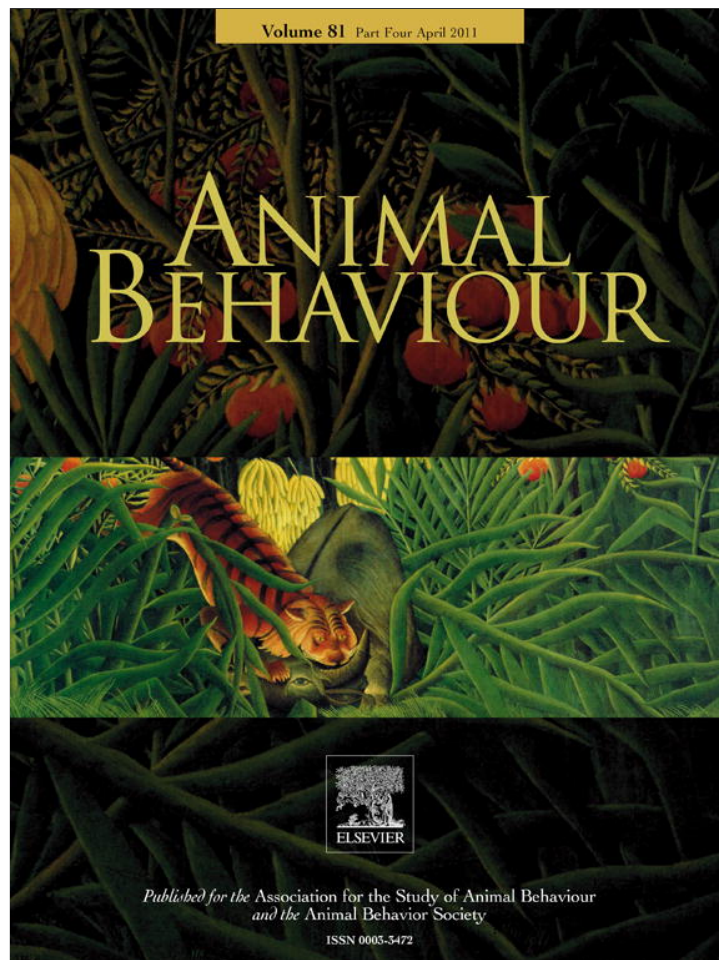


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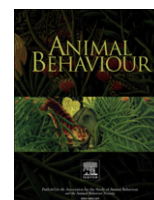
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Visual systems and vigilance behaviour of two ground-foraging avian prey species: white-crowned sparrows and California towhees

Esteban Fernández-Juricic^{a,*}, Megan D. Gall^a, Tracy Dolan^b, Colleen O'Rourke^b, Sarah Thomas^b, Jacqueline R. Lynch^a

^a Department of Biological Sciences, Purdue University

^b Department of Biological Sciences, California State University Long Beach

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Predator–prey interactions are regulated by the ability of individuals to detect, and then approach or avoid, each other. In visually guided organisms, the prevalent view is that predators have large binocular visual fields and high acuity, whereas prey have wide lateral areas and low acuity, which could affect vigilance behaviour. We characterized the configuration of the visual system (visual fields, retinal topography, visual acuity) and vigilance behaviour (head movement rate) of two ground-foraging avian prey (white-crowned sparrow, *Zonotrichia leucophrys*, California towhee, *Pipilo crissalis*) with laterally placed eyes. We found that the binocular field of both species (45°) was actually wider than those of some of their avian predators. Both species also had a single retinal specialization (high ganglion cell density area) located in the centro-temporal sector of the retina, which projected into the lateral and frontal part of the head. Wide binocular fields may increase binocular contrast to detect and visually guide the bill towards prey items. Both species had wider lateral visual fields and faster head movement rates than some of their predators, probably to enhance detection and visual tracking of predators. California towhees made faster sideways movements of the head than did white-crowned sparrows, probably to cover visual space more quickly with their retinal specialization because of the comparatively lower spatial resolution of their retinal periphery. Alternatively, California towhees might move their heads more rapidly to monitor for potential risks (e.g. competitors, predators), as they rely mostly on personal information because of their degree of territoriality. Our findings suggest that the visual system and vigilance behaviour of these two avian prey species combine traits to enhance predator detection through large visual coverage and fast head movements, but also to enhance food detection at close range through enhanced binocular vision.

