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Visual fields, eye movements, and scanning behavior of a sit-and-wait predator, the black phoebe (*Sayornis nigricans*)

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Abstract Foraging mode influences the dominant sensory modality used by a forager and likely the strategies of information gathering used in foraging and anti-predator contexts. We assessed three components of visual information gathering in a sit-and-wait avian predator, the black phoebe (*Sayornis nigricans*): configuration of the visual field, degree of eye movement, and scanning behavior through head-movement rates. We found that black phoebes have larger lateral visual fields than similarly sized ground-foraging passerines, as well as relatively narrower binocular and blind areas. Black phoebes moved their eyes, but eye movement amplitude was relatively smaller than in other passerines. Black phoebes may compensate for eye movement constraints with head movements. The rate of head movements increased before attacking prey in comparison to non-foraging contexts and before movements between perches. These findings suggest that black phoebes use their lateral visual fields, likely subtended by areas of high acuity in the retina, to track prey items in a three-dimensional space through active head movements. These head movements may increase depth perception, motion detection and tracking. Studying information gathering through head movement changes, rather than body posture changes (head-up, head-down) as generally presented in the literature, may allow us to better understand the mechanisms of information gathering from a comparative perspective.

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Introduction

The ability of a forager to gather information about prey items and potential predators is dependent upon sensory capabilities (Getty and Pulliam 1993). However, the main sensory modality used for information gathering can be influenced by foraging mode. For instance, snakes using a sit-and-wait strategy rely more heavily on visual cues, while those using an active foraging strategy use mostly chemical cues (Vincent et al. 2005). Foraging mode can also play an important role in the trade-off between foraging and predation risk. For instance, Huey and Pianka (1981) found that two species of lacertid lizards classified as sit-and-wait predators foraged on more active prey items but experienced lower predation than four species of lizards classified as active foragers. Although strategies to gather information in active avian foragers have been described before (e.g., Elgar 1989; Getty and Pulliam 1993; Martin 2007), there is relatively less information on sit-and-wait foragers. In this study, we focused on three factors associated with visual information gathering in an avian sit-and-wait predator: the configuration of visual fields, degree of eye movement, and scanning behavior.

Birds rely primarily on visual cues when gathering information (Meyer 1977). When the head is static, information gathering is limited by the configuration of the

visual field, which determines the amount of space visible around the head (Martin 1986a). Birds can move their eyes to increase the amount of space scanned around the head. Additionally, head movements can increase the quantity and also the quality of information gathered because they allow the higher acuity areas of the retina (e.g., fovea; Meyer 1977) to scan a wider portion of space (Dawkins and Woodington 2000; Dawkins 2002).

The visual field is composed of three main parts: the binocular area (the portion of the visual field where the eyes overlap), the lateral area (the area served by only one eye), and the blind area above or at the rear of the head (Martin 1993; 1999a). Binocularity functions primarily in the visual guidance of the bill tip during the acquisition, manipulation, and inspection of objects during foraging or chick-feeding (Martin et al. 2005, 2007). Thus, species that require visual-guidance of the bill tip usually have binocular areas that are 20–40° in width. Binocularity in the front of the head usually results in a blind area at the rear of the head from which no information can be extracted. This visual configuration appears to be quite common and is found in a range of bird species (Martin 1986a, 1999a, b; Martin and Katzir 1994; Fernández-Juricic et al. 2008).

The size of the binocular and blind areas can be altered by eye movements, which varies substantially between bird species (Martin 1986a, Martin et al. 2008, Fernández-Juricic et al. 2008, Blackwell et al. 2009). In species that track cryptic or evasive prey items, such as herons and great cormorants, eye movements allow individuals to enhance the ability to detect flushing prey (Martin and Katzir 1994; Martin et al. 2008). When these eye movements are not of sufficient amplitude to track moving prey or monitor the environment birds may compensate with scanning behavior (Wallman and Letelier 1993).

Most studies have defined scanning behavior as the amount of time spent in a head-up (vigilant) body position or the number of head-up events per unit time (Elgar 1989; Lima and Bednekoff 1999; Bednekoff and Lima 2002). At this coarse level, the configuration of the visual field can influence scanning behavior. For instance, in a between-species comparison, Guillemain et al. (2002) found that the species with a blind area behind the head scanned longer than the species without a blind area, probably due to differences in visual coverage. However, individuals with identical scanning rates using the head-up head-down paradigm could have highly different rates of head movements within a scanning bout, which could affect the information being obtained. A recent study by Jones et al. (2007) suggests that the mechanism of information gathering in birds may be better understood using head movements as a proxy of information gathering.

