NATURAL HISTORY NOTE

The Hawk-Eyed Songbird: Retinal Morphology, Eye Shape, and Visual Fields of an Aerial Insectivore

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ABSTRACT: Swallows are a unique group of songbirds because they are active-pursuit predators that execute all aspects of hunting prey in flight: search, detection, pursuit, and capture. We show that swallows have evolved a visual system that is unlike that of any other studied songbird. Swallows have a bifoveate retina that provides sharp lateral and frontal vision, an unusually long eye that enhances spatial resolution, a large posterior blind area, and a narrow binocular field. We also show that swallows and diurnal raptors (hawks and falcons) have converged on a similar visual configuration but that, interestingly, predatory songbirds that ambush prey (flycatchers) have not converged on the same suite of traits. Despite the commonly held belief that predators rely on binocular vision, the temporal (frontally projecting) fovea present in swallows—but not present in other songbirds—is likely not involved in binocular vision. Instead, swallows have four nonoverlapping foveae in a 100° arc around the beak, which can improve the tracking of frontally located aerial prey that are engaging in evasive maneuvers. Overall, vision in pursuit predators reflects the complex sensory demands of hunting in the air at high speeds and emphasizes the importance of acute frontal vision in predators.

Keywords: vision, bird, predator, swallow, raptor, flycatcher.

Introduction

Chasing prey is a challenging visual task for predators of all sizes and taxa. From cheetahs to hawks to ancient Cambrian arthropods, predators that take part in the chase have exceptional visual specializations (Tucker 2000; Ahnelt et al. 2005; Paterson et al. 2011). Diurnal raptors, in particular, have notoriously excellent vision (Jones et al. 2007; Land and Nilsson 2012). They have two foveae in each retina that provide the birds with acute vision directed forward and to either side of the head (Chievitz 1891; Reymond 1985, 1987). The diurnal-raptor eye itself is quite long, which increases focal length and consequently visual acuity (Reymond 1985, 1987). The diurnal-raptor visual field is characterized by a large blind area behind the head but a relatively small area of binocular overlap in front of the head (Martin and Katzir 1999; O'Rourke et al. 2010; Potier et al. 2016). Although diurnal raptors are a polyphyletic group that consists of the orders Accipitriformes and Falconiformes—hawks and falcons, respectively (Hackett et al. 2008; Jarvis et al. 2014)—both groups have independently converged on many of the same morphological traits, including the aforementioned visual specializations.

The other group of birds that have well-studied vision are passerine songbirds (order Passeriformes), which make up over 50% of all extant bird species. Many passerines are opportunistic foragers that are commonly granivorous during the nonbreeding season and omnivorous during the breeding season. The typical passerine has only a single, centrally placed fovea in each eye that projects to either side of the head, and unlike that of raptors, the passerine eye has a short focal length (table A1, available online; Dolan and Fernández-Juricic 2010; Moore et al. 2013, 2015, 2017; Tyrrell et al. 2013; Baumhardt et al. 2014). The typical passerine visual field includes a relatively wide binocular field in front of the head that is approximately symmetrical in size with the blind area behind the head (table A1; Martin 1986; Fernández-Juricic et al. 2008; Blackwell et al. 2009; Moore et al. 2013, 2015; Tyrrell et al. 2013; Baumhardt et al. 2014).

Given the foraging differences between predatory raptors and opportunistic passerines, it is not surprising that their visual systems are organized differently. It is even known that some passerines that are typically ambush predators have a third type of retinal configuration, with an area temporalis in addition to a fovea centralis (tyrant flycatchers; Coimbra et al. 2006, 2009). However, there are few recent studies on key visual-system properties of passerines that are also active-pursuit predators. Unlike other passerines, swallows (family Hirundinidae, order Passeriformes) are also active, obligate predators. More importantly, swallows could have a more visually difficult task than stalking and ambush predators (e.g., cheetahs, flycatchers), because swallows execute all four aspects of hunting prey (search, detection, pursuit, and cap-

ture) in flight, adding additional components to the high-speed chase. In fact, it has been shown that swallows have two foveae in each eye, a trait they share with other active predators, such as hawks, falcons, terns, and kingfishers (Chievitz 1891; Slonaker 1897; Wood 1917; Rochon-Duvigneaud 1943).

To better understand the visual requirements of passerine active predators, we characterized different components of spatial vision of an active-pursuit predator (tree swallow *Tachycineta bicolor*) and two ambush predators for comparison (Acadian flycatcher *Empidonax virescens* and least flycatcher *Empidonax minimus*; hereafter *Empidonax* flycatchers). More specifically, we measured eye shape; the number, position, types, and spatial resolving power of centers of acute vision; and the size of the binocular, lateral, and blind fields. This information allowed us to draw comparisons between predatory passerines, opportunistic passerines, and diurnal raptors in terms of the key traits driving their sensory world that could lead to variation in their foraging strategies.

Methods

Animals

Five tree swallows, six Acadian flycatchers, and six least flycatchers were captured with mist nets and nest box traps in Tippecanoe, Indiana. The Purdue Institutional Animal Care and Use Committee (1201000567 and 1112000398) approved all experimental procedures with animals.

Eye Shape and Tissue Sampling

Animals were euthanized with CO_2, and their eyes were removed immediately by cutting away the conjunctivia and severing the optic nerve. We then measured the axial diameter (eye length) and transverse diameter (eye width) of seven tree swallow eyes (four individuals), eight Acadian flycatcher eyes (five individuals), and 11 least flycatcher eyes (six individuals), using digital calipers (0.01-mm accuracy). To standardize eye shape across species with variable eye sizes, we calculated the ratio of axial diameter to transverse diameter. High values suggest particularly long eyes with long focal lengths, whereas low values suggest short eyes.

