N=2989$ terrestrial species and $N=464$ aquatic species. Data for aquatic species included $N=42$ families and represented 46% of the aquatic avifauna (Table S1). The average number of specimens measured per species was 1.3 (range: 1–8), and I calculated mean species-specific axial length for use in subsequent analyses.

2.3 | Terrestrial habitats

A total of 99 species (21%) were listed by Bird Life International as being partially dependent upon forests (generally mangroves or sub-tropical/tropical moist forest). Given the relatively dark light environments found within forests and that terrestrial birds specialising in forests have larger eyes (Ausprey, 2021), I scored species as being either associated or not associated with forests and included this binary score as a covariate in analyses. In addition, a small minority of included species exclusively used terrestrial habitats ($N=25$, 5%). Of these, 17 species (3.6%) exclusively used non-forested habitats, such as grassland, scrub, desert, pastures, or scattered shrubs. These habitats are largely open and likely have similar light environments to

most aquatic habitats. For this reason, I did not include a separate covariate for non-forested terrestrial associations.

2.4 | Mass, diet, and migratory tendency

I extracted data on mass and migratory tendency from the AVONET database and diet from the Elton Traits database (Tobias et al., 2022; Wilman et al., 2014). I aggregated dietary percentiles into two groups: (1) % vertebrate and invertebrate diet and (2) % plant-based diet.

2.5 | Foraging behaviour

I used Birds of the World to group species into five broad foraging categories (Billerman et al., 2022):

1. Plunge-divers ($N=23$): Species that soar or hover >2m above the water and plunge-dive to capture fish and other prey within a few meters of the water's surface. This included gannets and boobies (Sulidae), tropicbirds (Phaethontidae), skuas and jaegers (Stercorariidae), pelicans (Pelecanidae), and some species of gulls and terns (Laridae).
2. Stalkers ($N=69$): Species that hunt while standing, walking, or running before striking or pouncing on prey either in water or on the shoreline. This included herons and egrets (Ardeidae), plovers (Charadriidae), as well as some species of storks (Ciconiidae) and sandpipers (Scolopacidae).
3. Seize-plunge-dippers ($N=90$): Oceanic species that use a wide variety of manoeuvres involving the capture of fish and invertebrate prey within a few meters above and/or below the water surface, such as surface-seizing, surface-plunging, surface-dipping, pattering, and contact-dipping. This included storm-petrels (Hydrobatidae), albatrosses (Diomedidae), petrels and shearwaters (Procellariidae) and some species of gulls and terns (Laridae).
4. Underwater-pursuers ($N=74$): Species that pursue or identify prey exclusively underwater, sometimes at great depths. This included auks (Alcidae), penguins (Spheniscidae), grebes (Podicipedidae), cormorants (Phalacrocoracidae), diving ducks (Anatidae), loons (Gaviidae), as well as some species of petrels and shearwaters (Procellariidae).
5. Surface-feeders ($N=208$): A broad category including any type of manoeuvre performed on or near the surface of water or land that does not require long-distance prey recognition. This included manoeuvres such as dabbling and head dipping (ducks: Anatidae), pecking and/or probing (sandpipers: Scolopacidae; jacanas: Jacanidae; rails: Rallidae; ibises: Threskiornithidae), chiselling (oystercatchers: Haematopodidae), filtering (flamingos: Phoenicopteridae), and scything/sweeping (avocets: Recurvirostridae). This category included species that initially detect prey tactility via sensors in the bill, as well as species that graze upon or dig up vegetation on land.

2.6 | Myopic versus hyperopic foraging

I defined all species using foraging manoeuvres that do not require long-distance prey recognition as being myopic, which included only species from the 'Surface-feeders' foraging group. All other species and foraging groups used foraging manoeuvres requiring long-distance prey recognition and were classified as hyperopic.

2.7 | Nocturnality

I scored species as being nocturnal only if they clearly specialised in crepuscular or nocturnal foraging behaviour as described in Birds of the World species accounts. This excluded many species known to forage throughout both the day and night (e.g. certain shorebirds and ducks).

2.8 | Waders and body height

I created an additional foraging group that consisted of all species that forage exclusively while standing, walking, or running. This group was referred to as 'Waders' and included all species from the 'Stalkers' group with select species from the 'Surface-feeders' group ($N=210$ species). I further divided this group into four categories: run-peck (species that chase prey before striking), nocturnal specialists, stalkers (species that hunt while standing or walking before striking prey from a distance), and species that peck, probe or scythe. Comprehensive data on the exact height of wading species when foraging does not exist. Instead, I used body length sourced from Birds of the World as a proxy for the distance that a species has to visualise its prey.

2.9 | Diving height and depth

For species that plunge-dive, I sourced approximate heights from Birds of the World ($N=21$ species). For species that underwater-pursue, I sourced dive depths from the Penguin database, which curates depth measurements generated by biologging devices attached to wild diving birds (Ropert-Coudert et al., 2018) ($N=22$ species).

2.10 | Olfactory detection

Many species of seabirds use olfaction to detect mainly dead animal material over vast oceanic distances (Nevitt, 2008). I did not include olfaction as a covariate, because (1) the extent of its occurrence among seabirds remains poorly defined and (2) its existence does not inherently alter detectability within short distances. That is, a

species may use smell to orient towards food over large distances (i.e. many kilometres), but likely uses its eyes to ultimately target the food source at small scales.

2.11 | Phylogeny

I used 100 hypothetical trees from a previously published avian phylogeny and pruned the tips to include the species used in this analysis (Jetz et al., 2012).

