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Letter

Mammalian retinal specializations for high acuity vision evolve in response to both foraging strategies and morphological constraints

Emily E.K. Kopania and Nathan L. Clark

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, United States

Corresponding author: Department of Biological Sciences, University of Pittsburgh, 103 Clapp Hall, Fifth and Ruskin Avenues, Pittsburgh, PA 15213, United States. Email: emk270@pitt.edu

Abstract

Vision is a complex sensory system that requires coordination among cellular and morphological traits, and it remains unclear how functional relationships among traits interact with ecological selective pressures to shape the evolution of vision. Many species have specialized high visual acuity regions in the retina defined by patterns of ganglion cell density, which may evolve in response to ecological traits. For example, ganglion cell density can increase radially towards the center of the retina to form an area centralis, which is thought to improve acuity towards the center of the visual field in predators. Another example is the horizontal streak, where ganglion cells are dense in a horizontal pattern across the retina, which is thought to be beneficial in horizon-dominated habitats. At the morphological level, many have proposed that predation selects for high orbit convergence angles, or forward-facing eyes. We tested these hypotheses in a phylogenetic framework across eutherian mammals and found support for the association between the horizontal streak and horizon-dominated habitats. However, we did not find a significant association between orbit convergence and predation. We also tested if retinal specializations evolve in response to orbit convergence angles. We found that horizontal streaks were associated with side-facing eyes, potentially facilitating panoramic vision. Previous studies observed that some species with side-facing eyes have an area centralis shifted towards the temporal side of the retina, such that the high acuity region would project forward, but this relationship had not been tested quantitatively. We found that the temporal distance of the area centralis from the center of the retina was inversely correlated with orbit convergence, as predicted. Our work shows a strong relationship between orbit convergence and retinal specializations. We find support that both visual ecology and functional interactions among traits play important roles in the evolution of ocular traits across mammals.

Keywords: vision, orbit convergence, area centralis, horizontal streak, phylogenetic comparative methods, mammals

Introduction

Many species rely on visual cues for important behaviors such as detecting predators, finding food, and finding mates (Caves et al., 2018). Vision-related traits exhibit remarkable divergence across taxa, and these differences may be adaptations to different visual environments (Baker & Venditti, 2019; Caves et al., 2017, 2018; Nilsson, 2021). Some vision-related traits are associated with habitats or behaviors even after accounting for shared evolutionary history, suggesting that these traits may evolve in response to selective pressures imposed by the visual environment (Baker & Venditti, 2019; Cantlay et al., 2023; Caves et al., 2017, 2024; Chong et al., 2024; Potier et al., 2017, 2023). For example, visual acuity, or spatial resolving power, is associated with habitat complexity in both fish and birds (Caves et al., 2017, 2024), and relative corneal size increases in nocturnal mammals (Baker & Venditti, 2019). However, developmental and functional constraints are also expected to play an important role in the evolution of ocular traits (Nilsson, 2021). For many ocular traits, it remains unclear if they are associated with ecological traits that may impose selective pressures on vision. Additionally, vision is a complex sensory system that integrates traits from the cellular level, such as the arrangements of retinal cell types, to the morphological level, such as the size and orientation of the eyes. These cellular and morphological traits may be evolving in response to the same selective pressures and could also impose functional constraints on each other, so understanding their relationships is important for gaining a complete understanding of the evolution of vision (Hughes, 1977).

One such trait is orbit convergence, or the angle of the orbits (i.e., eye sockets) relative to the anterior–posterior axis of the skull (Figure 1A). A higher orbit convergence angle corresponds to more forward-facing eyes, with an angle of 90° indicating that the orbits face directly forward. Orbit convergence is highly correlated with binocular overlap, or the extent to which the visual fields of each eye overlap, which is thought to facilitate visual acuity and depth perception (Heesy, 2004; Read, 2021). Lower orbit convergence

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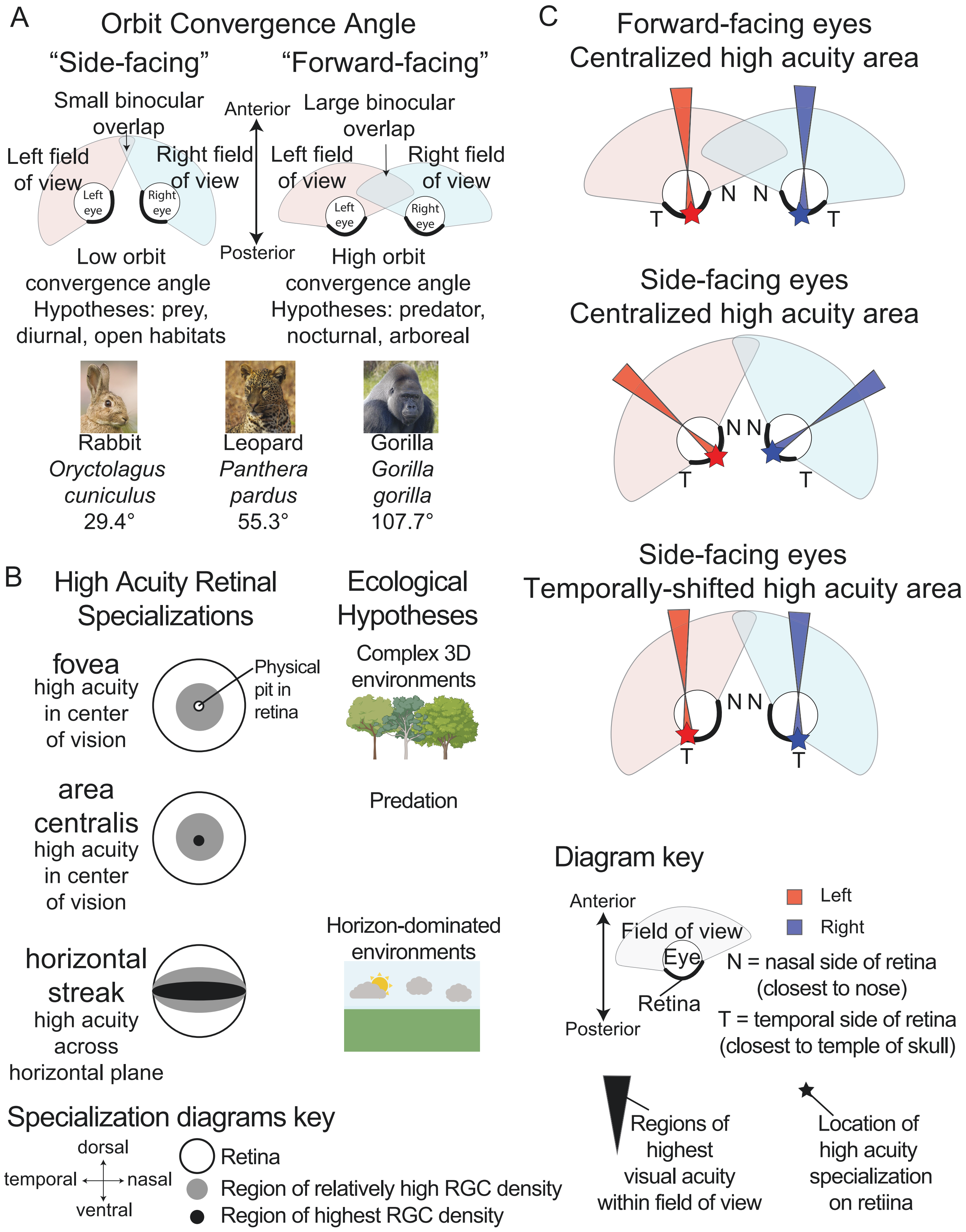