We then hemisected the eyes at the ora serrata, removed the vitreous humor, and fixed the retinae in the eyecup with 4% paraformaldehyde in 0.1 M phosphate-buffered saline (PBS), pH 7.4. Three tree swallow, three Acadian flycatcher, and two least flycatcher retinae were extracted from their eyecups by cutting away the sclera and peeling away the choroid. The retinae were then bleached in 3% H_2O_2 in PBS for ~12 h to clear the pigmented epithelium. Retinae were flattened by making radial cuts, whole-mounted onto gelatinized slides, and stained with cresyl violet, following Ullmann et al.

(2012), to allow for retinal ganglion cell visualization. Images were taken of the whole-mounted retinae before and after staining to correct for shrinkage that may have occurred during the staining process.

Retinal ganglion cells were counted at 344 ± 6 (mean $\pm$ SE) sites across each retina with the Optical Fractionator method within StereoInvestigator software (MBF Bioscience, Williston, VT), a Zeiss Axio Imager.M2 microscope (Carl Zeiss Microscopy, Göttingen, Germany) at $1,000 \times$ total magnification, and a Zeiss AxioCam MRm camera (Carl Zeiss Microscopy). At the periphery of the retina, the ganglion cell layer can include other cell types (e.g., amacrine cells, glial cells). These cells were identified and excluded on the basis of their soma size, shape, Nissl accumulation in the cytoplasm, and staining of the nucleus (Ehrlich 1981; Stone 1981). In the retinal periphery, a counting frame of 50 μm $\times$ 50 μm was used at each 750×750-μm site to estimate cell density, with an area-sampling fraction (i.e., proportion of each grid that was occupied by the counting frame) of 0.0044. At the center of the retina, we conducted higher-resolution sampling in an oval area encompassing both foveae in the tree swallows and a similar-sized oval area in the flycatchers. A counting frame of 25 μm $\times$ 25 μm was used at each 250×250-μm perifoveal site, with an area-sampling fraction of 0.01. At less than 0.10, our mean Schaeffer's coefficient of 0.029 ± 0.001 indicates that the stereological sampling strategy was appropriate (Glaser and Wilson 1998). To visualize the distribution of ganglion cells across the retina, we constructed topographic maps in R (ver. 3.3.0), following Garza-Gisholt et al. (2014).

We estimated the theoretical spatial resolving power in cycles/degree for each center of acute vision, using the peak retinal ganglion cell density and focal length of each eye, following Ullmann et al. (2012). Axial length was used as a proxy for focal length by taking axial length $\times$ 0.6 (Ullmann et al. 2012).

To confirm the presence of foveae, we performed histological cross sections on two tree swallow eyes, four Acadian flycatcher eyes, and four least flycatcher eyes. After the eye was hemisected and fixed in 4% paraformaldehyde (see above), the eyecup was cut into a 2-mm-wide strip along the nasotemporal axis, with the fovea in the center of the strip. We then embedded the tissue in paraffin wax and serial-sectioned it, using a Thermo Scientific Shandon Finesse ME microtome (Waltham, MA). Sections were stained with hemotoxylin/eosin in a Thermo Scientific Shandon Varistain 24–3.

Visual Fields

We measured the visual-field configuration of three tree swallows, three Acadian flycatchers, and three least flycatchers, using the ophthalmoscopic-reflex technique. Live, fully alert individuals were restrained at the center of a visual-field ap-

paratus (see Martin 1984), with the bill held parallel to the ground. The observer moved a Keeler Professional ophthalmoscope around the perimeter arm of the apparatus until the retinal reflex disappeared from the ophthalmoscope viewfinder. This position corresponds to the margin of the retinal visual field. The margin of the retinal visual field was always measured for both eyes, but we could record only one at a time rather than both eyes simultaneously. Visual-field dimensions were measured with the eyes at rest, with the eyes fully adducted in a forward position, and with the eyes fully abducted in a rear position. Eye movements were readily induced by light tapping sounds or small flashes of light in the visual periphery. To measure eye movement amplitude, an eye was induced to take an adducted or abducted position, and the limit of the visual field was noted. We continued to induce the same type of eye movement until the most extreme recorded eye position was adopted multiple times (following Martin and Katzir 1994; Martin 2007). Although only one eye was observed at a time, the adduction measurements are likely representative of a converged visual-field state where both eyes are adducted simultaneously (as shown by Tyrrell et al. 2015). The abduction measurements, however, are likely a slight overestimation of the diverged visual-field state where both eyes are abducted simultaneously (Tyrrell et al. 2015). A complete set of measurements was taken at every 10° vertical increment around the head, starting 60° below the beak and ending directly behind the head.

We also measured the angular projection of the optic axis (i.e., the line passing through the center of the cornea and the lens) and the projection of the fovea. To measure the optic axis, we mounted an light-emitting diode onto the side of the ophthalmoscope and took the optic axis as the point where the three discernible Purkinje images were aligned (Martin 1984). We measured the projection of each fovea using the following equation:

$$\text{forward fovea projection} = \frac{s \times f}{2} + \frac{b + f}{2} - 90,$$

where s is the location of the fovea in Cartesian coordinates on a 0–1 scale (see Moore et al. 2012), f is the field of view for a single eye in degrees, and b is the blind-area width in degrees. We present means ± standard errors throughout.

Results

Retinal Configuration

Every tree swallow retina examined contained a central fovea and a temporal fovea, both of which were easily visible on whole mounts under a stereomicroscope (fig. A1, available online). The presence of both foveae was confirmed via histological cross sections (fig. A1). Retinal ganglion cell counting revealed two peaks of cell density corresponding to the central and temporal foveae (fig. 1a). The central fovea had a peak cell density of $57,700 \pm 1,126$ cells/mm², and the temporal fovea had a peak cell density of $40,174 \pm 5,280$ cells/mm².