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Vigilance behaviour has been studied mostly from a functional (Elgar 1989; Lima 1998; Curio 2005) rather than a mechanistic perspective (Beauchamp 2003; Fernández-Juricic et al. 2004). One important question is what proximate factors affect the way in which animals gather information that is relevant to fitness (Dall et al. 2005). In visually guided organisms, the configuration of the visual system determines the quality and quantity of information gathered, eventually affecting decision making (e.g. detection of food items, the timing of flying away from a predator, etc.; Cronin 2008). For instance, in bird species with laterally placed eyes, individuals first turn their heads sideways to inspect food on the ground laterally, then turn to their binocular fields before pecking

at a food item (Bischof 1988; Hodos 1993). These bird species are generally thought to have one retinal specialization at the centre of the retina projecting laterally; that is, an area with a high density of retinal ganglion cells (fovea or area centralis) that provides high visual acuity (Collin 1999). The retinal ganglion cell axons carry the visual information gathered in the photoreceptors to the central nervous system through the optic nerve (Meyer 1977).

Interestingly, the type and position of retinal specializations and the configuration of the visual fields vary substantially between species (Collin 1999; Martin & Osorio 2008), which may result in differences between species in scanning behaviour when individuals gather information about food and predators (e.g. O'Rourke et al. 2010a, b; Fernández-Juricic et al. 2010). For instance, a comparison between the Eurasian wigeon, *Anas penelope*, and the northern shoveler, *Anas clypeata*, found that the former has the wider blind area at the rear of the head, and as a result spends more time in head-up vigilance to enhance visual coverage (Guillemain

* Correspondence: E. Fernández-Juricic, Department of Biological Sciences, Lilly Hall of Life Sciences, Purdue University, 915 W. State Street, West Lafayette, IN 47907, U.S.A.

E-mail address: efernan@purdue.edu (E. Fernández-Juricic).

et al. 2002). This increase in vigilance may compensate for the decrease in predator detection probabilities when animals are head-down foraging (Lima & Bednekoff 1999; Tisdale & Fernández-Juricic 2009).

Scanning behaviour has been traditionally studied as the movement of the body from head-down to head-up postures (i.e. from foraging to vigilance). However, this proxy of scanning can be considered too coarse (Fernández-Juricic et al. 2004), because even when the head is up (1) visual acuity varies in different parts of the visual field depending on the type and position of the retinal specialization (Meyer 1977; Collin 1999), and (2) the width of the blind area can limit visual coverage (Guillemain et al. 2002) and thus predator detection abilities (Devereux et al. 2006). Recent studies have shown that head movements are probably better indicators of scanning behaviour (reviewed in Fernández-Juricic 2010), as birds move their heads to monitor the environment with the high acuity provided by the retinal specialization. Changes in the rate and duration of head movements have been associated with different foraging strategies (Land 1999; Gall & Fernández-Juricic 2009), predator scanning before (Jones et al. 2009) and after (Jones et al. 2007) predator attacks, and conspecific monitoring (Dawkins 2002). The rate of head movement gives an indication of how frequently an individual shifts its visual fields to enhance visual coverage, estimate the distance to an object and explore a visual target with the retinal specialization (Dunlap & Mowrer 1930; Dawkins 2002; Kral 2003).

In this study, we characterized the configuration of the visual system and scanning behaviour in birds with laterally placed eyes that forage on the ground. We assessed the variation in three visual properties (visual field configuration, retinal topography, visual acuity) and scanning behaviour (head up/down patterns, head movement rate) in two species: the white-crowned sparrow, *Zonotrichia leucophrys*, and the California towhee, *Pipilo crissalis*. We chose two species with relatively similar foraging behaviour that belong to the Emberizidae family to reduce variability in phylogenetic history and feeding ecology, although our study species are not necessarily closely related within the family (DaCosta et al. 2009). Both species are ground foragers with conical bills that feed on plant matter (mostly seeds during the nonbreeding season) and animal matter (mostly invertebrates during the breeding season). Additionally, both species inhabit a mix of shrubby and grassy vegetation, and forage relatively close to cover (Chilton et al. 1995; Kunzmann et al. 2002). However, the white-crowned sparrow is smaller and more social than the California towhee, which is considered a solitary species (Chilton et al. 1995; Kunzmann et al. 2002).