Figure 1. Ocular trait evolutionary hypotheses. (A) Diagrams depicting different orbit convergence angles, hypotheses for ecological conditions that may act on orbit convergence, and example species depicting the range of orbit convergence angles in mammals. Eye diagrams are shown from the dorsal perspective such that the top is the anterior direction and the bottom is the posterior direction. The left semicircle in red represents the left eye's field of view, the right semicircle in blue represents the right eye's field of view, and the purple area in between represents the overlap between the two, or the binocular overlap. Rabbit photo by JJ Harrison and used under Creative Commons Attribution-Share Alike 3.0 Unported license. Leopard photo by Thomas Fuhrmann and gorilla photo by Thurundir, both used under Creative Commons Attribution-Share Alike 4.0 International license. (B) Retinal specialization diagrams and hypotheses for ecological conditions they may be associated with. Specialization diagrams are adapted

angles correspond to more side-facing eyes, which may facilitate panoramic vision and allow animals to have a wider field of view (Heesy, 2007; Hughes, 1977; Walls, 1942). Within mammals, primates have exceptionally high orbit convergence angles, and this has been hypothesized to be an adaptation to arboreal lifestyles or nocturnal predation in the ancestral primate species (Cartmill, 1972, 1974; Heesy, 2007). Outside of primates, carnivores tend to have high orbit convergence, while groups with more herbivorous species such as lagomorphs and artiodactyls tend to have low orbit convergence (Hughes, 1977; Walls, 1942). These observations led to the hypothesis that high orbit convergence is adaptive in predators, whereas low orbit convergence is beneficial in species that experience high predation rates to facilitate predator detection across a wider visual field (Hughes, 1977; Walls, 1942). This is often assumed to be the case, but this pattern has not been tested broadly across mammals in a phylogenetic framework. Some studies have focused on a few species or particular clades (Casares-Hidalgo et al., 2019; Noble et al., 2000; Pilatti & Astúa, 2016; Smith et al., 2018; Vega-Zuniga et al., 2013), but these groups do not encapsulate all the variation in orbit convergence that exists across mammals. Others have found that orbit convergence is associated with nocturnal predators (Heesy, 2007) or with body mass specifically in forested environments (Changizi & Shimojo, 2008), but these studies did not correct for phylogenetic relatedness. Thus, it remains unclear if arboreality, nocturnality, predation, or some combination of these traits are associated with high orbit convergence across mammals.

Cellular phenotypes in the eye, such as specialized regions of high acuity, have also diverged across taxa and may be associated with ecological traits. Retinal regions of high acuity impart the ability to see fine spatial details, and they arise from localized concentrations of ganglion cells, which send the visual signal to the brain (Caves et al., 2018; Collin, 1999; Moore et al., 2017). Most vertebrates do not have consistent ganglion cell density throughout the retina, but instead have regions of high and low density; the human retina, for example, ranges over 100-fold from 200 cells/mm^2 near the periphery to 38,000 cells/mm^2 towards the center (Curcio & Allen, 1990). Many vertebrate taxa including mammals have evolved different high acuity retinal specializations, which are defined by patterns of high retinal ganglion cell density (Collin, 1999; Moore et al., 2017). One specialization, the fovea, is an indentation in the retina surrounded by a region of high cell density (Figure 1B). Other retinal specializations include the area centralis, a centralized region of high cell density, and horizontal streak, an elongated region of high cell density stretching across the retina (Figure 1B). These specializations have evolved repeatedly across vertebrates, suggesting they may have adaptive potential and may evolve in response to different aspects of visual ecology (Collin, 1999; Moore et al., 2017). Within mammals, only primates have a fovea (Bringmann et al., 2018), but the area centralis and horizontal streak may have evolved multiple times independently. Many have proposed hypotheses regarding the ecological drivers that select for these retinal specializations. For example, the area centralis is thought to help detect prey movement and therefore may be an adaptation for predation (Moore et al., 2017; Yoshimatsu et al., 2020). The horizontal streak is hypothesized to be associated with "horizon-dominated" environments, particularly ground-foraging species in relatively unobstructed environments such as grasslands or deserts (Hughes, 1977). Some mammal species support these predictions (Hughes, 1977; Moore et al., 2017; Navarro-Sempere et al., 2018), but these hypotheses have not been directly tested across mammals in a phylogenetic framework.

Ecological traits such as predation, nocturnality, or horizon-dominated environments may impose selective pressures on both orbit convergence and high acuity retinal specializations. For example, a horizontal streak in combination with low orbit convergence may facilitate panoramic vision (Hughes, 1977). High orbit convergence and the fovea are both thought to improve depth perception, which may be beneficial for predators to detect prey (Bringmann, 2019; Cartmill, 1972; Heesy, 2004; Moore et al., 2017; Steenstrup & Munk, 1980). These traits may also impose functional or developmental constraints on each other. Species with low orbit convergence (i.e., side-facing eyes) and an area centralis may be more likely to have the area centralis located towards the temporal side of the retina, closer to the temple of the skull. This temporal shift of the area centralis in species with side-facing eyes is predicted to facilitate high acuity vision towards the front, despite the side-facing orbits (Figure 1C; Collin, 1999; Hughes, 1977; Moore et al., 2012). While some studies have found support for these predictions in particular species (Collin, 1999; Moore et al., 2012), it remains unclear if orbit convergence is correlated with the types and position of retinal specializations across mammals.

Here, we test if orbit convergence and retinal specializations are associated with ecological traits (Table 1), and with each other, through a phylogenetic comparative study across eutherian mammals. We used the most complete mammal phylogeny to date based on genomic data (Genereux et al., 2020), measured orbit convergence from museum specimens, and combined these data with published data on orbit convergence, retinal specializations (Supplementary Table S1), and ecological traits (Wilman et al., 2014) to address four main questions:

(1) Which ecological traits are associated with orbit convergence after controlling for phylogeny?
(2) Is the area centralis associated with predator species?
(3) Is the horizontal streak associated with horizon-dominated environments?
(4) Is there a relationship between orbit convergence and high acuity retinal specializations?

Methods

Samples and data collection

We measured orbit convergence from museum specimens from the Carnegie Museum of Natural History for 28 mammal species (Supplementary Table S1) using a custom-built dihedral goniometer to measure the angle between the plane of the orbit and the sagittal plane (Supplementary Figure S1) (Noble et al., 2000; Ross,

from Moore et al. (2017). RGC = retinal ganglion cell. Arboreal and horizon-dominated environments created using Biorender. Cheetah silhouette is a public domain image from PhyloPic. (C) Predicted directions of high acuity vision based on orbit convergence angle and position of high acuity retinal specialization. Species with forward-facing eyes and centrally located high acuity specializations will have the highest visual acuity towards the front (top), whereas species with side-facing eyes and centrally located high acuity specializations will have the highest visual acuity towards the sides (middle). Thus, species with side-facing eyes are predicted to have high acuity specializations located more towards the temporal side of the retina to facilitate higher visual acuity towards the front (bottom) (Collin, 1999).

Table 1. Definitions of ecological traits and hypotheses for associations with ocular traits.