3 | ANALYSES

3.1 | Eye size allometry

Eye size exhibits strong body mass allometry, such that larger species tend to have larger eyes (Howland et al., 2004). In order to control for allometric relationships, I extracted the residuals of the ordinary least-squares regression of $\log(\text{eye size}) \sim \log(\text{body mass})$. These residuals reflect species-specific adaptations to variable light environments, as has been demonstrated previously for terrestrial birds (Ausprey, 2021). I repeated this analysis twice: once across all terrestrial and aquatic species measured by Ritland (1982) to compare eye size variation among the two groups, and once for only aquatic species in order to examine ecological correlates in eye size variation specific to that group. I used residuals rather than ratios of eye size to body mass (Smith, 1999), because ratios do not explicitly incorporate an allometric scaling factor.

3.2 | Ecological versus phylogenetic models

Because eye size is a morphological character expected to correlate with evolution, it was necessary to incorporate correlational structures reflecting phylogenetic relationships in regression analyses (Pagel, 1994). However, when ecological traits are strongly correlated with evolution, phylogenetic effects often mask ecological patterns, especially when traits exhibit large amounts of phylogenetic signal. For this reason, I used both ordinary least-squares and phylogenetic regression to represent (1) ecological models of trait correlation and (2) phylogenetic models that explicitly quantify correlated trait evolution. Phylogenetic models were constructed using the function *phylolm* in the package *phylolm* while incorporating a model of evolution based upon Pagel's lambda (λ) (Tung Ho & Ané, 2014). These analyses were looped across 100 hypothetical trees from the Bird Tree phylogeny (Jetz et al., 2012), with inference made from median coefficients.

First, I compared differences in eye-body mass allometry and residual eye size variation between aquatic and terrestrial bird species. I first examined differences in allometric relationships by regressing log absolute eye size on log body mass, with an

interaction term for terrestrial versus aquatic, and then used regression to quantify the difference in residual eye size variation between the two groups. Second, I created a global model incorporating binary variables for myopic versus hyperopic foraging, nocturnal specialisation versus general activity, migratory versus nonmigratory activity, and forest use versus open habitats, as well as a continuous variable for the percentage of invertebrates and animals in the diet. This model was used to estimate the relative amount of variation attributable to evolution and ecology using the *rr2* package (Ives, 2019). Third, I used univariate regression models to quantify pairwise differences in residual eye size among the five broad foraging groups. Fourth, I used additive regression models to estimate the marginal effects of binary variables for foraging behaviour, forest associations, nocturnal specialisation and migratory tendency using the function *emmeans* from the package *emmeans* (Lenth, 2020). Fifth, I regressed the relationship between residual eye size and the percent diet composed of animal and invertebrate prey with an interaction term for nocturnal activity. I restricted this analysis to surface foragers, because the diets of the other four foraging groups rarely included plant material. Sixth, I extracted all data for the 'Waders' foraging group and used a univariate regression model to quantify pairwise contrasts in residual eye size between the four foraging subgroups (run-peck, nocturnal, stalking and peck-probe-scythe). I also regressed the relationship between residual eye size and log body length, with an interaction term for the four foraging subgroups. Finally, I estimated the role of eye size in predicting dive heights of plunge-divers and depths of underwater-pursuers using additive regression models, with log dive height or depth as the dependent variables and residual eye size and log body mass as the predictor variables. For underwater-pursuers, I also used linear mixed models to analyse depths for individual birds, coding species as a random intercept using the function *lmer* in the package *lme4* (Bates et al., 2015). All pairwise comparisons were calculated using the package *emmeans* (Lenth, 2020). I projected interspecific variation in residual eye size and ancestral state reconstructions on the phylogenetic tree using the function *contMap* from the package *phytools* (Revell, 2012). I conducted all analyses in R (v. 4.2.1) (R Core Team, 2022). This study did not require ethical approval or permits.

4 | RESULTS

4.1 | Aquatic versus terrestrial species

The slope for the allometric relationship between log absolute eye size and log body mass was larger for terrestrial ($\beta=0.000571$, 95% CI=0.000561–0.000581) compared to aquatic ($\beta=0.000462$, 95% CI=0.000436–0.000487) species (Figure 1). This was due to a significant interaction between the two groups ($\beta=0.030$, $p<0.001$, $\lambda=0.89$). Hence, while aquatic species had significantly smaller eyes than terrestrial species on average ($\beta=-0.11$, $p=0.002$, $\lambda=0.89$), differences varied with body size. Small species (10g) had similar eye sizes between the two groups, whereas eye sizes of large species (10kg) were on average 1.4× larger for terrestrial species.

Residual eye size was significantly smaller for aquatic species ($\beta=-0.11$, $p=0.005$, $\lambda=0.89$). Mean residual eye size of aquatic species was -0.12 ± 0.01 SE versus 0.02 ± 0.01 SE for terrestrial species.

4.2 | Phylogenetic and ecological contributions to eye size variation

Residual eye size varied widely across the aquatic bird tree of life (Figure 2). Eye size was highly conserved ($\lambda=0.94$), and families showed marked differences in the range of size values (Figure S1). The ecological model explained 39% of residual eye size variation ($R^2=0.39$), with foraging behaviour explaining the majority ($R^2=0.26$). Given the large amount of signal for eye size variation, the relative contribution of ecology was reduced when introducing phylogenetic structure into the analysis. Phylogeny alone explained 65% of variation in eye size ($R^2=0.65$), with the ecological variables explaining an additional 13% ($R^2=0.13$) split between foraging behaviour ($R^2=0.07$) and the remaining variables ($R^2=0.06$).