In this study, we assessed the configuration of the visual fields, degree of eye movement, and variations in head movement rate across different contexts in a passerine sit-and-wait predator: the black phoebe (Sayoris nigricans). We also present preliminary information on the density of retinal ganglion cells in different parts of the retina and estimates of spatial resolving power. This visually guided flycatcher tracks individual prey items (e.g., flies, bees, and wasps; Ohlendorf 1976; Wolf 1997) from a perch and then flies in pursuit of them. This foraging mode makes the black phoebe a good model species because it is highly dependent on visual information about the location of prey items in three-dimensional space (Gall and Fernández-Juricic 2009).

We predicted that black phoebes would have wide binocular areas to allow for visual guidance of the bill during aerial prey capture and that these binocular areas would have a relatively long vertical extent to maximize visual coverage above the head while seeking prey. Wide binocularity is expected to generate a relatively large blind area behind the head. Individuals could compensate for a wide blind area with relatively large amplitude eye movements and/or head movements to track prey while perching. Head movements are expected to vary between contexts and depend on whether the target of attention is present within the visual field or not. We predicted that black phoebes would move their head (scanning) at a faster rate prior to a foraging flight (e.g., visual tracking of a mobile prey item) than they would while at rest on a perch or before a flight resulting in movement between perches.

Methods

Visual fields

All visual field measurements were conducted at California State University Long Beach (IACUC protocol no. 220) between May and July of 2007. We determined the retinal visual field using an ophthalmoscopic reflex technique (Martin 1984; see also Fernández-Juricic et al. 2008 for a detailed description of the procedures). An individual was positioned with its head aligned at the pivot points of the visual field apparatus and secured to a foam block using Velcro straps. We used a coordinate system in which 0° was directly above the bird's head, 90° was at the horizontal plane in front of the head, and 270° was at the horizontal plane behind the head. The bill position was fixed at the angle normally adopted while the bird was perching (90°) by taping it to a metal bill holder. The bill holder was replaced with a wire for measurements below the bill because the bill holder obstructed our view of the eye. The projection of the retinal margins of each eye was recorded with an accuracy of ±0.5° at each elevation using a Keeler Professional ophthalmoscope. We also recorded the margins of the pecten, a vascular structure in the eye.

We took measurements at elevations separated by 10° increments in the median sagittal plane of the bird.

We recorded the at-rest visual field of two adult black phoebes and the maximum (eyes diverged in front of the head) and minimum (eyes converged in front of the head) visual fields of four black phoebes (two adults and two juveniles). Black phoebes are sexually monomorphic, so we were unable to determine the sex of the individuals sampled. Juveniles were identified by the presence of cinnamon wing bars. Our sample sizes were similar to those in previous studies on visual fields (Martin 1984, 1986a; Martin and Katzir 1999). A recent study (Fernández-Juricic et al. 2008) suggested that the degree of inter-individual variability in visual field configuration within a species is relatively low. Actually, the coefficient of variation in the width of the binocular area across all elevations in black phoebes (CV = 28%, $N = 4$) was similar to that of house sparrows (CV = 28%, $N = 19$ individuals) and house finches (CV = 44%, $N = 14$; Fernández-Juricic et al. 2008) recorded over more individuals.

To determine the minimum and maximum visual fields, we elicited eye movements using a small light source and sounds (tapping or finger snapping). First, the position of the retinal field margins produced by the movement of the eyes towards the front of the head at each elevation (from 90° to 270°) in the sagittal plane was recorded. Then the position of the retinal margins produced by the movement of the eyes towards the rear of the head at each elevation was recorded. We calculated the difference between these values as the maximum amplitude of eye movement at each elevation. We recorded the position of the retinal margins when the eyes were at rest (from elevation 150° to 250°).

We calculated the extent of the binocular and lateral visual fields, and the extent of the blind areas behind the head in the horizontal plane. We used the following assumptions: (a) the maximum binocular overlap is produced when eyes are converged (i.e., rotated maximally forward), and (b) the minimum binocular overlap is produced when eyes are diverged (i.e., rotated maximally backwards). The extent of the lateral field for each eye in the plane of the bill was calculated using the formula [(360 − (mean blind field + mean binocular field))/2]. The vertical extent of the binocular field was calculated from the number of consecutive 10° elevations that had binocular overlap with the eyes at rest.