Ecological trait	Definition	Orbit convergence prediction	Retinal specialization prediction
Diet—predator	Species labeled as predators if EltonTraits diet categories for invertebrates and vertebrates sum to at least 70% of diet	Higher orbit convergence in predators	Predators more likely to have an area centralis
Diet—herbivore	Species labeled as herbivores if EltonTraits diet categories for plant material sum to at least 70% of diet	Lower in herbivores	NA
Activity pattern	Species labeled as nocturnal if nocturnal = 1 and crepuscular and diurnal = 0 in EltonTraits database; species labeled as diurnal if nocturnal and crepuscular = 0 and diurnal = 1 in EltonTraits database; all other combinations labeled as crepuscular/cathemeral	Higher in nocturnal species	NA
Nocturnal predation	Species labeled as both “predator” and “nocturnal” based on the above diet and activity pattern definitions	Higher in nocturnal predators	NA
Foraging substrate	Foraging strategies from EltonTraits were used, with the addition of a “fossorial” category (see *Methods* for list of foraging strategy categories and fossorial species)	Higher in arboreal foragers and lower in ground foragers	Ground foragers more likely to have a horizontal streak (horizon-dominated environment)
Predators in complex, 3D environments	Species labeled as predators and also as arboreal or marine foragers	NA	Predators in complex, 3D environments more likely to have an area centralis
Small, ground-foraging herbivore	For orbit convergence, we tested if interaction terms between foraging strategy and herbivory or size and herbivory had a significant effect on orbit convergence. For retinal specializations, we placed ground-foraging herbivores <100 kg in this category	Lower in small, ground-foraging herbivores	Small, ground-foraging herbivores more likely to have a horizontal streak
Unobstructed, horizon-dominated habitats	Species that primarily reside in grassland, savannah, tundra, or desert habitats (Myers et al., 2024)	NA	Species in unobstructed horizon-dominated habitats more likely to have a horizontal streak (terrain hypothesis, Hughes, 1977)

Note. NA = Not applicable.

1995). We stabilized skulls using clay or rice and measured the vertical distance from the base of the goniometer to the inion, basion, and prosthion of the skull to ensure the sagittal plane was parallel with the bottom of the goniometer. We then folded the top part of the goniometer and adjusted the position of the skull until three pins of equal length touched three points on the orbit. We used the orbitale superius, orbitale anterius, and orbitale inferius to mark the plane of the orbit (Heesy, 2004; Ross, 1995). For some specimens, there was no orbitale inferius or it was difficult to identify, so we used the orbitale posterius instead (Casares-Hidalgo et al., 2019) (Supplementary Table S1). We then used a digital protractor (Insize Co., Ltd) to measure the angle between the two planes of the goniometer. To collect data from species representing a wide range of sizes, we had three sizes of goniometers built (3 inches^2, 12 inches^2, and 36 inches^2). We also obtained orbit convergence measurements from another 63 species from published sources (Casares-Hidalgo et al., 2019; Heesy, 2004, 2005) for a total of 91 species with orbit convergence data. These studies used a MicroScribe coordinate data stylus to mark skull landmarks in three-dimensional space and calculate the orbit convergence angle based on the positions of these landmarks. To verify the consistency of our method with the coordinate data stylus approach, we measured orbit convergence for nine species that also had values reported in previous studies, and we found that our measurements were consistent with those reported in the literature (Supplementary Figure S2).

We used information on retinal specializations for 82 species from published studies that categorized retinal specializations based on retinal ganglion cell density (Supplementary Table S1). For 26 species that had a fovea or area centralis and high-resolution retinal topography map images, we measured the relative distance and angle of the specialization from the center point of the retina by implementing the method from (Moore et al., 2012) in Fiji (Schindelin et al., 2012) (Supplementary Figure S3, Supplementary Table S2). We manually marked the outermost points of the retinal topographic maps on the dorsal, ventral, nasal, and temporal axes, and marked the center of the retinal specialization. We then used built-in ImageJ macros to calculate the minimum bounding circle of the retina, the center point of the retina, the radius of the retina, and the distance and angle of the retinal specialization from the center point. We normalized the specialization distance by the retina radius, and then used trigonometry functions to calculate the temporal distance of the retina from the center using the specialization distance and angle. For both orbit convergence and retinal specializations, carnivores, artiodactyls, and primates had the most data available. However, we had data for at least one species from most major mammalian clades, including Afrotheria (elephant, manatee), Xenarthra (sloths), Perissodactyla (horse, rhinoceros), Lagomorpha (hare, rabbit), Scandentia (tree shrew), as well as several rodents and bats (Supplementary Table S1).

We used ecological and body mass data from the EltonTraits 1.0 dataset (Wilman et al., 2014). It is not feasible to categorize species into binary "predator" and "prey" groups, because many species can be both, and data on rates of predation do not exist for most mammal species. Instead, we categorized species as "predators" or "not predators," and separately categorized species as "herbivores" or "not herbivores" using the EltonTraits data, which provides percentages of different diet categories. Species were considered "predators" if invertebrates and vertebrates were greater than or equal to 70% of their diets, excluding scavengers. Species were considered "herbivores" if greater than or equal to 70% of their diets were plant material. Thus, it is possible for species to be categorized as neither predators nor herbivores if they are omnivorous or scavengers. We also tested our hypotheses with species assigned to diet categories based on 100% and 50% thresholds.

For activity pattern, the EltonTraits data list diurnal, crepuscular, and nocturnal as separate, binary categories, such that it is possible for species to be any combination of these three categories. We categorized species as exclusively diurnal, exclusively nocturnal, or crepuscular/cathemeral (crepuscular or any other combination of activity patterns). For foraging substrate, the EltonTraits database categorizes species as marine, ground, scansorial, arboreal, or aerial. We added a "fossorial" category and changed *Heterocephalus glaber*, *Fukomys damarensis*, *Ellobius lutescens*, and *Ellobius talpinus* from "ground" to "fossorial" since they are known to spend the majority of their lives underground and do not have fully developed eyes (Partha et al., 2017). We used ground foraging as a proxy for horizon-dominated environments and considered both marine and arboreal species to be foraging in complex, three-dimensional environments. We considered species to be in "unobstructed, horizon-dominated" habitats if they primarily reside in grassland, savannah, desert, or tundra biomes (Myers et al., 2024) (Supplementary Table S1).

We used the Zoonomia mammal phylogeny (Genereux et al., 2020). For 11 species, we used orbit convergence and retinal specialization data from a closely related species when data were not available for the species in the Zoonomia dataset (Supplementary Table S3). In these cases, we used the ecological data for the same species as the ocular trait data. In four additional cases, we used ecological or orbit convergence data from a subspecies or congeneric species because none were available from the same species as the retinal specialization data (Supplementary Table S3). We ran all analyses with these 15 species included and excluded to verify that our results were similar.