4.3 | Foraging behaviour

There was strong evidence for correlated evolution between eye size and foraging behaviour. The ecological model showed stalkers and plunge-divers having the largest eyes, followed by

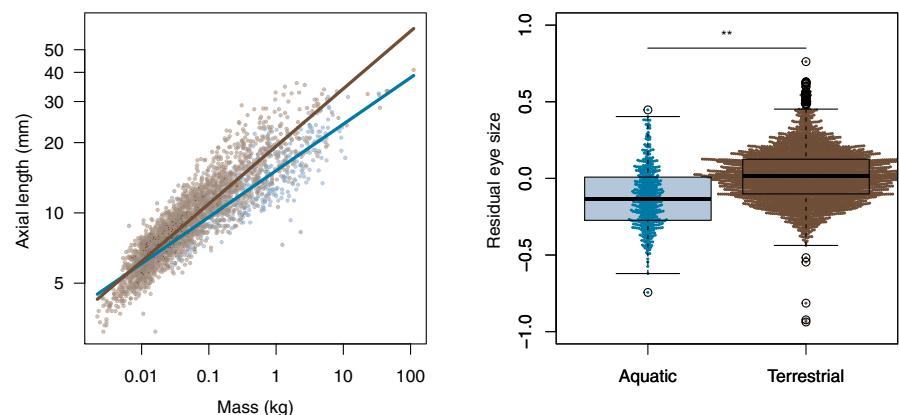


FIGURE 1 Variation in body mass allometry of absolute eye size (axial length) and residual eye size between terrestrial ($N=2989$ species) and aquatic ($N=464$ species) birds. $**p<0.01$.

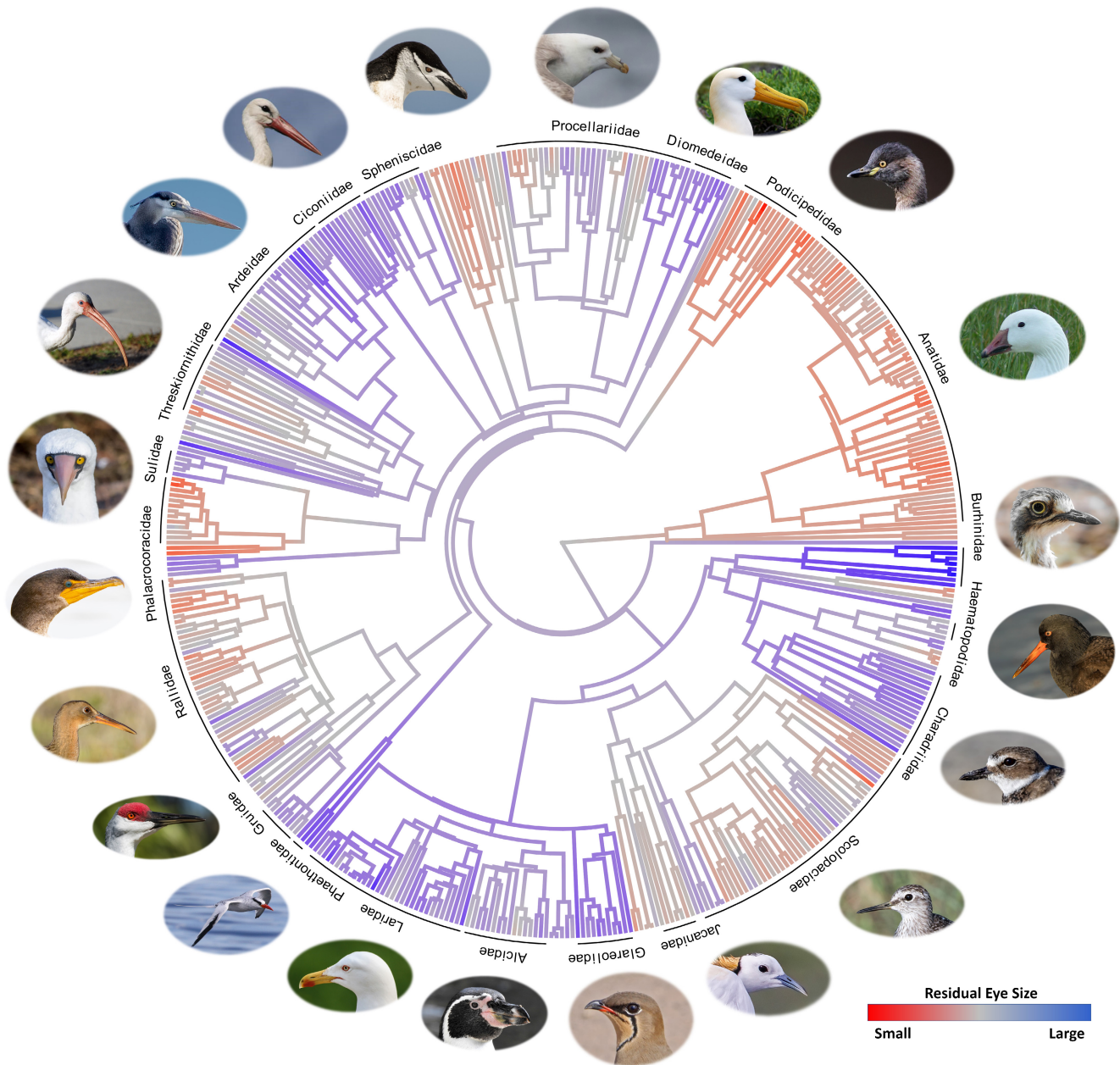


FIGURE 2 Variation in residual eye size (axial length) across the aquatic bird tree of life ($N=464$ species). Select families are noted. All photos are reproduced under a Creative Commons licence: M. Bonnie, D. Joyce, D. Behm, W. Tregaskis, A. Morffew, L. Leszczynski, Z. Jackson, N. Borrow, D. Miller, D. Freeman, H. Patibanda, T. Ruggeri, T. Benson, V. Pickering, P. Kavanagh, E. Ellingson, B. Matsubara, K. Koshy, K. Mortara, M. Guffey, M. Barrison.