Retinal ganglion cell density

The number retinal ganglion cells per unit area was estimated following Boire et al. (2001). Two adult individuals were euthanized in a CO_2 chamber following CSULB IACUC protocol #220. The eye was excised and its anterior portion removed. The eye was then placed in a solution of 2.5% gluteraldehyde in 0.1 M phosphate buffer (pH = 7.2) for 5 min, and then rinsed with phosphate buffered saline (PBS).We removed the retina from the eye cup using a small paintbrush. Two of the four retinas were torn during this procedure and were not processed further. The two remaining retinas (one right, one left) were then placed in a solution of 4% paraformaldehyde for >12 h. The retinas were then rinsed with PBS. We took tissue samples from different areas of the retina; therefore, the data we present here should be considered preliminary. The retinal tissue was covered with a glass microscope slide and then placed on a gelatinized slide with a few drops of PBS and a small weight to ensure it would lay flat. The slides were then placed in a dish containing several drops of formalin on a 60°C hot plate for 2 h. The tissue was allowed to dry in the same dish for an additional 24 h. We then removed the cover slip and subsequently hydrated with distilled water adulterated with glacial acetic acid. After staining in a 0.25% cresyl violet solution for ∼6 min, the tissue was rinsed quickly with distilled water and dehydrated in an alcohol series and cleared. The tissue was cover-slipped with Permount for microscopic observations.

We took pictures of the ganglion cell layer with a Moticam 2000 microscope camera using Motic Image Plus 2.0. We measured the area of the retina with ImageJ (http://rsb.info.nih.gov/ij/) before and after processing, and calculated a percentage change in tissue size. Cell density was estimated by dividing the number of cells in each picture by the corrected tissue area. Stained ganglion cells were then counted under the microscope at 40× power. To calculated visual acuity, we used the sampling theorem (Hughes 1977) and estimated the highest detectable spatial frequency following Williams and Coletta (1987).

Scanning behavior

We sampled 98 adult individuals of unknown sex in 14 urban parks in Los Angeles and Orange counties in California between March and May of 2007. An additional 30 adult individuals of unknown sex were observed in July and August of 2008. We did not include juvenile birds in our analyses. Black phoebes are highly territorial (Wolf 1997), with territories that are smaller in the breeding (0.5–0.8 ha) than in the non-breeding season (9–11 ha). We did not tag individuals but we mapped the locations of the sampled individuals in each study area, which allowed us to minimize the chances of sampling a given individual more than once. Some study areas were visited more than once; however, we did not return to the same area of the park and individuals were sampled at least 500 m away from each other.

An individual was followed until it alighted on a perch, and then video-taped using a Canon ZX 50 digital camera

until it initiated a flight. We noted whether a flight resulted in a foraging attempt or a change of patch. Foraging flights were identified visually by their highly stereotyped flight shape and acoustically by bill snaps that occur when an insect was captured. Flights were classified as patch changes if an individual flew directly towards another perch in a different tree.

We measured head movement rate from videos using JWatcher 1.0 (Blumstein et al. 2000). Head movement rate for pre-flight scanning was measured from 15 s of video immediately prior to the initiation of a flight. This is the approximate duration of a head movement bout prior to foraging (Gall and Fernández-Juricic 2009). To determine scanning rate while individuals were perching, we analyzed 30 s of video with a start time chosen using a random number table. We used only video segments that occurred at least 30 s after an individual alighted on a perch and 30 s before an individual initiated a flight to avoid including pre-flight scanning. All head movement rates are presented as head movements per second.

We used general linear models to analyze the scanning behavior data. We determined differences in head movement rate between contexts with two comparisons: (a) resting on a perch versus prior to a foraging flight ($n = 98$ individuals), and (b) prior to moving between patches versus prior to a foraging flight ($n = 30$ individuals). All results are reported as means $\pm$ SE throughout.

Results

Visual field configuration

With the eyes at rest, the binocular overlap extended vertically 190° from 60° below the bill (elevation 150°) to 40° behind the head (elevation 320°) (Fig. 1). The binocular field was widest 10° above the plane of the bill (elevation 80°) with the eyes at rest (Fig. 1). The mean width of the binocular field $\pm$ SE in the plane of the bill was $31° \pm 1.0°$. The mean blind area $\pm$ SE directly behind the head was $21.5° \pm 2.5°$.