Phylogenetic analyses

We visualized traits on the phylogeny using phytools V2.1-1 (Revell, 2012). We also used phytools to calculate phylogenetic signal for orbit convergence using the function *phylosig* with 1,000 simulations. To test for an association between orbit convergence and ecological traits, we used phylogenetic generalized least squares (PGLS [Martins & Hansen, 1997]) implemented in the R package nlme V3.1-164 (Pinheiro et al., 2020) with a Pagel's λ approach to model the underlying phylogenetic correlation structure. There is some evidence that orbit convergence scales allometrically with skull length in primates (Nett & Ravosa, 2019) and other mammal families (Noble et al., 2000), but this is not supported across carnivores (Casares-Hidalgo et al., 2019), so the consistency of these scaling relationships across mammals is unclear. Therefore, we used the $\log_{10}$ of body mass to control for potential allometric scaling relationships (Cantlay et al., 2023; Changizi & Shimojo, 2008; Potier et al., 2023) and ran our models both with and without body mass as a covariate. Because activity pattern had three categories, we used a post-hoc Tukey test to compare means using the *glht* function in the package multcomp V1.4-25. We tested for associations between orbit convergence and ecological traits for 88 species, with orbit convergence as the response variable. For tests involving foraging substrate (i.e., arboreal vs. ground foraging), we removed four aquatic pinniped species for a total of 84 species in the analyses (Table 2). In some cases, we sought to test if orbit convergence was associated with a combination of ecological traits, such as nocturnal predation. We tested these hypotheses by incorporating interaction terms into our PGLS models (Tables 1 and 2) and reran models with

Table 2. Results from PGLS analyses comparing orbit convergence with ecological traits. ":" indicates interaction terms.

Model (PGLS with Pagel's λ correlation structure)	Term	Number of species	Coefficients			
			Value	*SE*	*t*-Value	*p*-Value
Orbit convergence ~ log(body mass) + predation	intercept	88	32.54	6.94	4.69	0.00
	log(body mass)		2.51	1.38	1.81	0.07
	predation		–1.47	3.71	–0.39	0.69
Orbit convergence ~ log(body mass) + herbivore	intercept	84	29.17	6.96	4.19	0.00
	log(body mass)		2.94	1.35	2.17	0.03
	herbivore		2.16	3.04	0.71	0.48
Orbit convergence ~ log(body mass) + activity pattern	intercept	88	31.15	7.30	4.27	0.00
	log(body mass)		2.46	1.40	1.75	0.08
	activity pattern [nocturnal]		1.47	3.21	0.46	0.65
	activity pattern [diurnal]		1.83	2.64	0.69	0.49
Orbit convergence ~ log(body mass) + predation + activity pattern + predation:activity	intercept	88	31.92	7.48	4.27	0.00
	log(body mass)		2.54	1.47	1.73	0.09
	predation		–3.34	4.99	–0.67	0.51
	activity pattern [nocturnal]		0.24	3.85	0.06	0.95
	activity pattern [diurnal]		1.27	3.57	0.36	0.72
	predation:activity pattern [nocturnal]		3.78	6.15	0.61	0.54
	predation:activity pattern [diurnal]		0.97	5.51	0.18	0.86
Orbit convergence ~ log(body mass) + predation + activity pattern	intercept	88	31.41	7.39	4.25	0.00
	log(body mass)		2.48	1.41	1.75	0.08
	predation		–1.40	3.75	–0.37	0.71
	activity pattern [nocturnal]		1.43	3.23	0.44	0.66
	activity pattern [diurnal]		1.81	2.65	0.68	0.50
Orbit convergence ~ log(body mass) + foraging strategy	intercept	84	29.96	6.87	4.36	0.00
	log(body mass)		2.94	1.38	2.13	0.04
	foraging strategy [ground]		1.28	3.14	0.41	0.69
Orbit convergence ~ log(body mass) + foraging strategy + herbivore + foraging strategy:herbivore	intercept	84	29.85	7.65	3.90	0.00
	log(body mass)		2.82	1.40	2.01	0.05
	foraging strategy [ground]		–1.12	4.87	–0.23	0.82
	herbivore		–0.17	4.32	–0.04	0.97
	foraging strategy [ground]:herbivore		4.90	5.25	0.93	0.35
Orbit convergence ~ log(body mass) + foraging strategy + herbivore + log(body mass):herbivore	intercept	84	27.91	8.54	3.27	0.00
	log(body mass)		2.87	1.94	1.47	0.14
	foraging strategy [ground]		1.91	3.21	0.59	0.55
	herbivore		2.99	8.13	0.37	0.71
	log(body mass):herbivore		–0.13	2.18	–0.06	0.95
Orbit convergence ~ log(body mass) + foraging strategy + herbivore	intercept	84	28.15	7.23	3.89	0.00
	log(body mass)		2.79	1.40	1.99	0.05
	foraging strategy [ground]		1.95	3.19	0.61	0.54
	herbivore		2.54	3.10	0.82	0.41

Note. PGLS = phylogenetic generalized least squares.

interaction terms removed if the interaction terms were not significant (Engqvist, 2005).

Retinal specializations can vary greatly in their absolute and relative retinal ganglion cell densities, but collecting quantitative data consistently across species is challenging, and most existing data on retinal specializations describe them as discrete, categorical traits (Moore et al., 2012). We therefore encoded each retinal specialization as a binary variable (e.g., horizontal streak present or absent). We estimated Pagel's λ for these binary traits using the *fitDiscrete* function in geiger V2.0.11 with *transform="lambda"* (Pennell et al., 2014). To test the relationships between retinal specializations and ecological traits, we encoded ecological traits as binary traits and compared the likelihood ratios between dependent and independent models of discrete trait evolution using a maximum likelihood estimation approach in BayesTraits V4.0.1 (Pagel, 1994; Pagel & Meade, 2006). For hypotheses involving multiple ecological traits (e.g., ground-foraging herbivore < 100 kg), we encoded species with all of these traits as "trait present" and all other species as "trait absent." Because many species have multiple retinal specializations, such as an area centralis within a horizontal streak, we tested each hypothesis twice: once including species that have only the focal retinal specialization and once including all species that have the focal retinal specialization, even if it is in combination with other specializations. We corrected for multiple tests using Benjamini–Hochberg (BH) correction.

To test for differences in orbit convergence between species that have only an area centralis or fovea (22 species) compared to those that have only a horizontal streak (11 species), we used the same PGLS approach that we used to test for associations between orbit convergence and ecological traits. We used the model $orbit\ convergence \sim retinal\ specialization + \log(body\ mass)$. We verified this result with a simulation-based phylogenetic ANOVA (Garland et al., 1993) using the phytools function *phylANOVA* with 10,000 simulations (Revell, 2012). We tested if the relative temporal position of the retinal specialization showed a negative correlation with orbit convergence using PGLS with the model $temporal\ shift \sim orbit\ convergence + \log(body\ mass)$. All statistical tests and R packages were implemented using R version 4.3.2.

Results

No support for associations between ecological traits and orbit convergence

We first evaluated the evolution of orbit convergence across 91 eutherian mammals (Figure 2A). We found that phylogenetic signal was relatively high, with Pagel's $\lambda = 0.78$, where $\lambda = 0$ indicates no phylogenetic signal and $\lambda = 1$ represents a Brownian motion model of evolution ($p < 0.001$ based on a likelihood ratio test (LRT) comparing $\lambda = 0.78$ to $\lambda = 0$). In other words, more closely related species tended to have more similar orbit convergence values. We then asked if orbit convergence angle is associated with ecological traits after controlling for phylogeny (Table 2). Surprisingly, we did not find a significant difference in orbit convergence between predators and non-predators or between herbivores and non-herbivores based on a PGLS test ($p = 0.69$; $p = 0.48$; Figure 2B and C). There was also no significant difference when considering an interaction between herbivory and ground foraging (PGLS $p = 0.35$) or herbivory and body mass (PGLS $p = 0.95$).