From a visual ecology perspective, the prevalent predator–prey paradigm is that predatory species have wide binocular fields to facilitate visual detection and manipulation of prey, whereas prey species have wide lateral visual fields and narrow blind areas to be able to detect predators through panoramic vision (Johnson 1901; Walls 1942). This view has been supported in some taxonomic groups (Hughes 1977), but remains controversial in some mammal groups (Heesy 2009) and even in birds (Martin 2009). Within birds, raptors that prey on our study species (e.g. red-tailed hawk, *Buteo jamaicensis*, Cooper's hawk, *Accipiter cooperii*, and American kestrel, *Falco sparverius*; Chilton et al. 1995; Kunzmann et al. 2002) have binocular fields of 33–39°, lateral areas of 122–132° and blind areas of 60–82° (O'Rourke et al. 2010a). Based on the aforementioned predator–prey paradigm, we predicted that white-crowned sparrows and California towhees would have narrower binocular fields and blind areas and wider lateral areas than their raptor predators. We predicted that the retinal specialization of these ground foragers would be at the centre of the retina, projecting laterally because of the position of the eyes, to increase visual

resolution in the lateral visual field (Dolan & Fernández-Juricic 2010).

We hypothesized that scanning behaviour of predators and prey would vary because of differences in body size and eye size (Brooke et al. 1999). Predators have larger eyes and thus higher visual acuity than prey (Kiltie 2000), which may reduce the need of predators to scan the surroundings as often as prey. We predicted that white-crowned sparrows and California towhees would have higher scanning rates than some of their avian predators (red-tailed hawks, 19.34 ± 3.34 head movements/m; Cooper's hawks, 35.45 ± 4.47 head movements/m; American kestrels, 18.10 ± 1.51 head movements/m; O'Rourke et al. 2010b). Using the eye size–visual acuity relationship (Kiltie 2000), we also predicted that the scanning behaviour of our two study species would differ: white-crowned sparrows should show relatively higher scanning rates than California towhees to compensate for their smaller eye size and lower visual acuity. Making a two-species comparison limits our inference about cause–effect relationships as any between-species difference in phylogeny, ecology and physiology could be influencing scanning behaviour. Therefore, we used all studied visual traits (acuity visual field configuration, degree of eye movement, retinal topography) to provide some post hoc interpretations that could be tested in the future.

METHODS

The protocol for this study was approved by the California State University Long Beach Institutional Animal Care and Use Committee (protocol no. 248). White-crowned sparrows and California towhees were captured from different populations in southern California. Animals were housed on campus with one to four birds per cage ($0.80 \times 0.55 \times 0.60$ m). Birds were kept on a 12:12 h light:dark cycle at approximately 25 °C. Food and water were provided ad libitum. We first measured the scanning behaviour of all individuals. We then measured visual fields of 27 individuals chosen at random. Most individuals were later released at their site of capture, but five white-crowned sparrows and four California towhees were used for retinal analysis. Details of each of these procedures are described below.

Visual Fields

We successfully measured visual fields of 12 white-crowned sparrows and 15 California towhees with two methods (see below). Measurements were taken using a visual field apparatus, following an ophthalmoscopic reflex technique (Martin 1984), which is a procedure widely used in comparative visual ecology (Martin 2007; Martin & Osorio 2008). Each individual was restrained in the centre of the visual field apparatus with its body and bill in a horizontal position. We used an angular coordinate system to measure the visual fields (see example in Fig. 4). The head of the bird lies at the centre of this space defined as a globe. The horizontal axis of the globe travels through both eyes. The 0° elevation lies directly above the head of the bird, the 90° elevation lies directly in front of the bird's head, and the 270° elevation lies directly behind the bird's head on the horizontal plane. We held the head of each bird at a 90° angle, based on the natural head position recorded for individuals while perched. Using a Keeler Professional ophthalmoscope, we measured the retinal margins of each eye in 10° increments ($\pm 0.5^\circ$) at elevations ranging from 150° to 260° (elevations outside this range were obstructed by the apparatus).

We measured visual fields using two methods: (1) when eyes were at rest and (2) when eyes were converged towards the bill tip and diverged towards the back of the head. In the first method, we

measured visual fields without eliciting eye movements. We also measured the projection of the pecten, a vascular structure in the retina that projects a blind spot into the visual field (Meyer 1977). In the second method, we elicited eye movements with flashes of light or sounds directed at the front or rear of the bird's head. When the eyes converged towards the bill or diverged towards the rear of the head, we recorded the maximum and minimum positions of the retinal field margins. The difference between maximum and minimum positions represented the degree of eye movement. We also calculated the maximum and minimum size of the binocular, lateral and blind areas with eyes converged and with eyes diverged. The lateral area (monocular area – binocular area) was calculated as follows: $(360 - (\text{mean blind area} + \text{mean binocular area})/2)$ (Fernández-Juricic et al. 2008). The monocular area encompasses the whole extent of the visual field served by a single eye, including the area of binocular overlap with the other eye. For a given eye, the lateral visual field represents the sector of the visual field without binocular overlap.