Empidonax flycatcher retinae contained a central fovea but did not have an obvious temporal fovea. In addition, serial cross sectioning of six retinae failed to reveal a temporal fovea. Retinal ganglion cell counting did, however, reveal two peaks of cell density corresponding to a central fovea and an area temporalis (i.e., a region of elevated cell density in the temporal portion of the retina but lacking a foveal pit; fig. 1b). Acadian flycatchers had a peak cell density of $63,762 \pm 6,925$ cells/mm² in the central fovea and $45,177 \pm 5,507$ cells/mm² in the area temporalis. Least flycatchers had a peak cell density of $56,028 \pm 3,699$ cells/mm² in the central fovea and $38,113 \pm 1,642$ cells/mm² in the area temporalis. Collectively, the *Empidonax* flycatchers had a peak density of $60,668 \pm 4,917$ cells/mm² in the central fovea and $42,351 \pm 3,931$ cells/mm² in the area temporalis. For reference, Inzunza et al. (1991) found the central fovea of the black-chested buzzard-eagle (*Geranoaetus melanoleucus*) and American kestrel (*Falco sparverius*) to have peak retinal ganglion cell densities of 65,000 and 62,000 cells/mm², respectively, and the temporal fovea of both species peak densities of 45,000 cells/mm².

The central fovea of the tree swallow (11.0 ± 0.1 cycles/degree) had significantly higher spatial resolving power than that of *Empidonax* flycatchers (9.7 ± 0.4 cycles/degree; $t_6 = 2.52$, $P = .045$). The temporal fovea of the tree swallow (9.1 ± 0.4 cycles/degree) also had significantly higher spatial resolving power than the area temporalis of *Empidonax* flycatchers (8.1 ± 0.3 cycles/degree; $t_6 = 2.58$, $P = .042$).

Eye Shape

With an axial diameter of 8.30 ± 0.07 mm and a transverse diameter of 8.39 ± 0.06 mm, tree swallows had a relatively long eye (axial/transverse = 0.99 ± 0.01). This eye shape is similar to that of falcons (axial/transverse = 1.00; Reymond 1987) and hawks (axial/transverse = 1.08; Reymond 1985; fig. 1c). *Empidonax* flycatchers had wider (transverse diameter = 8.61 ± 0.04 mm) but shorter (axial diameter = 6.93 ± 0.06 mm) eyes than tree swallows. *Empidonax* flycatcher eye shape (axial/transverse = 0.80 ± 0.01) was similar to that of typical songbirds (fig. 1d). A sampling of 26 other passerine species showed an axial/transverse ratio of 0.77 ± 0.01 with a range of 0.72–0.86, with statistical outliers being less than 0.72 or greater than 0.83
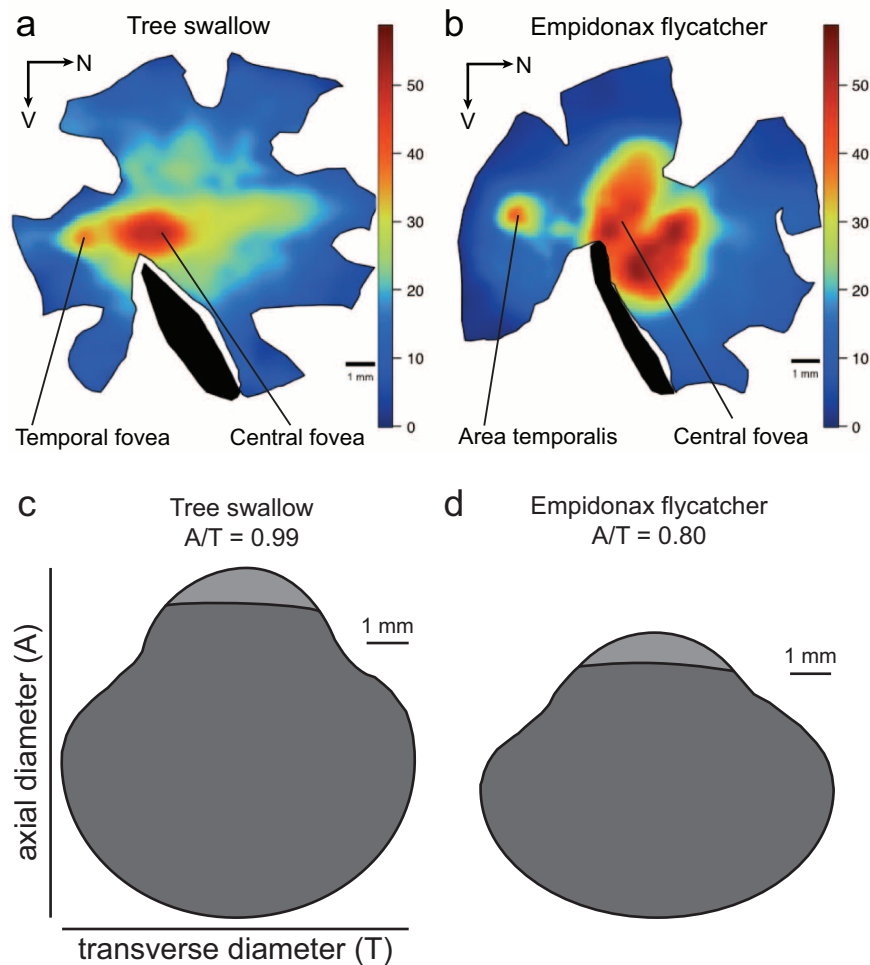
Figure 1: *a*, *b*, Topographic maps of retinal ganglion cell distribution for one exemplar tree swallow (*a*) and one exemplar *Empidonax* flycatcher (*b*; Acadian flycatcher). Tree swallows are bifoveate, while *Empidonax* flycatchers have a central fovea and an area temporalis. The oblique black bar indicates the pecten. *c*, *d*, Representations of eye shape profile in tree swallows (*c*) and *Empidonax* flycatchers (*d*). A/T is the species mean for axial diameter divided by transverse diameter. For reference, the A/T is 0.77, 1.00, and 1.08 for typical passerines, falcons, and hawks, respectively (see table A1, available online, for sources and species).