Some have hypothesized that high orbit convergence facilitates vision in low light, and thus nocturnal species are predicted to have higher orbit convergence (Cartmill, 1972; Heesy, 2007; Read, 2021). However, we did not find support for this hypothesis (PGLS $p = 0.65$; Figure 2D). The nocturnal predation hypothesis predicts that the combination of nocturnality and predation selects for higher orbit convergence, but there was also no significant interaction between predation and nocturnality (PGLS $p = 0.54$; Table 2). Because high orbit convergence is thought to improve depth perception, orbit convergence may be higher in arboreal species (Changizi & Shimojo, 2008), while lower orbit convergence may facilitate panoramic vision in ground-foraging species (Heesy, 2007; Hughes, 1977). Although there was a trend towards higher orbit convergence in arboreal species compared to ground-foraging species, this relationship was not significant after phylogenetic correction (PGLS $p = 0.69$; Figure 2E). We reran our models with nonsignificant interaction terms removed (Engqvist, 2005) and still did not find significant statistical support for associations between orbit convergence and ecological traits (Table 2). We also saw similar results whether we included body mass as a covariate or not and with different diet threshold cutoffs for categorizing species as predators or herbivores (Supplementary Table S4). Overall, shared evolutionary history plays an important role in the patterns of orbit convergence across mammals, and we could not separate these effects from potential associations with ecological traits.

The area centralis is not associated with predator species

To understand broad patterns of retinal specialization evolution, we overlaid retinal specialization data from 82 species on the mammal phylogeny and found evidence that both the area centralis and horizontal streak have evolved repeatedly in mammals (Figure 3). Other specializations also occur in mammals, including the fovea in primates and the presence of a vertical streak or "anakatabatic area," which is common in artiodactyls (Supplementary Table S1). We focused on the area centralis and horizontal streak, because they appear to be the most common specializations and show evidence for multiple independent gains or losses across the mammalian phylogeny. We calculated Pagel's λ for the area centralis and horizontal streak separately, with each encoded as a binary trait (present or absent) and found that $\lambda = 1$ for both, suggesting that retinal specializations tend to follow a Brownian motion model of evolution across mammals. It is important to note that this Pagel's λ value cannot be directly compared to that calculated for orbit convergence because different sets of species were included in these different datasets, and because the methods for calculating Pagel's λ are different for continuous versus discrete traits.

We tested for an association between predation and the presence of an area centralis across the mammal phylogeny and did not find support for this hypothesis (LRT = 4.043; BH-corrected $p = 0.185$; Table 3). This was true for species with any presence of an area centralis and species with only an area centralis (Table 3). We also tested if the area centralis was associated with predators that forage in three-dimensional environments (arboreal and marine), where depth perception may be particularly important. We observed high transition rates to an area centralis given this trait, but this association was not significant after multiple test correction (LRT = 6.511; BH-corrected $p = 0.096$; Table 3). When we defined predators based on 50% or 100% invertebrate or vertebrate diets, we saw similar results (Supplementary Table S5).

The horizontal streak is associated with horizon-dominated environments

As a proxy for horizon-dominated habitats, we tested for an association between ground foraging and the presence of a horizontal streak (possibly in combination with other retinal specializations)

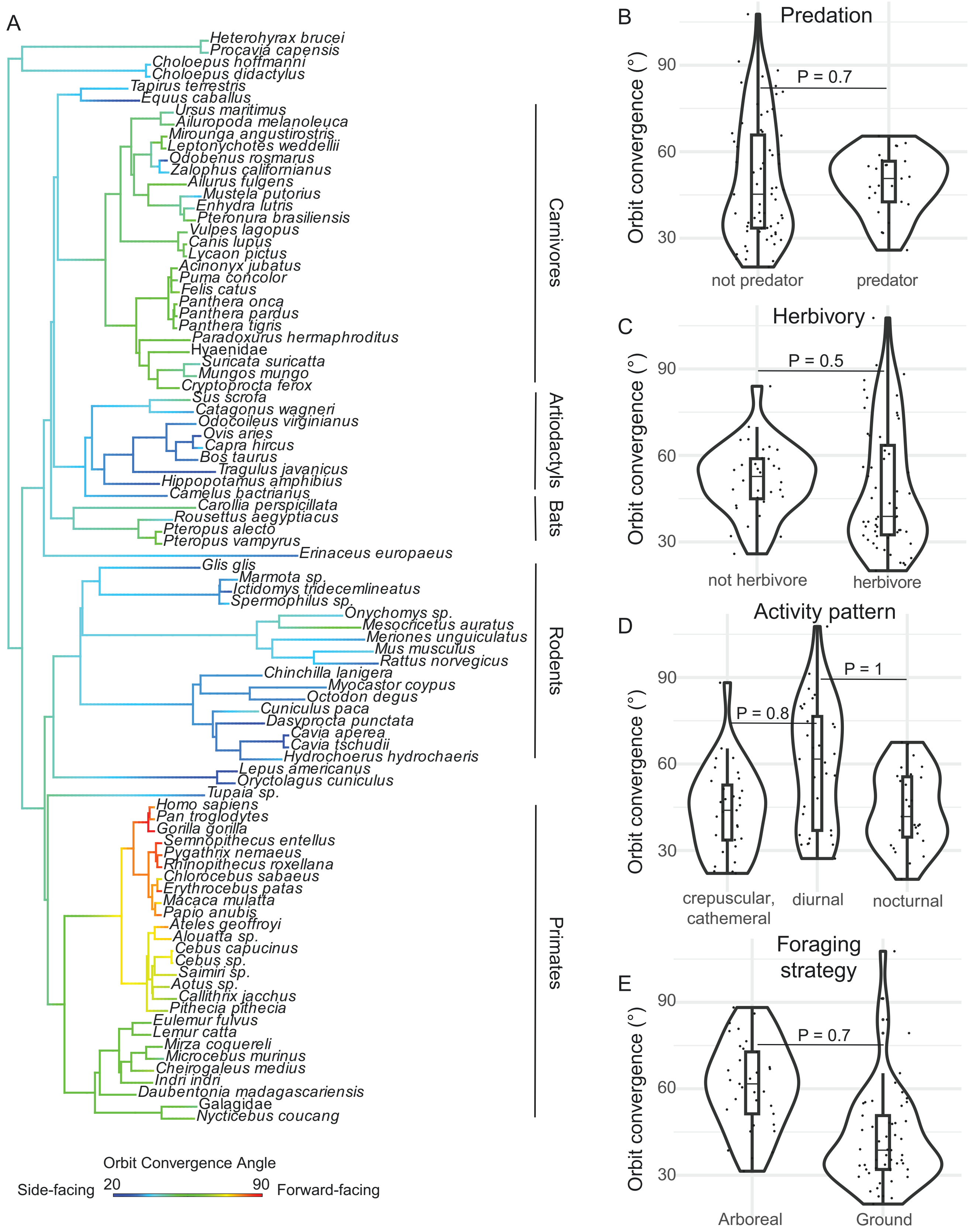

Figure 2. Orbit convergence evolution across mammals. (A) Orbit convergence angles for 91 species overlaid on the mammalian phylogeny (Genereux et al., 2020), with warmer colors representing higher angles or more “forward-facing” eyes (e.g., primates). (B–E) Violin plots comparing orbit convergence angles for species in different ecological categories. Each point represents a species, and thick horizontal lines within the violin plots represent the median orbit convergence angle for species in the given ecological category. *p*-Values are based on phylogenetic generalized least squares with body mass as a covariate. *p*-Values in (D) are based on a post-hoc Tukey test.