Retinal Ganglion Cell Density and Visual Acuity

We extracted retinas from five white-crowned sparrows and four California towhees (these were individuals used in the visual field measurements), and successfully processed four and three retinas, respectively. We chose one representative retina per species to draw topographic maps, which represent changes in the density of ganglion cells (number of cells/mm²) across the retina (see Supplementary Appendix 1 for methods used to remove, stain and photograph the retinas and to count the number of retinal ganglion cells).

Visual acuity can vary with eye size and shape, photoreceptor density, retinal ganglion cell density and other optical properties of the eyes (Kirk & Kay 2004). Given the similar activity patterns of our study species, we assumed that they also have similar eye shapes and optics. We estimated visual acuity based on eye size and on the areas in the retina with the highest 25th percentile of retinal ganglion cell density (Dolan & Fernández-Juricic 2010), following the sampling theorem (Hughes 1977). We estimated the posterior nodal distance (PND), which is the length between the posterior nodal point of the eye and the anterior surface of the retina (Reymond 1985) by measuring the axial length of the eye and multiplying it by 0.60, which is the axial length to PND ratio in diurnal birds (Hughes 1977; Martin 1993). PND is a proxy of the area of the retina on to which an image is projected. We estimated spatial resolving power by calculating the retinal magnification factor (RMF), which is the linear distance on the retina that subtends 1° (Pettigrew et al. 1988), as follows:

$$\text{RMF} = \frac{2\pi\text{PND}}{360}$$

Our estimate of visual acuity was F_n , the highest spatial frequency that can be detected in cycles per degree:

$$F_n = \frac{\text{RMF}}{2} \sqrt{\frac{2D}{\sqrt{3}}}$$

where D represents retinal ganglion cell density in cells/mm² (Williams & Coletta 1987).

Scanning Behaviour

We measured the scanning behaviour of California towhees and white-crowned sparrows in the laboratory. Each bird was placed in a rectangular 1.20 × 0.90 × 0.40 m (L × W × H) wire-mesh

enclosure on top of a 1.5 m high table in one corner of the room. We covered all sides of the enclosure with cardboard except that we made six 0.18 × 0.03 m openings to allow access for video cameras (two openings on each long side, one opening on each short side and one opening on the top). Even if the animals looked through these openings, no objects but the cameras were visible to them. The area around the table was surrounded by black cloth that extended from the floor to the ceiling of the room to reduce visual distraction (e.g. video recording equipment, computers, observers, etc.).

Four video cameras recorded the behaviour of the animals in the enclosure: two camcorders were located 0.5 m from the short sides of the enclosure, one camcorder was on top of the enclosure, and one wide-angle pinhole camera was hidden in one corner of the enclosure. At the bottom of the enclosure, we placed lining paper that was replaced after each trial. The cage was illuminated from above by four high-flicker-frequency (20 000 Hz) fluorescent bulbs to avoid behavioural reactions to regular fluorescent light (Greenwood et al. 2004; Evans et al. 2006), as birds have a higher flicker-fusion frequency than humans (D'Eath 1998). We used 43 white-crowned sparrows and 19 California towhees for these behavioural observations. Body mass of these individuals varied significantly between species (white-crowned sparrows, 30.17 ± 0.61 g; California towhees, 43.01 ± 0.91 g; $F_{1,60} = 138.86$, $P < 0.001$). Temperature in the room varied between 22.1 and 26.8 °C, and light intensity varied between 1390 and 1930 lx.

On a given trial, we uniformly dispersed 1 g of millet seeds throughout the bottom of the enclosure. We then placed a single individual within the enclosure, let it acclimatize for 1 min, and then videorecorded its behaviour for 4 min. Individuals scanned (moving the head sideways while in a head-up posture), moved around (flying, jumping, hopping, walking), searched for food (moving or not moving the head while in a head-down posture) and pecked (head-down). We recorded these behaviours from the videos with JWatcher 1.0 (Blumstein & Daniel 2007). A given head movement started whenever an individual would change the orientation of its head and ended when the individual stopped moving its head to a new orientation. Although birds show a variety of head movements that vary in amplitude and orientation, we lumped all head movements into a single category because of the difficulty of distinguishing between head movements types. We believe our estimate of head movement rate reflects scanning rather than food searching, as food-searching behaviour was generally performed in the head-down posture, which we recorded separately. However, we recorded the frequency of different types of body movement because the orientation of the eyes changes as the body moves in space, and hence can alter the position of the retinal specialization and the range of visual coverage.