We were unable to accurately record eye movement at elevations below the bill due to obstructions by the visual field apparatus, so we only present minimum and maximum binocular fields in the celestial hemisphere. Black phoebes had an average binocular overlap $\pm$ SE of $40° \pm 1.9°$ with the eyes converged and of $4° \pm 5.4°$ with the eyes diverged in the plane of the bill (Fig. 2). The binocular field was widest in the plane of the bill (Fig. 3). The average width of the blind area $\pm$ SE directly behind the head was $49° \pm 10.6°$ when the eyes were converged in front of the head, and $33° \pm 4.8°$ when the eyes were diverged from the front of the head.
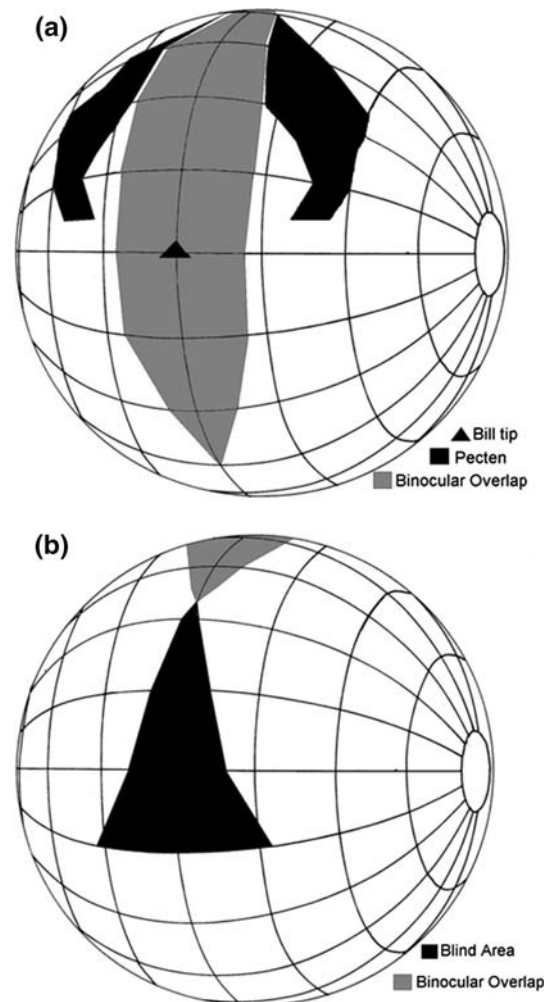

Fig. 1 Three-dimensional representation of the mean ($N = 2$) adult retinal field when the eyes are at rest in black phoebes. The head is at the center of the sphere with the tip of the bill projected towards triangle (**a**). The visual field as presented from directly behind the head with the head at the center of the sphere (**b**). The grid is at 20° intervals. *Unshaded areas* indicated areas of lateral monocular vision

The vertical extent of the binocular field was 140° when the eyes were diverged, with a gap in binocularity above the head (e.g., binocularity was abolished directly above the head, 0° elevation, but was present in front of and behind the head). The vertical extent of the binocular field was 100° when the eyes were converged (Fig. 3). The greatest average degree of eye movement $\pm$ SE in the celestial hemisphere was $18° \pm 2.7°$ and occurred in the plane of the bill (Fig. 4). The average amplitude of eye movement $\pm$ SE was $11.15° \pm 0.66°$ across all elevations.

Retinal ganglion cell density

Our preliminary estimate of overall cell density $\pm$ SE for both eyes was $27,673 \pm 575$ cells/mm^2. Cell density $\pm$ SE
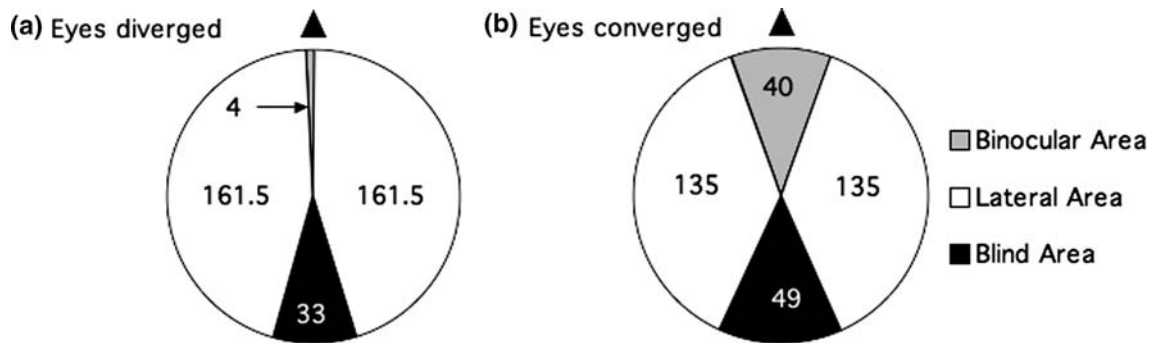
Fig. 2 Sections through the retinal visual fields in the plane of the bill for black phoebes ($N = 4$). Mean minimum visual fields are measured with the eyes converged maximally towards the bill (**a**) and mean maximum visual fields are obtained when the eyes are diverged maximally away from the bill (**b**). The direction of the bill is indicated by a *black triangle*. The size of each segment is indicated in degrees