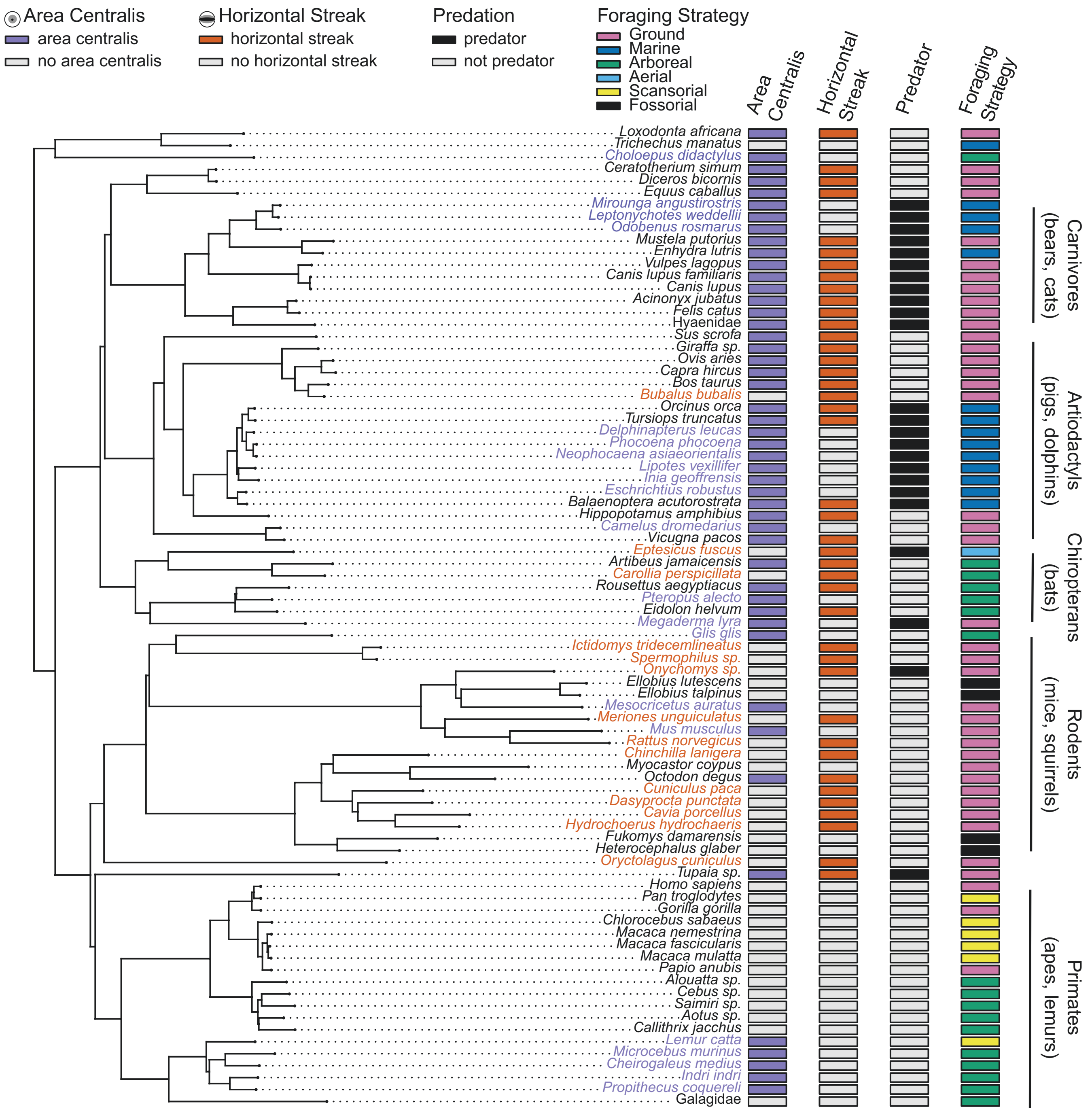

Figure 3. Retinal specializations for 82 species overlaid on a mammalian phylogeny (Genereux et al., 2020). Columns to the right indicate the retinal specializations and ecological traits for each species. Species in purple have only an area centralis, and species in orange have only a horizontal streak. Major taxonomic groups are labeled on the right, with common names of representative species in these clades.

and found a significant relationship between these traits, with transition rates indicating a higher probability of having a horizontal streak given the presence of ground foraging (LRT = 15.938; BH-corrected $p = 0.003$; Table 3). This relationship was no longer significant when we narrowed the foreground set to species with only a horizontal streak. The horizontal streak may be particularly common in species in horizon-dominated habitats that experience high predation to help detect predators across a wider field of view. We tested if the horizontal streak is associated with ground-foraging herbivores with body mass less than 100 kg, as a proxy for prey species. These likely prey species were more likely to have only a horizontal streak (LRT = 9.238; BH-corrected $p = 0.049$; Table 3). This result held when we used a cutoff of 50% plant diet to define herbivores but was no longer significant with a strict 100% plant diet cutoff (Supplementary Table S5). We also asked if species in unobstructed, horizon-dominated environments were more likely to have horizontal streaks (Hughes, 1977). These species trended towards having a horizontal streak, but the relationship was not significant after multiple test correction (LRT = 8.163; BH-corrected $p = 0.056$; Table 3). We tested

Table 3. Results from hypothesis tests comparing retinal specializations to ecological traits. The independent column gives the log likelihood of the null model in which the two traits are evolving independently across the phylogeny. The dependent column gives the log likelihood value of the model in which the evolution of one trait depends on the other. LRT is the likelihood ratio test value, the *p*-values were determined using a chi-squared test with 2 df, and BH *p*-values were corrected for multiple tests using the Benjamini–Hochberg method. The last four columns show the transition rates to or away from the focal retinal specialization given the presence or absence of the ecological trait. Rows in bold are significant after multiple test correction.

							Rate to specialization		Rate away from specialization	
Retinal specialization	**Ecological trait**	**Independent**	**Dependent**	**LRT**	***p*-Value**	**BH *p*-value**	**Ecological trait absent**	**Ecological trait present**	**Ecological trait absent**	**Ecological trait present**
Area centralis (any)	Predator	–50.780	–48.759	4.043	0.132	0.185	2.482	0.671	3.980	0
Area centralis (only)	Predator	–51.828	–50.855	1.946	0.378	0.378	1.575	10.712	8.966	23.146
Area centralis (any)	Predator; marine or arboreal foraging	–43.373	–40.117	6.511	0.039	0.096	2.185	100.000	4.451	0.000
Area centralis (only)	Predator; marine or arboreal foraging	–44.421	–42.513	3.817	0.148	0.185	1.390	63.147	10.593	36.992
Horizontal streak (any)	**Ground foraging**	**–84.792**	**–76.823**	**15.938**	**3.46E-04**	**0.003**	**0.000**	**33.012**	**18.719**	**4.359**
Horizontal streak (only)	Ground foraging	–69.287	–66.775	5.024	0.081	0.135	1.656	3.757	29.711	2.616
Horizontal streak (any)	Herbivore; ground foraging; <100 kg	–74.293	–71.604	5.379	0.068	0.135	3.997	92.306	5.092	17.952
Horizontal streak (only)	**Herbivore; ground foraging; <100 kg**	**–58.788**	**–54.170**	**9.238**	**0.010**	**0.049**	**2.662**	**9.249**	**34.191**	**3.641**
Horizontal streak (any)	Unobstructed horizon-dominated	–78.490	–74.408	8.163	0.017	0.056	4.303	83.183	8.352	7.198
Horizontal streak (only)	Unobstructed horizon-dominated	–62.985	–62.286	1.398	0.497	0.497	1.265	3.544	7.009	0.745

these hypotheses with a subset of 67 species for which we had phylogenetic, ecological, and retinal specialization data for the exact same species and saw similar results (Supplementary Table S5). Our results suggest that the horizontal streak may evolve in response to foraging strategy.