seize-patter-dippers, and finally surface feeders and underwater pursuit-divers (Figure 3A; Table S2). Despite large amounts of phylogenetic signal ($\lambda=0.93$), results for the phylogenetic model were similar, except that seize-patter-dippers were only significantly different from underwater pursuit-divers.

When grouping foraging behaviours into myopic (near-sighted) versus hyperopic (far-sighted) categories, species using hyperopic manoeuvres had significantly larger eyes for both the ecological ($\beta=0.132$, $p<0.001$) and phylogenetic models ($\beta=0.039$, $p=0.023$), although the latter had a smaller effect size due to phylogenetic effects (Figure 3B).

4.4 | Nocturnal activity

As expected, nocturnal species had significantly larger eyes for both the ecological ($\beta=0.145$, $p<0.001$) and phylogenetic ($\beta=0.086$, $p<0.001$) models, although the latter had a smaller effect size due to phylogenetic effects (Figure 3C). When comparing the additive relationship between foraging behaviour and nocturnal activity, species with the smallest eyes tended to be diurnal myopic foragers, while species with the largest eyes were nocturnal hyperopic foragers (Figure 3D; Table S3).

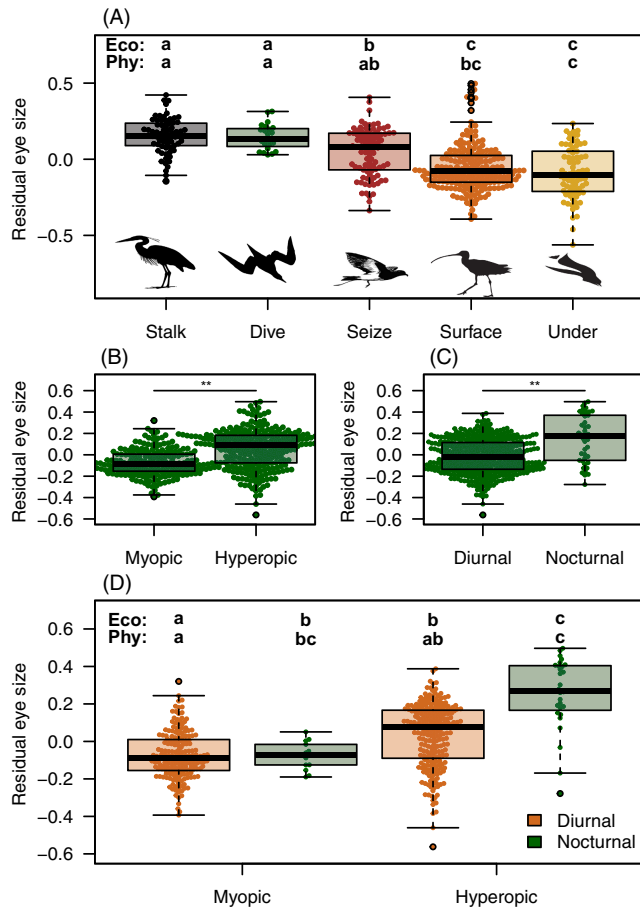


FIGURE 3 Foraging behaviour (A, B), nocturnal activity (C), and their interaction (D) drive eye size variation for $N = 464$ species of aquatic birds. $**p < 0.01$. Unique lowercase letters indicate significance among pairwise contrasts for ecological (Eco) and phylogenetic (Phy) models ($p < 0.05$).

4.5 | Forest associations

Species that associated with forests had significantly larger eyes for both the ecological ($\beta = 0.044$, $p = 0.013$) and phylogenetic ($\beta = 0.042$, $p < 0.001$) models.

4.6 | Migratory tendency

There was no difference in residual eyes size between resident and migratory species for both the ecological ($\beta = 0.017$, $p = 0.281$) and phylogenetic ($\beta = 0.010$, $p = 0.322$) models.

4.7 | Diet

For surface foragers, diurnal species that consumed larger amounts of vertebrate and invertebrate prey had significantly larger eyes for both the ecological ($\beta = 0.002$, $p < 0.001$) and phylogenetic ($\beta = 0.0006$, $p = 0.040$, $\lambda = 0.94$) models, although the latter had

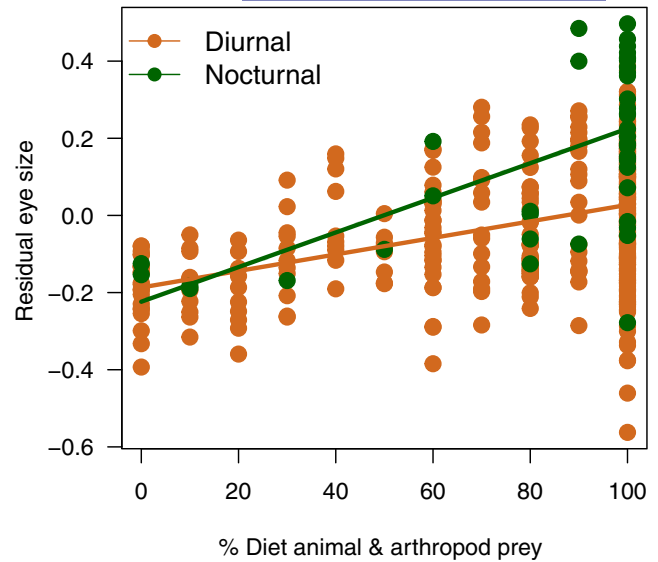


FIGURE 4 Surface feeders that consume more animal and invertebrate prey have larger eyes, especially for nocturnal species. $N = 208$ species.