(table A1). Flycatchers fall within that range, but tree swallows are extreme statistical outliers.

Visual Fields

With their eyes at rest, tree swallows had a 23.0° ± 1.6° binocular field in front of the head and a 53.0° ± 4.5° blind area behind the head. The tree swallow has a blind area that is 2.3 times the size of its binocular field, which is identical to the 2.3 blind:binocular ratio in accipitrid hawks (Martin and Katzir 1999; O'Rourke et al. 2010; Potier et al. 2016) and similar to the 2.1 ratio in falcons (O'Rourke et al. 2010; fig. 2). *Empidonax* flycatchers had a resting binocular field of 24.1° ± 2.7° that is similar in size to the blind area

behind the head (26.6° ± 1.9°). With a 1.1 blind:binocular ratio, flycatchers were more similar to typical passerines (1.0 blind:binocular ratio; fig. 2). The blind:binocular ratio for all passerines had a range of 0.7–2.4, with statistical outliers being less than 0.4 or greater than 1.5 (table A1). Once again, flycatchers fall within that range, but tree swallows—and European starlings (*Sturnus vulgaris*)—are extreme statistical outliers.

The tree swallow optic axis (42.8° ± 1.7° forward, 1.5° ± 1.3° down) aligned closely with the projection of its central fovea (40.3° ± 0.7° forward, 3.6° ± 2.1° down). The temporal fovea in the tree swallows projected 68.9° ± 1.4° forward and 2.6° ± 4.2° down. Even with the more forward projection, the temporal fovea did not project into the binocular field. Instead, it projected into the lateral field,
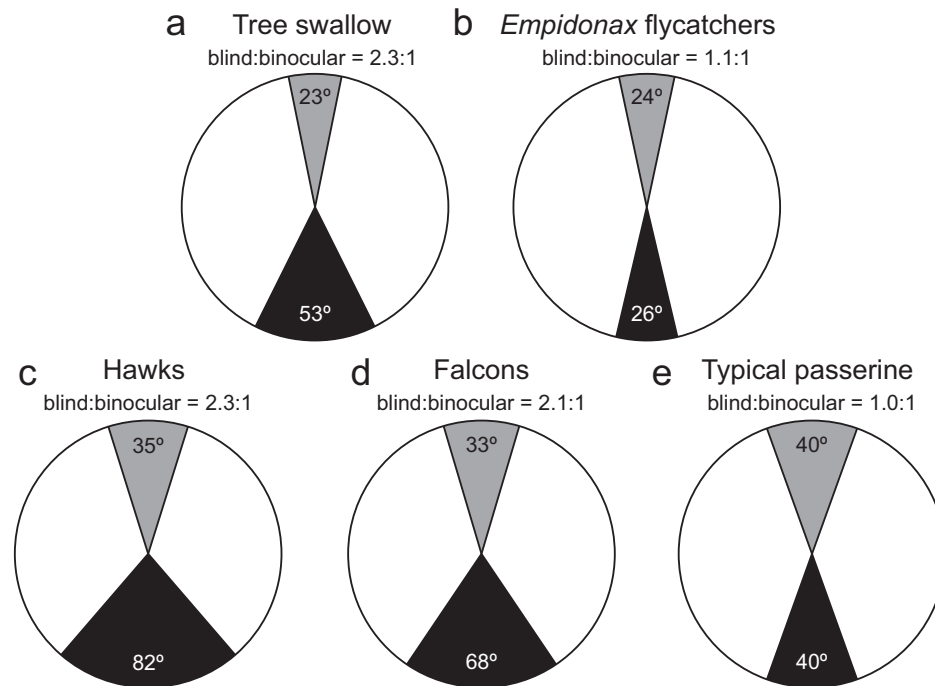
Figure 2: Horizontal section of the visual field along the plane parallel to the ground in tree swallows (*a*), *Empidonax* flycatchers (*b*), hawks (*c*), falcons (*d*), and typical passerines (*e*). Visual fields for typical passerines, falcons, and hawks are mean values from those available in the literature (table A1, available online, for sources and species). Blind : binocular ratios of 2.3, 2.3, and 2.1 indicate that the blind area is over twice the size of the binocular field in tree swallows, hawks, and falcons, respectively. *Empidonax* flycatchers, like other passerines, have similar-sized blind areas and binocular fields.

$9.6° \pm 1.4°$ outside the margin of the binocular field (fig. 3*a*). The central *Empidonax* flycatcher fovea projected $21.7° \pm 1.2°$ forward and $5.5° \pm 1.1°$ down. The area temporalis projected $76.0° \pm 0.8°$ forward and $0.9° \pm 3.1°$ down, lying outside the binocular field by $2.0° \pm 0.8°$ (fig. 3*b*).