There is a strong association between orbit convergence and retinal specializations

We then asked if there is a relationship between orbit convergence and retinal specializations. Both the horizontal streak and more side-facing eyes are thought to facilitate panoramic vision in open, horizon-dominated environments, and therefore we predicted that they would tend to occur together (Hughes, 1977). Consistent with this prediction, we found that orbit convergence was significantly lower in species that had only a horizontal streak compared to species that had only a fovea or area centralis (PGLS $p = 0.0398$; Figure 4A; Supplementary Table S6). We also tested this relationship using a simulation-based phylogenetic ANOVA (Garland et al., 1993) and again saw significantly lower orbit convergence for species with only a horizontal streak ($p = 0.0195$).

Previous studies have observed that species with lower orbit convergence tend to have temporally shifted retinal specializations, which would allow for higher acuity in the binocular field, the region in front of an animal where the visual fields of both eyes overlap (Figure 1C; Collin, 1999; Moore et al., 2012). Essentially, in these cases, the lateral shift serves to redirect the high acuity area so that it faces more forward with respect to the head, despite the side-facing orientation of the eyes themselves. We asked if the relative temporal distance of the area centralis or fovea from the center of the retina was correlated with orbit convergence and found strong support for an inverse relationship between these measurements (PGLS $p = 0.0047$; Figure 4B; Supplementary Figure S4; Supplementary Table S6). That is, species with more laterally placed eyes tend to have more temporally shifted retinal specializations, as predicted. The regression line intercepts the y-axis close to 1, which would mean that species with eyes facing directly sideways would have retinal specializations shifted almost completely to the temporal side of the retina. This suggests that the high acuity retinal specialization tends to project forward, regardless of the position of the eyes in the head. These relationships between orbit convergence and retinal specializations held when we narrowed our dataset to only species with phylogenetic, retinal specialization, and orbit convergence data from the same species (Supplementary Table S6).

Discussion

It is still unclear how selective pressures influence many ocular traits, or what evolutionary forces underlie divergence in these traits across species. Ecological correlates of ocular traits can provide insight into their potential roles as visual adaptations (Baker & Venditti, 2019; Cantlay et al., 2023; Caves et al., 2017, 2024; Potier et al., 2017, 2023). Additionally, multiple traits involved in vision are predicted to evolve in response to similar ecological traits, but the way these ocular traits interact with each other may also shape their evolutionary patterns (Collin, 1999; Hughes, 1977; Walls, 1942). We tested hypotheses regarding the ecological selective pressures acting on orbit convergence and high acuity retinal specializations and found mixed evidence supporting these hypotheses. However, we did find strong evidence for correlations between these traits across the mammal phylogeny, suggesting that functional interactions between ocular traits may play an important role in their evolution.

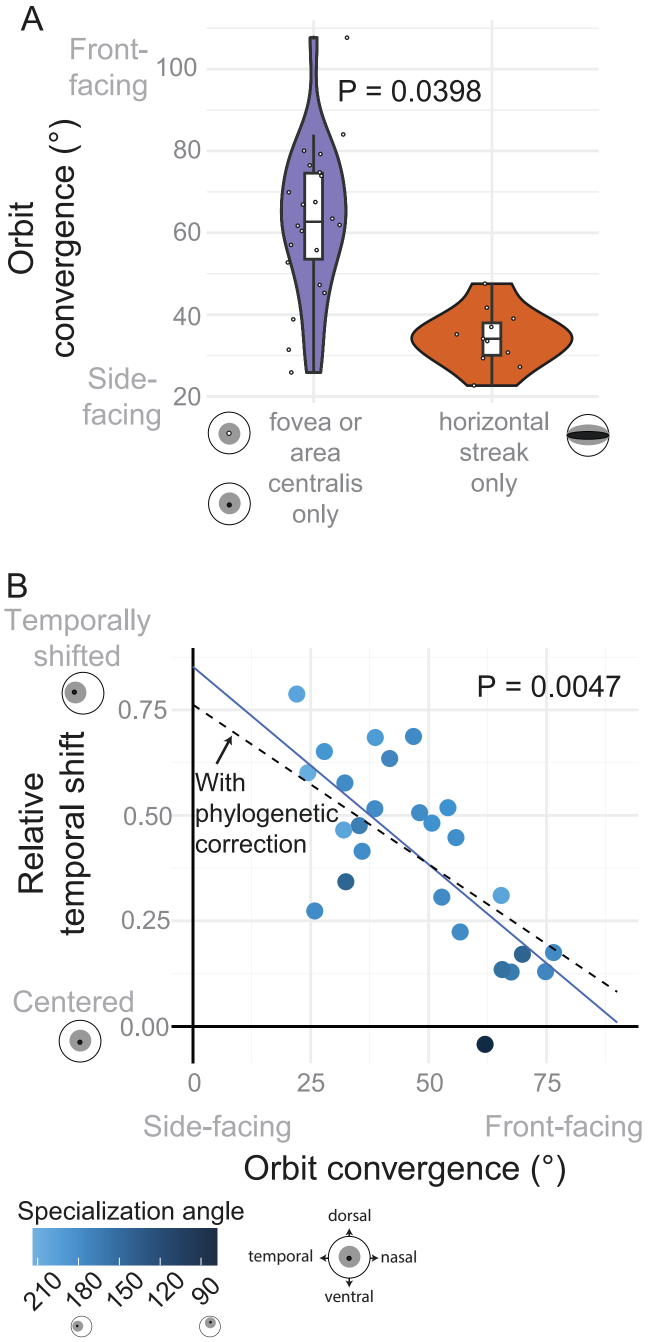

Figure 4. The relationship between retinal specializations and orbit convergence. (A) Violin plot showing the relationship between orbit convergence and presence of different retinal specialization types. Each point represents a species (33 total), and thick horizontal lines within the violin plot represent the median orbit convergence angle for species with the given retinal specialization. (B) Scatter plot showing the negative correlation between orbit convergence and relative temporal distance of the fovea or area centralis from the center of the retina (26 species). Points are colored based on the angle of the retinal specialization relative to the horizontal plane of the retina. The dashed line represents the slope and intercept of the phylogenetic generalized least squares analysis, and the solid line shows the regression without phylogenetic correction. See Supplementary Figure S4 for species names corresponding to each point. *p*-Values in both plots are based on phylogenetic generalized least squares with body mass as a covariate.