a smaller effect size due to phylogenetic effects (Figure 4). There was a significant behavioural interaction, such that the positive relationship between residual eye size and consumption of prey was stronger for nocturnal species (Eco: $\beta = 0.002$, $p = 0.004$; Phy: $\beta = 0.002$, $p = 0.026$).

4.8 | Waders

When examining foraging behaviours for wading species, the ecological model showed that species using run-peck manoeuvres (e.g. plovers) had the largest eyes, followed by nocturnal species (e.g. night-herons) and stalkers (e.g. herons) with intermediate eyes sizes, and species using pecking, probing or scything manoeuvres with the smallest eyes (e.g. shorebirds and avocets) (Figure 5; Table S4). Due to large amounts of signal ($\lambda = 0.93$), the phylogenetic model showed only significant differences between peck-probe-scything species and nocturnal and run-peck species.

The hypothesis that taller species visualising prey at longer distances would have larger eyes was strongly supported. Eye size was positively correlated with body length irrespective of foraging groups for both the ecological ($\beta = 0.30$, $p < 0.001$) and phylogenetic ($\beta = 0.23$, $p = 0.006$) models. For the ecological model, there was a positive correlation between residual eye size and body length for species that peck-probe-scythe ($\beta = 0.25$, $p < 0.001$). There was a further significant positive interaction with stalkers ($\beta = 0.33$, $p = 0.043$), nocturnal species ($\beta = 1.31$, $p < 0.001$), and run-peck species ($\beta = 0.68$, $p < 0.001$) (Figure 5). Hence, the positive relationship between eye size and body length was strongest for nocturnal species, followed by run-peck species, stalkers and

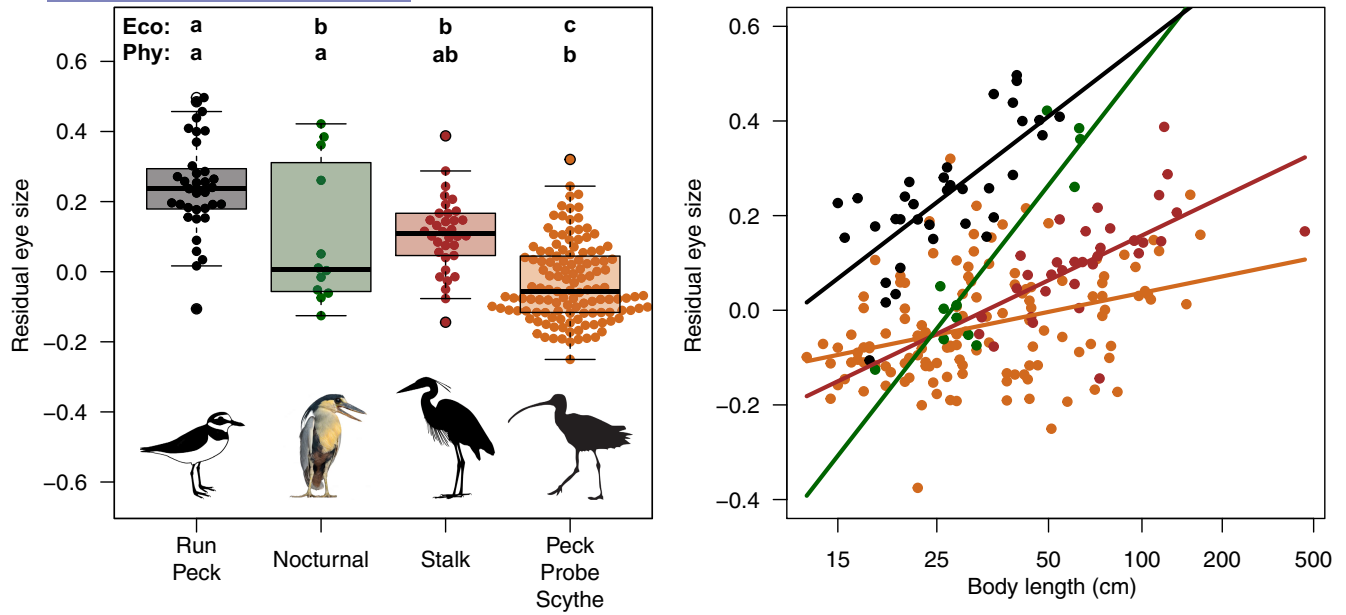


FIGURE 5 Foraging behaviour and body length predicts variation in residual eye size for $N=210$ wader species. Unique lowercase letters indicate significance among pairwise contrasts for ecological (Eco) and phylogenetic (Phy) models ($p < 0.05$). Solid regression lines indicate significant slopes ($p < 0.05$).