Fig. 3 The average width of the binocular and blind area ($\pm$SE) in black phoebes ($N = 4$) as a function of elevation in the median sagittal plane when the eyes are maximally converged and maximally diverged. Contiguous elevations are show beginning directly behind the head (270°) and moving to directly in front of the head (90°). *Negative values* (below the *x*-axis) indicate blind areas, while *positive values* (above the *x*-axis) indicate areas of binocular overlap
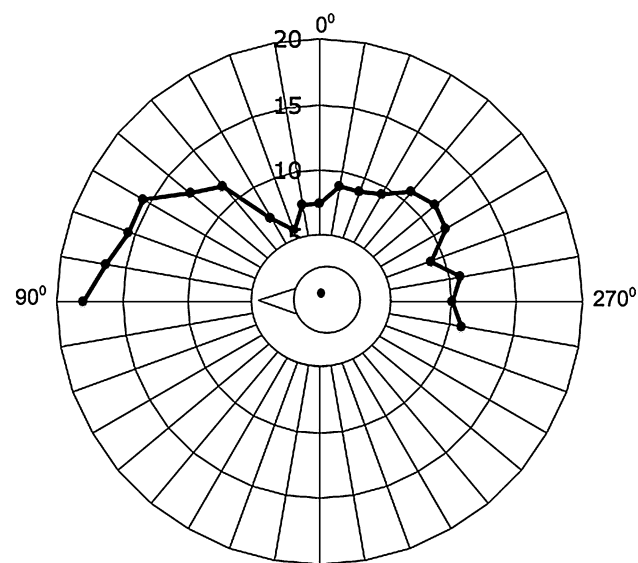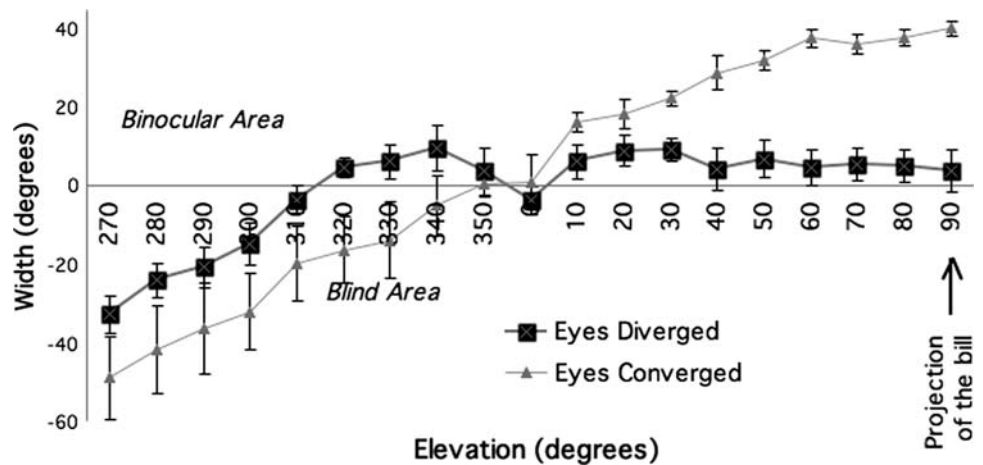
Fig. 4 Mean amplitude of eye movements as a function of elevation in the median sagittal plane in black phoebes ($N = 4$)

in the periphery of both eyes was $17,391 \pm 1,333$ cells/mm^2. Both black phoebes appeared to have two areas with high density of retinal ganglion cells. The highest cell density area can be considered the area centralis, with $37,363 \pm 851$ cells/mm^2 in the right eye and $44,417 \pm 993$ cells/mm^2 in the left eye. This translates into a visual acuity of 7.47 ± 0.09 cycles/degree in the right eye, and 8.88 ± 0.09 cycles/degree in the left eye. Both birds had another area with high density, with $30,026 \pm 910$ cells/mm^2 in the left eye and $31,266 \pm 1,058$ cells/mm^2 in the right eye.