Ecological correlates of orbit convergence and retinal specializations

Phylogenetic comparative methods can give insight into adaptive evolution, especially for traits evolving over longer evolutionary timescales that cannot be directly tested for selection within populations (Harmon, 2019). As genome sequencing has become more accessible and affordable, phylogenetic inference has improved, generating well-resolved phylogenetic trees consisting of many species across long evolutionary timescales (Feng et al., 2020; Genereux et al., 2020; Shen et al., 2018; Suvorov et al., 2022; Upham et al., 2019). While the importance of controlling for shared evolutionary history is well-established (Felsenstein, 1985; Harmon, 2019), many older hypotheses about the relationships among cellular or morphological phenotypes and ecological traits have not been revisited using current phylogenies and phylogenetic comparative methods. Testing these hypotheses with modern phylogenetic methods and resources can reveal new insights about trait evolution and putative ecological selective pressures acting on traits (Baker & Venditti, 2019; Baker et al., 2016; Benun Sutton & Wilson, 2019; Davis et al., 2016; Harmon, 2019; Jarvis & Marshall, 2023). Additionally, broad comparative studies often have uneven taxonomic sampling, as is true in our dataset that has proportionally more carnivores, primates, and artiodactyls compared to known mammalian diversity. While this could potentially bias results, phylogenetic comparative methods address this by incorporating species relatedness or branch lengths into the underlying models (Martins & Hansen, 1997; Pagel, 1994).

We tested several long-standing hypotheses regarding ecological selective pressures acting on visual traits. Surprisingly, we did not find support for most of these hypotheses in mammals. After controlling for phylogeny, we found that orbit convergence was not associated with diet, activity pattern, or foraging substrate (Figure 2). This contrasts with previous work that did not account for shared evolutionary history (Heesy, 2007), but is consistent with findings in carnivores and marsupials (Casares-Hidalgo et al., 2019; Pilatti & Astúa, 2016). Phylogenetic relationships and ecological correlates thought to influence orbit convergence may be confounded in mammals, because high orbit convergence seems to be concentrated in a few mammalian clades with similar relevant ecological traits. For example, carnivores tend to have high orbit convergence associated with predation, but they are also a monophyletic clade and may have similar orbit convergence due to their shared evolutionary history (Casares-Hidalgo et al., 2019). Consistent with this, carnivoran species with primarily herbivorous diets such as the panda (*Ailuropoda melanoleuca*) and red panda (*Ailurus fulgens*) maintain higher orbit convergence angles similar to those of other carnivorans (Figure 2A; Supplementary Table S1). Another interesting example is the grasshopper mouse (*Onychomys leucogaster*), a nocturnal predator that hunts large insects but has a relatively low orbit convergence similar to other rodents (Figure 2A; Supplementary Table S1). Constraints imposed by skull morphology may play an important role in the evolution of orbit convergence in mammals (Casares-Hidalgo et al., 2019; Pilatti & Astúa, 2016; Ross, 1995). There are stark differences in the overall skull morphology of the mammals included in our analysis, which may have a larger influence among major clades on orbit morphology than any ecological selective pressures. This may partially explain differences in our results compared to previous work, which found support for the nocturnal predation hypothesis as an explanation for the highly convergent orbits of primates (Heesy, 2007; Noble et al., 2000; Ravosa & Savakova, 2004). Ecological traits such as nocturnal predation may select for smaller scale changes in orbit convergence within some clades, but not enough to drive larger scale patterns of orbit convergence across eutherian mammals.

We found some evidence for associations between retinal specializations and ecology, although we did not find support that the area centralis was associated with predation (Figure 3). We defined predation based on diet composition because these data were widely available across species in our dataset. However, different hunting strategies may impose different selective pressures on vision, such as chase versus ambush predation (Banks et al., 2015). The area centralis and other ocular traits may evolve in response to more specific selective pressures imposed by these different predation strategies, but we did not have behavioral data at this level of detail to make comparisons across species. We found a significant association between the horizontal streak and ground foraging, supporting the hypothesis that horizon-dominated habitats may select for the presence of a horizontal streak. We also found that species with only a horizontal streak were more likely to be small, herbivorous ground foragers. There was a weak association between ground-foraging species in unobstructed habitats and the presence of the horizontal streak. However, this was not significant, and the strongest relationship we observed was with ground foraging. It may be that ground foraging alone is enough to select for the presence of a horizontal streak, regardless of how open the habitat is or the diet of a species. Previous studies have found variation in retinal specializations associated with foraging terrain complexity in artiodactyls (Schiviz et al., 2008) and marsupials (Navarro-Sempere et al., 2018). Our work shows that these patterns persist across deeper evolutionary time scales and across species with greater variation in habitats and foraging strategies.

Challenges of retinal specialization data

Retinal specializations are usually binned into categories due to historical precedent and available methodologies (Hughes, 1977). However, patterns of retinal ganglion cell density are often more complex than these categories, and many species have specializations that fit multiple categories (Figure 3; Supplementary Table S1). Quantitative data, such as changes in ganglion cell density across the retina, provide a more complete understanding of the evolution of retinal specializations (Moore et al., 2012; Schiviz et al., 2008). Indeed, we found strong support for a negative correlation between the temporal shift of the specialization and orbit convergence, which required quantitative data. Future work on retinal specializations should include detailed retinal topography maps as well as raw data on ganglion cell density across the retina, allowing comparative work to test hypotheses about the evolution of quantitative retinal specialization traits (Moore et al., 2012).

Evolutionary relationships between ocular traits

The strongest relationships we observed were those between orbit convergence and retinal specializations. Orbit convergence was significantly lower in species with only a horizontal streak compared to those with a fovea or area centralis (Figure 4A), which may reflect similar selective pressures for panoramic vision and a wide field of view acting on both orbit convergence and patterns of retinal ganglion cell density. We also found a strong negative correlation between the temporal shift of the high acuity specialization from the center of the retina and orbit convergence, meaning that the high acuity area shifts temporally in species with side-facing eyes (Figure 4B). This would provide the highest visual acuity in front of an animal even if the eyes are facing sideways (Figure 1C) (Collin, 1999; Moore et al., 2012). Consistent with this, many species with side-facing eyes such as goats, rabbits, and squirrels appear to have depth perception and fixate their gaze forwards based on behavioral observations (Hughes, 1977). Previous studies predicted that species with low orbit convergence would have temporally shifted retinal specializations based on observations in some species (Collin, 1999; Hughes, 1977), but we provide, to our knowledge, the first quantitative support for this relationship in a phylogenetic framework.

In this study, we used phylogenetic comparative approaches and ocular trait data from a broad sample of eutherian mammals to show that the occurrence and position of retinal specializations evolved in response to both ecological selective pressures and other ocular traits. Orbit convergence is likely constrained by cranial morphology (Cox, 2008; Finarelli & Goswami, 2009; Pilatti & Astúa, 2016; Ross, 1995), whereas the arrangement of ganglion cells within the retina is likely subject to fewer constraints. Therefore, high acuity retinal specializations may be a more evolutionarily available trait that can evolve on shorter time scales to adapt to ecological selective pressures on vision and compensate for other ocular traits such as orbit convergence. Vision, like many sensory processes, requires the coordination of multiple traits across molecular, cellular, and morphological levels. Testing how these traits evolve in relation to one another in the context of visual ecology provides a more complete understanding of the evolution of sensory systems.

Supplementary material

Supplementary material is available online at *Evolution Letters*.

Data and code availability

Orbit convergence data that we measured from museum specimens are available in Supplementary Table S1. Sources from the literature for orbit convergence and retinal specializations are available in Supplementary Table S1 and in the Supplementary Material under Supplementary References. Scripts for ImageJ macros and phylogenetic analyses are available on GitHub (https://github.com/ekopania/mammal_retinas).

Author contributions

E.E.K.K. performed the literature searches and data analyses with support from N.L.C. E.E.K.K. and N.L.C. funded this work, collected data on orbit convergence, and wrote the manuscript.

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