With both eyes adducted in a converged state, tree swallows had a $39.4° \pm 2.5°$ binocular field in front of the head and a $68.4° \pm 1.5°$ blind area behind the head. In this converged state, the tree swallow's central fovea projected $48.3° \pm 0.7°$ forward and the temporal fovea projected $77.0° \pm 1.4°$ forward (fig. 4). Therefore, the two temporal foveae never view a shared point in space, but they do fall within the periphery of the binocular field when both eyes are adducted. *Empidonax* flycatchers had a $39.2° \pm 4.7°$ binocular field and a $53.3° \pm 4.9°$ blind area with the eyes converged, their central fovea projected $31.9° \pm 1.2°$ forward, and their area temporalis projected $84.4° \pm 0.8°$ forward. With both eyes abducted in a diverged state, tree swallows had a $0.5° \pm 3.9°$ binocular field in front of the head and a $35.9° \pm 6.2°$ blind area behind the head, whereas *Empidonax* flycatchers had a $2.0° \pm 2.2°$ binocular field and a $5.5° \pm 4.5°$ blind area. The tree swallow had a maximum eye movement amplitude of $19.5° \pm 2.8°$ in the plane of the beak, and *Empidonax* flycatchers had a maximum

eye movement amplitude of $18.6° \pm 3.3°$. All data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.n7140 (Tyrrell and Fernández-Juricic 2017*b*).

Discussion

Overall, several tree swallow visual-system properties are similar to those of diurnal raptors. This study shows that a songbird—the tree swallow—has a bifoveate retina (figs. 1*a*, A1) rather than the single fovea present in other songbirds (Dolan and Fernández-Juricic 2010; Moore et al. 2013, 2015, 2017; Tyrrell et al. 2013; Baumhardt et al. 2014), corroborating previous work with barn swallows (*Hirundo rustica*), bank swallows (*Riparia riparia*), common house martins (*Delichon urbicum*), and tree swallows (Chievitz 1891; Slonaker 1897; Rochon-Duvigneaud 1943). Furthermore, our flycatcher results support previous studies (Coimbra et al. 2006, 2009) that described other tyrant flycatchers as having a centrally placed fovea as well as an area temporalis (fig. 1*b*). Although both groups of predatory songbirds studied here have a second, frontally directed center of acute vision, the fovea of the active-pursuit swallow represents a higher degree of retinal specialization for acute vision than the area temporalis of the ambushing flycatcher. The presence of a fo-
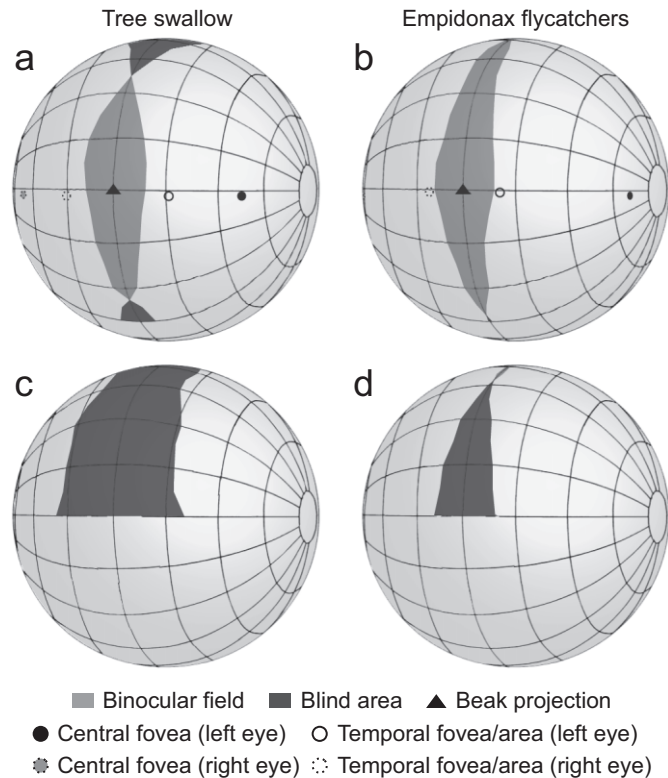
Tree swallow   Empidonax flycatchers

Figure 3: Three-dimensional representation of the visual field and point projections of the centers of acute vision in tree swallows (*a, c*) and *Empidonax* flycatchers (*b, d*); *a* and *b* show the visual fields in front of the head, and *c* and *d* show the visual field and blind areas behind the head.

veal pit has been hypothesized to serve numerous different functions (Moore et al. 2016), including image magnification (Walls 1942) and object-tracking enhancement (Pumphrey 1948).

In addition to the second fovea, tree swallows possess a raptor-like eye shape that is nearly as long as it is wide (fig. 1c). *Empidonax* flycatchers, however, have short eyes that are similar to those of typical passerines (fig. 1d). The unusually long eyes of tree swallows and diurnal raptors increase the focal length and, consequently, the visual acuity they can achieve. Our results actually show that tree swallows and *Empidonax* flycatchers have similar retinal ganglion cell densities, but tree swallows have a significantly higher theoretical spatial resolving power because of their longer focal length. Birds already have very large eyes in general, and in some cases the volume of a single eye can be greater than the volume of the entire brain (Burton 2008). Therefore, space in the avian skull is limited. If tree swallows and raptors were to increase axial length and transverse length proportionally, the eye would occupy more space in the avian skull and limit brain size. But by increasing axial length without a concomitant increase in transverse length, swallows and raptors achieve higher visual acuity without bal-

looning the size of the orbit and challenging brain size to accommodate the eye.