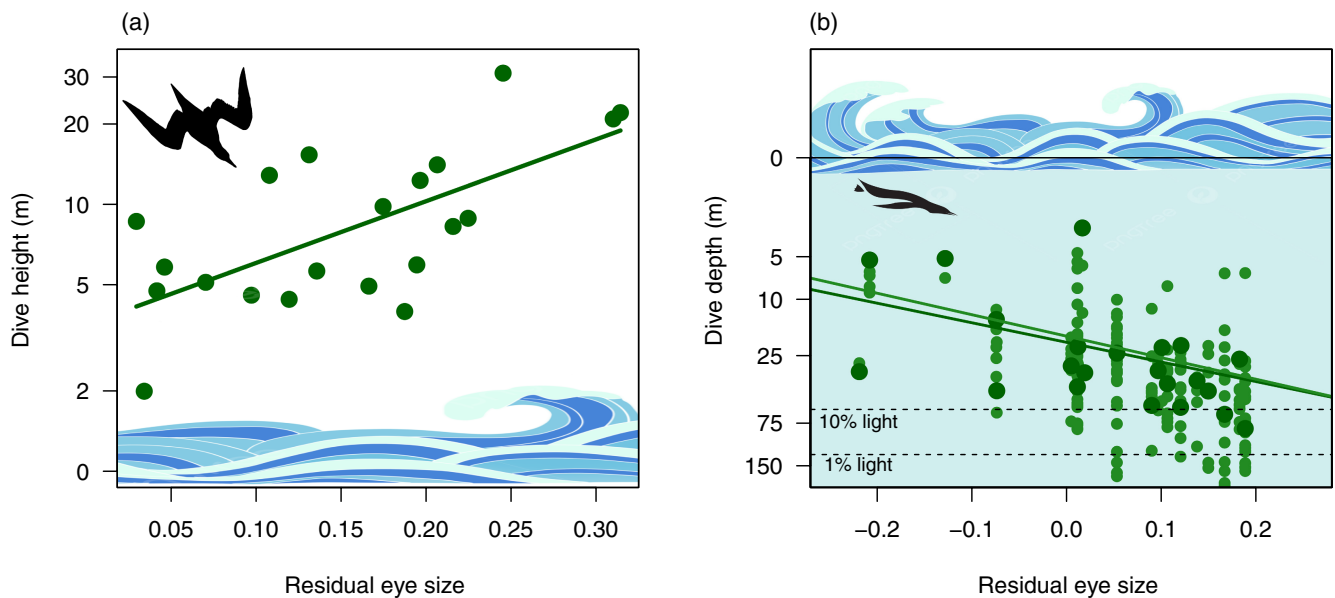


FIGURE 6 Eye size predicts (a) dive height for $N=21$ species of plunge-divers and (b) dive depth for $N=22$ species of underwater pursuit-divers. In (b) small light green dots are individual measurements fit with a linear mixed model using species as a random intercept; large dark green dots are species means fit by phylogenetic regression. Values are partial residuals for residual eye size after accounting for log body mass. The depths at which 10% (60m) and 1% (125m) of light remain in clear ocean water are from (Hill, 1962).

peck-probe-scythers. The phylogenetic model showed a similar positive relationship with body length for species that peck-probe-sweep ($\beta=0.16$, $p=0.05$) and a significant positive interaction for nocturnal species ($\beta=0.98$, $p=0.005$). There was no significant interaction with stalkers ($\beta=0.29$, $p=0.17$) or species that run-peck ($\beta=0.38$, $p=0.12$). Hence, phylogenetic effects masked ecological differences among foraging groups for the relationship with body length ($\lambda=0.89$).

4.9 | Plunge-divers and underwater-pursuers

Plunge-divers that initiated dives from greater heights tended to have larger eyes ($\beta=5.34$, $p=0.001$) and larger body masses ($\beta=0.49$, $p<0.001$) (Figure 6). Underwater pursuers that foraged at greater depths also had larger eyes (species means: $\beta=3.92$, $p=0.01$; individual values: $\beta=4.45$, $p=0.003$) and larger body masses (species means: $\beta=0.35$, $p=0.010$; individual values: $\beta=0.49$, $p=0.005$).

Values for ecological and phylogenetic models were identical due to zero phylogenetic signal.

5 | DISCUSSION

I found strong support for correlated evolution between eye size and ecological factors related to foraging behaviour, diet and nocturnality. Similar to terrestrial birds, species engaging in long-distance (hyperopic) prey recognition had larger eyes after correcting for body mass, while species using near-sited (myopic) foraging manoeuvres and eating plants had smaller eyes. For species that walk while searching for food ('waders'), taller species that presumably need enhanced visual acuity to identify prey at a greater distance had larger eyes. Plunge-divers had the largest relative eye sizes across all foraging groups, with species diving from the greatest heights having the largest eyes. Even illuminance gradients underwater seemed to drive eye size evolution, with larger eyes predicting greater diving depths where light levels fall to <10%. Phylogeny alone explained 62% of eye size variation, demonstrating the central role that visual systems have played in the evolution of the aquatic avifauna.

5.1 | Aquatic versus terrestrial species

As expected, aquatic species had significantly smaller eyes compared to terrestrial species, supporting the prediction that the relatively bright environments found in aquatic ecosystems negate the adaptive benefit of developing larger eyes that presumably improve visual acuity and sensitivity in darker conditions. This was further supported by the fact that aquatic species at least partially associated with enclosed habitats like forested wetlands or mangroves also had significantly larger eyes. There are two potential explanations for differences in eye size allometry between aquatic and terrestrial species. First, eyes are metabolically expensive organs to maintain (Laughlin et al., 1998; Moran et al., 2015), and bright aquatic environments likely provide sufficient illumination to facilitate visual recognition beyond the adaptive benefits of evolving larger eyes that improve visual acuity. Second, large eyes are particularly susceptible to disability glare (Fernandez-Juricic et al., 2012; Fernandez-Juricic & Tran, 2007), especially for species that lack optical adnexa that limit the amount of light entering the eye (Martin & Katzir, 2000). Such 'sun shades' are more common in larger species with eye axial lengths >18mm, and many species included in this analysis have eyes exceeding this value. Finally, there was a significant interaction between the two groups for the allometric relationship between body mass and absolute eye size, with the slope of the allometric curve being shallower for aquatic species. Hence, the difference in absolute eye size between terrestrial and aquatic species increased with body mass, emphasising the idea that the evolutionary constraints to eye size development are likely more extreme for larger species.