Scanning behavior

As predicted, black phoebes scanned their environment more rapidly immediately before initiating a foraging flight (1.02 ± 0.03 head movements/s) than they did when resting on a perch (i.e., background scanning, 0.79 ± 0.04 head movements/s; $F_{1,96} = 19.26$, $P < 0.001$). Furthermore, in a second set of observations, we found that individuals scanned more rapidly prior to initiating a foraging flight that resulted in prey capture (1.30 ± 0.087 head movements/s) than they did prior to flights that resulted in a change of perches (0.99 ± 0.087 head movements/s; $F_{1,28} = 6.56$, $P = 0.016$).

Discussion

Visual fields

We found that with the eyes at rest the vertical extent of the black phoebe binocular field (190°) was as long as in passerines that forage on the ground ($\sim$180°–200°, Electronic Supplementary Material; Martin 1986a; Fernández-Juricic et al. 2008). However, when the eyes are at rest black phoebes have binocular (31°) and blind areas (21.5°) that are smaller in width than other passerines. For instance, house finches (Carpodacus mexicanus) and house sparrows (Passer domesticus) (Fernández-Juricic et al. 2008) have wider binocular areas (40°–51°). The implication is that black phoebe lateral fields are relatively large and may play a role in visual tracking.

Black phoebes had an unusual gap in binocularity above the head that has not been shown in other species. This may be due to obstructions of the retinal projection by the feathered crest. Morphological characteristics of the skull can influence the configuration of the visual field (Martin and Piersma 2009). For instance, Martin and Coetzee (2004) have shown that the bill ornamentation of the hornbills can obstruct the binocular field. The width of the bill has also been associated with the degree of binocularity in ground-foraging passerine species (Fernández-Juricic et al. 2008).

The binocular area was widest in the plane of the bill for black phoebes, but for other passerines the widest binocular areas occurred in elevations 30°–40° below the bill (Martin 1986a; Fernández-Juricic et al. 2008). This is likely related to variations in foraging behavior. The other passerines described so far are ground foragers, thus binocularity below the bill may assist them in locating seeds or insects (Cabe 1993; Hill 1993; Lowther and Cink 2006). Flycatchers, like the black phoebe, may benefit from binocularity in the plane of the bill to allow for the estimation of prey position and time to contact an object, and hence the precise timing of bill movements before prey capture while flying (Coimbra et al. 2006; Martin 2007). While it is unclear whether binocularity in birds results in stereopsis (McFadden 1993; Davies and Green 1994), binocularity may be used for obtaining optic flow-field information (the perception of movement of an object relative to movements of the observer) and for visual guidance of flight (Gibson 1986; Martin and Katzir 1999).

Although, black phoebes can alter their binocular areas with eye movements (18°), these changes are not as substantial as those seen in other passerines, which show a larger degree of eye movement (e.g., 20°–30° in the plane of the bill, Martin 1986a; Fernández-Juricic et al. 2008; Blackwell et al. 2009). One possibility is that predators that track prey items, like black phoebes, move their heads to

compensate for the relatively limited degree of eye movements.

Overall, the black phoebe has a visual field that is more similar in many regards (e.g., degree of eye movement and binocular width) to active and dive-pursuit predators than to sit-and-wait predators. With the exception of the cattle egret, other species of diurnal sit-and-wait predators tended to have 44–61% narrower binocular areas and 28–100% smaller degree of eye movement than the black phoebe (Electronic Supplementary Material). This may be due to differences in the prey type. While black phoebes make short pursuit flights after insects, the other sit-and-wait predators generally do not take their aquatic prey in flight (e.g., herons) or are nocturnal (e.g., owls) (Electronic Supplementary Material). Therefore, black phoebes, along with active and dive-pursuit predators, may face the need to precisely control the bill while foraging and track prey items in three-dimensional space.