Flycatchers, like most other passerines, have a binocular field that is approximately symmetrical to the blind area at the rear of the head (fig. 2b). Yet tree swallows diverge from their passerine relatives, with a visual-field configuration that is more similar to that of diurnal raptors. Like raptors, tree swallows have a narrow binocular field, despite their predatory nature, and an asymmetric visual-field configuration where the large posterior blind area is over twice the size of the narrow anterior binocular field (fig. 2). While both tree swallows and raptors are predators, tree swallows are subject to higher risk of being depredated themselves. Actually, tree swallows have a somewhat smaller blind area behind the head—where predators are likely to approach—at an even greater expense to binocular vision. Among studied passerines, only European starlings (Martin 1986) have visual-field morphology similar to that of the tree swallow. Why starlings also have larger blind areas is difficult to establish, given the low number of species with multiple visual traits measured. Starling eye shape is similar to that of typical passerines (table A1; Martin 1986), but starlings do have a ramped retina (Martin 1986), track conspecifics with pe-
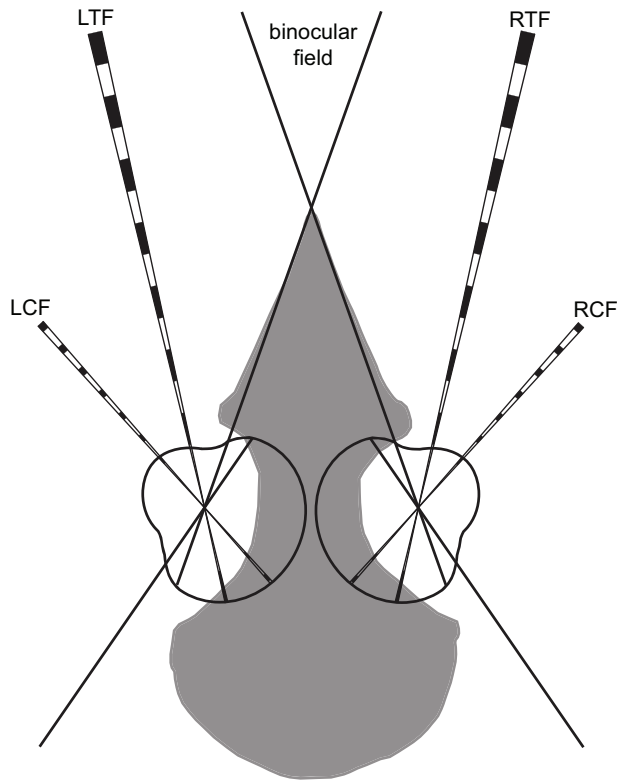
Figure 4: Top-view diagram of a tree swallow skull with the eyes in a fully converged position, showing the binocular field, the posterior blind area, and the foveal visual fields along the horizontal plane. LCF and LTF indicate the foveal visual field of the left eye's central fovea and temporal fovea, respectively. RTF and RCF indicate the foveal visual field of the right eye's temporal fovea and central fovea, respectively. Note that the temporal foveal visual fields will never cross to view a single, shared point, but they will enter the binocular field ~10 cm out from the focal point of the eye.

ripheral rather than foveal vision (Butler et al. 2016), and use a probing foraging technique to search for food in the ground (Beecher 1978). Further comparative studies considering these morphological and ecological factors would be needed to assess their relevance in explaining the similarities and differences with other songbirds.

Typically, when we think of animals with a temporally shifted fovea like that of the tree swallow, we envision a perceptual world akin to ours, where the foveae from the left and right eyes converge on a single point in the binocular field. The temporal fovea in the tree swallow retina does indeed project more frontally than its central fovea, but it does not intersect with the temporal fovea from the other eye or even fall within the binocular field at all (fig. 3a). This leaves the tree swallow with a visual system where each eye has two foveae that both serve monocular vision, not binocular vision. Knowing this, the first expectation may be

that tree swallows use large convergent eye movements to bring the temporal foveae of the left and right eyes together just before prey capture. Tree swallows are indeed capable of large convergent eye movements that bring their temporal foveae into the binocular field. However, it is important to note that, despite falling within the binocular field, the temporal fovea of the left eye and the temporal fovea of the right eye are still divergent from each other, falling close to the margins of the binocular field (fig. 4). This means that the foveae of each eye would not be able to view a single, shared point in space even when the eyes are converged. To achieve a state where the two temporal foveae are parallel to each other, tree swallows would have to move their eyes 13° more forward than the 20° of total eye movement of which they are already capable. To bring both temporal foveae into intersection at the tip of the beak, an additional 28° of forward movement would be necessary.

There is conflicting evidence as to whether the perceptual world of swallows is replicated in the visual system of other bifoveate birds (Slonaker 1897; Wood 1917; Lord 1956; Pettigrew 1978; Wallman and Pettigrew 1985; Tucker 2000; Kane and Zamani 2014). The temporal foveae of the left and right eyes also diverge from each other in American kestrels, broad-winged hawks, and common terns (Slonaker 1897; Wood 1917). More recent studies also found that the temporal foveae of the little eagle (*Haliaetus morphnoides*; Wallman and Pettigrew 1985) and the American kestrel (Pettigrew 1978) are diverged with the eyes at rest. In both diurnal-raptor species, the authors note that eye movements were observed that would allow both temporal foveae to fix on a single binocular target (Pettigrew 1978; Wallman and Pettigrew 1985). An important distinction between the little eagle and the American kestrel on the one hand and the tree swallow on the other is that, with the eyes in a resting position, the diurnal raptors' temporal foveae fall within the binocular field whereas the tree swallow foveae do not (fig. 3a). This is important because birds likely have no single neuron to control foveal alignment (Wallman and Pettigrew 1985). Therefore, the temporal foveae must rest within the binocular field so that binocular neurons with extremely large disparity can control fovea-aligning saccades (Wallman and Pettigrew 1985).

In either case, the temporal fovea does provide high-quality vision in a location more frontal than that of the central fovea, even if it is not binocular vision per se. Despite the commonly held belief that predators rely on binocular vision, swallows and diurnal raptors actually have narrow binocular fields. These lines of evidence suggest that avian binocular vision may serve a different set of functions in birds than it does in mammals (Martin 2009; Tyrrell and Fernández-Juricic 2017a).