5.2 | Ecological correlates and phylogenetic relationships

Ecological correlates of eye size variation were consistent with similar comparative assessments of the terrestrial avifauna: hyperopic foraging manoeuvres, carnivorous diets, and nocturnal activity predicted larger eye sizes (Ausprey, 2021; Beauchamp, 2023; Garamszegi et al., 2002; Hall & Ross, 2007; Liu et al., 2012; Martin & Piersma, 2009). These results also support past comparative analyses of shorebird communities that linked larger eye sizes to nocturnal behaviours (Thomas et al., 2006) and points to the pervasive role of light as a mediator in food acquisition that extends even to aquatic ecosystems with limited to no vegetation structure.

Phylogenetic relationships alone explained 62% of variation in residual eye size, and trait values were highly clustered at the family level (Figure S1). These results are almost identical to results found for the terrestrial avifauna (61%) (Ausprey, 2021), suggesting that avian visual systems have contributed similarly to avian evolution in both aquatic and terrestrial ecosystems. Furthermore, trait evolution has been found to have a predictive accuracy of 65% in explaining ecomorphological relationships across the full avian tree of life (Pigot et al., 2020), meaning that eye size has potentially made a similar contribution to avian evolution as other morphological traits such as bill size and shape and tarsus length.

5.3 | Plunge-divers

Species that hunt for fish and other aquatic fauna by scanning from above the water surface must navigate the challenges of identifying distant prey occupying variable environmental conditions. This involves factors that alter the clarity of water (e.g. turbidity), as well as the refraction of light and wind-induced glitter that change the apparent position of prey (Darby et al., 2022; Horváth & Varjú, 1990; Preisendorfer & Mobley, 1986). Given that plunge-divers do not dive to great depths (<5 m), the only way to increase the surveyable area and, hence, availability of prey, is by increasing the survey height, which comes at cost of reduced visual acuity (Eriksson, 1985). This may explain why plunge-divers foraging from greater heights have larger eyes, which presumably improve the spatial resolution and sensitivity of prey detection (Land & Nilsson, 2012).

Explanations for how plunge-diving species cope with variable environmental conditions appear less clear. Plunge-divers have long been thought to select relatively clear water when foraging that presumably eases the recognition of prey (Ainley, 1977). Indeed, capture success for Damara, Royal, Little and Sandwich Terns has been documented to improve with increasing clarity, and Sandwich Terns will switch to deeper dives in the clearest of conditions (Baptist & Leopold, 2010; Braby et al., 2011; Brenninkmeijer et al., 2002). However, some species, such as the Pied Kingfisher, are more successful in turbid water (Holbech et al., 2018), and many plunge-diving species are not necessarily more abundant in clear versus turbid waters (Haney & Stone, 1988). This could be explained by the

evasiveness of prey, which can better detect approaching predators in clearer waters due to Snell's Window (Katzir & Camhi, 1993; Lythgoe, 1979). Plunge-divers appear to partially surmount this obstacle by rapidly altering their visual capabilities upon striking the water's surface, such that they transform from excellent aerial spotters to highly effective underwater pursuers able to compensate for the delay incurred from initial detection to eventual capture (Machovsky-Capuska et al., 2012). What remains unknown is how plunge-divers compensate for potential disability glare associated with the scattered reflection of light from the water's surface (Lythgoe, 1979; Machovsky-Capuska et al., 2012), a problem presumably particularly acute for this group of species given their exceptionally large eyes.

5.4 | Waders

Species that detect and capture prey while walking face a similar trade-off between increased survey area associated with a higher vantage and reduced visual acuity, which may explain the pattern of taller species overall having larger eyes. This relationship was strongest for nocturnal specialists that presumably have to overcome extreme reductions in spatial resolution. Stalkers, (e.g. herons), showed the next strongest relationship, which makes sense given their sit-and-wait approach to prey capture. Herons, especially those that forage primarily in water, are well-known for their ability to behaviourally compensate for the refractive effects of water that make prey appear closer than reality by adjusting their attack angle mid-strike (Katzir et al., 1989, 1999; Katzir & Intrator, 1987). Furthermore, herons appear to tilt their heads towards the sun in an effort to move patches of glare on the water's surface away from their foraging targets (Krebs & Partridge, 1973). Given the wide array of prey that stalking species capture, including fish, amphibians, frogs, and macroinvertebrates (Niethammer & Kaiser, 1983; Willard, 1977), it makes sense that taller species that have to visualise at a greater distance should have larger eyes. Interestingly, even species that use more myopic picking, tactile, and filtering manoeuvres, such as shorebirds and avocets, had a subtle yet significant positive relationship between body height and eye size. This suggests that a sufficient number of captures involving optical recognition exist to promote the adaptive benefits of increased visual acuity. Finally, species that run and pounce (e.g. plovers) also showed a positive relationship between body height and eye size. Unlike sit-and-wait predators, these species run towards their prey, meaning that physical agility associated with non-visual morphological and behavioural traits may contribute to foraging success, as well.