In terms of the relationship between predation risk and visual field configuration, there are two important elements, the vertical extent of the binocular area and the width of the blind area behind the head (Martin 2007). The black phoebe is similar to other diurnal sit-and-wait predators (e.g., cattle egret Bubulcus ibis, reef heron Egretta gularis, squacco heron Ardeola ralloides) and non-visual foragers (e.g., woodcock (Scolopax rusticola), mallard Anas platyrhynchos) in the vertical extent of the binocular field (Electronic Supplementary Material). However, the black phoebe generally has a 16–21% larger blind area behind the head than diurnal sit-and-wait predators (Electronic Supplementary Material). One interpretation is that the predation pressure for black phoebes is different from the other species. However, such a conclusion is premature as ecological parameters related to the size of the blind area are not clear: black phoebes share similar widths with three species of tactile feeders [golden plovers (Pluvialis apricaria), lesser flamingos (Phoeniconaias minor), and blue duck (Hymenolaimus malacorhynchos)], two species of granivores (rock pigeon and house sparrow) and a piscivorous pursuit-dive forager [great cormorant (Phalacrocorax carbo)]. These species are diverse in body size, foraging mode, prey type, and predation pressure (e.g., aerial vs. terrestrial predators). Future research should compare the visual field configuration of closely related species that differ in foraging strategy and predation risk to better understand the factors that shape the visual field.

Retinal ganglion cell density

A recent study showed that two species of flycatchers, the great kiskadee (Pitangus sulphuratus) and the rusty margined flycatcher (Myiozetetes cayanensis) have a small central portion of the retina with high acuity (fovea) that

falls within the lateral visual field (Coimbra et al. 2006). These flycatchers also have a small secondary area with high acuity, located in the temporal portion of the retina projecting into the binocular field (Coimbra et al. 2006). The species that relies more heavily on insect prey (rusty margined flyctacher) has a higher concentration of retinal ganglion cells in the central fovea and temporal area than the species (great kiskadee) with a more generalist diet (Coimbra et al. 2006). Our preliminary evidence also suggests that black phoebes have two areas of high concentration of ganglion cells in their retinas. These findings indicate that the fovea and the temporal area in flycatchers subtend a small portion of the whole visual field, so rapid head movements can be used to keep a visual target in the line of sight with high acuity while tracking prey from a perch.

Scanning behavior

Previous behavioral analyses of scanning have assumed that individuals have comprehensive vision when head-up (reviewed in Fernández-Juricic et al. 2004). However, many species, like the black phoebe, have blind areas behind the head and may compensate for this reduced visual coverage through head movements (Guillemain et al. 2002). Individuals use these head movements to monitor their environment. Monitoring allows individuals to determine whether the visual landscape has changed over time (e.g., the approach of a predator introduces a new object into the visual field). Head movements can also be used to track a single visual target as it moves through space (e.g., the trajectory of the predator). Although, these behaviors may appear similar when scanning is explored at a coarse level (e.g., number of head-up events per unit time) they serve different functions. By providing an analysis of scanning behavior at a finer scale (e.g., number of head movements within a scan bout, Jones et al. 2007), we found that scanning behavior was adjusted to different contexts.

Black phoebes scanned more rapidly prior to a foraging flight than they did when resting on a perch or prior to a flight that resulted in a patch change. We assume that higher head-movement rate corresponds to greater scanning effort in order to obtain more information from the environment (Land 1999; Jones et al. 2007). Changes in head movement rates with context may be related to the configuration of the visual fields and the topography of the retina. Black phoebes have large lateral visual fields, subtended by the foveae (Meyer 1977; Nalbach et al. 1993; Coimbra et al. 2006). Taking turns placing the right and left lateral areas with the foveae on the object repeatedly may improve depth perception by motion parallax (Casperson 1999; Kral 2003). The fovea is also involved in motion

detection (Sillman 1973), which may assist in tracking stimuli that move at high speed (Maldonado et al. 1988), like the prey items of the black phoebe.

Conclusions

Overall, the black phoebe has large lateral areas, likely subtended by high acuity areas in the retina, which are used for prey searching in a three-dimensional space through active head movements while perching. Head movements in non-foraging contexts were found to be less pronounced than head movements in foraging contexts. This scanning strategy may be related to foraging mode, as other species (e.g., ground foragers) may actually show opposite patterns: higher head movement rates in non-foraging than in foraging contexts as prey is stationary and usually found in a two-dimensional plane. Assessing scanning at a fine scale could be used to better understand the relationship between the design of the sensory system and the investment in gathering different types of information.

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