Overall, predatory swallows have an extremely specialized visual system for a songbird, to the point that it has converged

with that of diurnal raptors on several characteristics, including a bifoveate retina, a long focal length, and an asymmetric visual field. Our study also shows that high-quality frontal vision is a shared trait among aerial predators, likely because of the visual demands of their foraging strategies. Despite a shared emphasis on frontal vision, it is ambiguous whether avian predators also share an emphasis on binocular vision itself. Even the central fovea of the tree swallow projects nearly 20° farther forward than that of flycatchers, giving swallows four separate foveae plus an afoveate binocular field in a single 100° arc (fig. 3a). Predators that chase prey have to react quickly to evasive maneuvers executed by the prey. With a total of four foveae already directed toward different potential escape paths, the swallow has acute vision waiting at every turn, and even abrupt changes in the escape trajectory by the prey can fall into any of the swallow foveae.

Acknowledgments

Literature Cited

Ahnelt, P. K., C. Schubert, A. Kuebber-Heiss, and E. M. Anger. 2005. Adaptive design in felid retinal cone topographies. Investigative Ophthalmology and Visual Science 46:4540.

Baumhardt, P. E., B. A. Moore, M. Doppler, and E. Fernández-Juricic. 2014. Do American goldfinches see their world like passive prey foragers? a study on visual fields, retinal topography, and sensitivity of photoreceptors. Brain, Behavior and Evolution 83:181–198.

Beecher, W. J. 1978. Feeding adaptations and evolution in the starlings. Bulletin of the Chicago Academy of Sciences 11:269–298.

Blackwell, B. F., E. Fernández-Juricic, T. W. Seamans, and T. Dolan. 2009. Avian visual system configuration and behavioural response to object approach. Animal Behaviour 77:673–684.

Burton, R. F. 2008. The scaling of eye size in adult birds: relationship to brain, head and body sizes. Vision Research 48:2345–2351.

Butler, S. R., E. C. Hosinski, J. R. Lucas, and E. Fernández-Juricic. 2016. Social birds copy each other's lateral scans while monitoring group mates with low-acuity vision. Animal Behaviour 121:21–31.

Chievitz, J. 1891. Über das Vorkommen der Area centralis retinae in den vier höheren Wirbelthierklassen. Archiv für Anatomische Entwicklung 1891:11–334.

Coimbra, J. P., M. L. V. Marceliano, B. L. da Silveira Andrade-da-Costa, and E. S. Yamada. 2006. The retina of tyrant flycatchers: topographic organization of neuronal density and size in the ganglion cell layer of the great kiskadee *Pitangus sulphuratus* and the rusty margined flycatcher *Myiozetetes cayanensis* (Aves: Tyrannidae). Brain, Behavior and Evolution 68:15–25.

Coimbra, J. P., N. Trévia, M. L. V. Marceliano, B. L. da Silveira Andrade-da-Costa, C. W. Picanço-Diniz, and E. S. Yamada. 2009.

Number and distribution of neurons in the retinal ganglion cell layer in relation to foraging behaviors of tyrant flycatchers. Journal of Comparative Neurology 514:66–73.

Dolan, T., and E. Fernández-Juricic. 2010. Retinal ganglion cell topography of five species of ground-foraging birds. Brain, Behavior and Evolution 75:111–121.

Ehrlich, D. 1981. Regional specialization of the chick retina as revealed by the size and density of neurons in the ganglion cell layer. Journal of Comparative Neurology 195:643–657.

Fernández-Juricic, E., M. D. Gall, T. Dolan, V. Tisdale, and G. R. Martin. 2008. The visual fields of two ground-foraging birds, house finches and house sparrows, allow for simultaneous foraging and anti-predator vigilance. Ibis 150:779–787.

Garza-Gisholt, E., J. M. Hemmi, N. S. Hart, and S. P. Collin. 2014. A comparison of spatial analysis methods for the construction of topographic maps of retinal cell density. PLoS ONE 9(4):e93485. doi:10.1371/journal.pone.0093485.

Glaser, E. M., and P. D. Wilson. 1998. The coefficient of error of optical fractionator population size estimates: a computer simulation comparing three estimators. Journal of Microscopy 192:163–171.

Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, et al. 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320:1763–1768.

Inzunza, O., H. Bravo, R. L. Smith, and M. Angel. 1991. Topography and morphology of retinal ganglion cells in falconiforms: a study on predatory and carrion-eating birds. Anatomical Record 229:271–277.

Jarvis, E. D., S. Mirarab, A. J. Aberer, B. Li, P. Houde, C. Li, S. Y. W. Ho, et al. 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. Science 346:1320–1331.

Jones, M. P., K. E. Pierce, and D. Ward. 2007. Avian vision: a review of form and function with special consideration to birds of prey. Journal of Exotic Pet Medicine 16:69–87.

Kane, S. A., and M. Zamani. 2014. Falcons pursue prey using visual motion cues: new perspectives from animal-borne cameras. Journal of Experimental Biology 217:225–234.

Land, M. F., and D.-E. Nilsson. 2012. Animal eyes. 2nd ed. Oxford University Press, Oxford.

Lord, R. D. 1956. A comparative study of the eyes of some falconiform and passerine birds. American Midland Naturalist 56:325–344.

Martin, G. R. 1984. The visual fields of the tawny owl, *Strix aluco* L. Vision Research 24:1739–1751.

———. 1986. The eye of a passeriform bird, the European starling (*Sturnus vulgaris*): eye movement amplitude, visual fields and schematic optics. Journal of Comparative Physiology A 159:545–557.

———. 2007. Visual fields and their functions in birds. Journal of Ornithology 148:S547–S562.