5.5 | Pursuit-divers

Pursuit-divers are largely visual foragers that must detect prey against rapidly changing illumination levels. Since both the visual availability of prey and visual acuity of predators improve in brighter

conditions (Stempniewicz et al., 2013; White et al., 2007), factors that degrade light availability, such as the angle of the sun, extent of clouds, or water turbidity, indirectly drive foraging behaviour (Darby et al., 2022). Although light levels change with environmental conditions, in clear ocean water light intensity attenuates to 1% at approximately 125m (Hill, 1962). While pursuit-divers forage over a wide range of depths, results from studies utilising depth loggers demonstrate strong interspecific variation in average diving depths (Halsey et al., 2006), and, as expected, I found that species diving deeper where water illumination is darker tend to have larger eyes that presumably improve visual sensitivity and spatial recognition.

There is strong evidence across species that foraging intensity peaks midday when light levels are at their brightest (Schreer et al., 2001; Shoji et al., 2014; Wilson et al., 1989), as well as diving depth (Chappell et al., 1993; Croxall et al., 1993; Wanless et al., 1999; White et al., 2008; Wilson et al., 1993). Even species foraging with little to no access to light, such as at night or during the winter at high latitudes, appear to track light availability. For example, nocturnally foraging Common Murres dive to greater depths and are more successful during light conditions approximating moonlight versus starlight (Regular et al., 2011). Interestingly, cormorants have among the smallest relative eye size of all pursuit-divers and extremely poor visual acuity, yet regularly forage at extremely low light levels similar to twilight (1–100 lux), including throughout the polar winter when luminosity falls to <1 lux (Grémillet et al., 2005; White et al., 2007). They apparently behaviourally compensate by utilising strike manoeuvres similar to those employed by herons after initial coarse visualisation (Grémillet et al., 2005). A large amount of variation in diving behaviour is explained by the diel migrations of prey communities through the vertical water column, as is the case for Common Murres that follow capelin movements upwards at dusk and downwards at dawn (Regular et al., 2010). However, experiments that control for prey availability show a strong positive correlation between foraging intensity and light intensity (Cannell & Cullen, 1998). Likewise, foraging depth is often correlated with light intensity during the daytime when prey is of limited availability (e.g. when prey rise upwards at dawn and dusk) (Elliott & Gaston, 2015). Furthermore, seabirds are attracted to artificial light, which has emerged as a major conservation concern near coastlines, oil rigs, and large fishing vessels (Ostaszewska et al., 2017). Cumulatively, the evidence suggests that underwater pursuit-divers are at least partially limited by light illumination, which would explain the apparent correlated evolution between diving depth and eye size.

5.6 | Additional factors

Visual acuity represents just one component of the avian visual system that contributes to the foraging efficiency of aquatic birds. For example, the cornea can no longer refract light upon immersion in water, and species adapted to underwater prey recognition compensate either with spherical lenses or specialised scleral ossicles and muscles in the iris that 'push' the lens forward and partially out of the

pupillary aperture (Cronin, 2012; Machovsky-Capuska et al., 2012). Both strategies collectively maximise refractive power and improve focus when underwater. Additionally, visual fields define the 3-dimensional area perceived by a bird and exhibit interspecific variation that is strongly correlated with foraging ecology, especially among aquatic species (Cantlay et al., 2023). Species that employ precision guided lunging manoeuvres, such as herons, tend to have binocular fields that extend perpendicular below the bill, while surface filtering ducks cannot see their own bills and instead have binocular vision extending in a narrow field surrounding the upper part of the head (Martin, 2007). Finally, many seabirds in the families Procellariidae and Diomidae use olfaction to detect prey over vast oceanic distances (Nevitt, 2008). Given that the sense of smell operates over far greater distances than sight, these species undoubtedly use olfaction to hone to a general foraging area before switching to visual cues when identifying exact targets (Martin, 1998). Future large-scale comparative analyses are needed to clarify the relative contribution of eye size in regulating foraging behaviour compared to other elements of the avian visual system (Martin & Piersma, 2009).

AUTHOR CONTRIBUTIONS

Ian J. Ausprey conceived the ideas, extracted and curated the data, performed the analyses, and wrote the manuscript.

ACKNOWLEDGEMENTS

Eye size measurements for terrestrial species were originally digitised by S. Montgomery and K. Perez, with funding provided by the Katherine Ordway Chair of Ecosystem Conservation at the Florida Museum of Natural History. I am indebted to Stanley Ritland and Alice Hutchison for the heroic amount of work that went into collecting the eye measurements. Open access funding provided by Universitat Bern.

CONFLICT OF INTEREST STATEMENT

I declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3xsj3txq7> (Ausprey & Ritland, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Taxonomic coverage of species sampled by Stanley Ritland and included in this analysis.

Table S2. Pairwise contrasts in residual eye size among foraging groups for $N=464$ species of aquatic birds.

Table S3. Pairwise contrasts for differences in residual eye size among ecological variables related to foraging behavior, nocturnal specialization, migratory tendency, and habitat.

Table S4. Pairwise contrasts in residual eye size variation among foraging behavioral groups for wading aquatic birds ($N=210$ species).

Figure S1. Residual eye size (axial length) for $N=464$ species of aquatic birds in $N=42$ families.

How to cite this article: Ausprey, I. J. (2024). Eye morphology contributes to the ecology and evolution of the aquatic avifauna. *Journal of Animal Ecology*, *00*, 1–13. <https://doi.org/10.1111/1365-2656.14141>