———. 2009. What is binocular vision for? a birds' eye view. Journal of Vision 9:1–19.

Martin, G. R., and G. Katzir. 1994. Visual fields and eye movements in herons (Ardeidae). Brain, Behavior and Evolution 44:74–85.

———. 1999. Visual fields in short-toed eagles, *Circaetus gallicus* (Accipitridae), and the function of binocularity in birds. Brain, Behavior and Evolution 53:55–66.

Moore, B. A., M. Doppler, J. E. Young, and E. Fernández-Juricic. 2013. Interspecific differences in the visual system and scanning behavior of three forest passerines that form heterospecific flocks. Journal of Comparative Physiology A 199:263–277.

Moore, B. A., J. M. Kamilar, S. P. Collin, O. R. P. Bininda-Emonds, N. J. Dominy, M. I. Hall, C. P. Heesy, et al. 2012. A novel method for comparative analysis of retinal specialization traits from topographic maps. Journal of Vision 12(12):13. doi:10.1167/12.12.13.

Moore, B. A., D. Pita, L. P. Tyrrell, and E. Fernández-Juricic. 2015. Vision in avian emberizid foragers: maximizing both binocular vision and fronto-lateral visual acuity. Journal of Experimental Biology 218:1347–1358.

Moore, B. A., L. P. Tyrrell, J. M. Kamilar, S. P. Collin, N. J. Dominy, M. I. Hall, C. P. Heesy, et al. 2016. Structure and functions of regional specializations in vertebrate retinas. Pages 351–372 in J. H. Kaas, ed. Evolution of nervous systems. Vol. 1. 2nd ed. Academic Press, Cambridge, MA.

Moore, B. A., L. P. Tyrrell, D. Pita, O. R. P. Bininda-Emonds, and E. Fernández-Juricic. 2017. Does retinal configuration make the head and eye of foveate birds move? Scientific Reports 7:38406. doi:10.1038/srep38406.

O'Rourke, C. T., M. I. Hall, T. Pitlik, and E. Fernández-Juricic. 2010. Hawk eyes I: diurnal raptors differ in visual fields and degree of eye movement. PLoS ONE 5(9):e12802. doi:10.1371/journal.pone.0012802.

Paterson, J. R., D. C. García-Bellido, M. S. Y. Lee, G. A. Brock, J. B. Jago, and G. D. Edgecombe. 2011. Acute vision in the giant Cambrian predator *Anomalocaris* and the origin of compound eyes. Nature 480:237–240.

Pettigrew, J. D. 1978. Comparison of the retinotopic organization of the visual wulst in nocturnal and diurnal raptors, with a note on the evolution of frontal vision. Pages 328–335 in S. J. Cool and E. L. Smith III, eds. Frontiers in visual science. Springer, New York.

Potier, S., F. Bonadonna, A. Kelber, G. R. Martin, P.-F. Isard, T. Dulaurent, and O. Duriez. 2016. Visual abilities in two raptors with different ecology. Journal of Experimental Biology 219:2639–2649.

Pumphrey, R. J. 1948. The theory of the fovea. Journal of Experimental Biology 25:299–312.

Reymond, L. 1985. Spatial visual acuity of the eagle *Aquila audax*: a behavioural, optical and anatomical investigation. Vision Research 25:1477–1491.

———. 1987. Spatial visual acuity of the falcon, *Falco berigora*: a behavioural, optical and anatomical investigation. Vision Research 27:1859–1874.

Rochon-Duvigneaud, A. 1943. Les yeux et le vision des vertébrés. Masson, Paris.

Slonaker, J. R. 1897. A comparative study of the area of acute vision in vertebrates. Journal of Morphology 13:445–493.

Stone, J. 1981. The whole mount handbook: a guide to the preparation and analysis of retinal whole mounts. Maitland, Sydney.

Tucker, V. A. 2000. The deep fovea, sideways vision and spiral flight paths in raptors. Journal of Experimental Biology 203:3745–3754.

Tyrrell, L. P., S. R. Butler, and E. Fernández-Juricic. 2015. Oculomotor strategy of an avian ground forager: tilted and weakly yoked eye saccades. Journal of Experimental Biology 218:2651–2657.

Tyrrell, L. P., and E. Fernández-Juricic. 2017a. Avian binocular vision: it's not just about what birds can see, it's about what they can't. PLoS ONE (forthcoming).

———. 2017b. Data from: The hawk-eyed songbird: retinal morphology, eye shape, and visual fields of an aerial insectivore. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.n7140.

Tyrrell, L. P., B. A. Moore, C. Loftis, and E. Fernández-Juricic. 2013. Looking above the prairie: localized and upward acute vision in a native grassland bird. Scientific Reports 3:3231. doi:10.1038/srep03231.

Ullmann, J. F. P., B. A. Moore, S. E. Temple, E. Fernández-Juricic, and S. P. Collin. 2012. The retinal wholemount technique: a window to understanding the brain and behaviour. Brain, Behavior and Evolution 79:26–44.

Wallman, J., and J. D. Pettigrew. 1985. Conjugate and disjunctive saccades in two avian species with contrasting oculomotor strategies. Journal of Neuroscience 5:1418–1428.

Walls, G. L. 1942. The vertebrate eye and its adaptive radiation. Hafner, New York.

Wood, C. A. 1917. The fundus oculi of birds especially as viewed by the ophthalmoscope: a study in comparative anatomy and physiology. Lakeside, Chicago.

References Cited Only in the Online Appendixes

Fernández-Juricic, E., C. O'Rourke, and T. Pitlik. 2010. Visual coverage and scanning behavior in two corvid species: American crow and Western scrub jay. Journal of Comparative Physiology A 196: 879–888.

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