We report the following variables: (1) head movement rate (number of sideways movements of the head/min while head-up); (2) head-up rate (number of events/min), which is one of the traditional measures of vigilance behaviour; (3) walk/hop rate (number of events/min); and (4) jump/fly rate (number of events/min). We do not report the interval duration between consecutive head movements as it was roughly the inverse of the head movement rate.

Statistical Analysis

We used general mixed linear models (Proc Mixed in SAS 9.2, SAS Institute, Cary, NC, U.S.A.) to analyse between-species differences in the width of the binocular field, blind area and pecten, the vertical extent of the binocular field and the degree of eye movement. Our models considered individual identity as the within-subject factor and included species, elevation in the visual field and the interaction between species and elevation as independent variables. We were particularly interested in the between-species

differences as well as the interaction between species and elevation to determine whether a given dependent factor varied between species at different elevations.

We used *t* tests to analyse species differences in eye axial length, RGC₂₅ density (highest 25th percentile of retinal ganglion cell density) and visual acuity. We also analysed how the percentage of counts in different retinal ganglion cell density classes (32–34, 32–22, 12–22, 2–12 cells/mm² × 10³) varied between species to establish the degree to which cell density changes from the area with the highest density (e.g. retinal specialization) to the rest of the retina (e.g. periphery). The results of a recent study suggest that the degree of change in retinal ganglion cell density across the retina could influence patterns of head movement (Dolan & Fernández-Juricic 2010). We ran a general linear model assessing the interaction effect between species and cell density range.

We used a general linear model (Statistica 9.0, StatSoft, Tulsa, OK, U.S.A.) to analyse differences between species in head movement rate, head-up rate, walk/hop rate and jump/fly rate. Temperature and light intensity were significantly correlated (Pearson product moment correlation: $r = 0.30$, $P = 0.018$), so we excluded light intensity from our statistical models. We log-transformed walk/hop rate and jump/fly rate to increase the normality of residuals. However, we present backtransformed means for clarity. We present means ± SE throughout.

RESULTS

Visual Fields

The bill tips of both white-crowned sparrows and California towhees projected into the binocular field around the horizontal plane (90°; Fig. 1). Within the range of elevations measured, the

binocular field of California towhees ($176.15 \pm 5.34^\circ$) was vertically longer than that of white-crowned sparrows ($150.00 \pm 7.86^\circ$; $F_{1,17} = 7.57$, $P < 0.014$; Fig. 2). This resulted in the binocular field extending higher above the top of the head of the California towhee, increasing its vertical visual coverage, compared to that of the white-crowned sparrow (Figs 1, 2).

The maximum average width of the binocular field occurred at elevation 80° (right above the bill projection into the binocular field) in both species (Fig. 2). At elevation 90° with the eyes at rest, the width of the binocular field was similar in both species (Fig. 1b, d). Across all recorded elevations, the average width of the binocular field did not differ significantly between white-crowned sparrows ($30.74 \pm 1.48^\circ$) and California towhees ($29.68 \pm 0.81^\circ$; Table 1).

At elevation 90° with the eyes at rest, we found that the blind area was about 10° wider in the white-crowned sparrow than in the California towhee (Fig. 2b, d). Across all recorded elevations, the blind area was significantly wider in the white-crowned sparrow ($23.40 \pm 1.82^\circ$) than in the California towhee ($19.04 \pm 1.41^\circ$; Table 1), but there was no significant interaction between species and elevation (Table 1). The maximum width of the blind area was recorded at elevation 260° (just below the back of the head) in both species (Fig. 2).

Across all recorded elevations, the degree of eye movement was significantly higher in white-crowned sparrows ($12.17 \pm 0.46^\circ$) than in California towhees ($10.61 \pm 0.39^\circ$; Table 1, Supplementary Appendix 2); however, there was no significant interaction between species and elevation (Table 1). Variation in the degree of eye movement (e.g. eyes converged or diverged) led to changes in the configuration of the visual field, particularly with regard to the width of the binocular and blind areas (Supplementary Appendix 2).

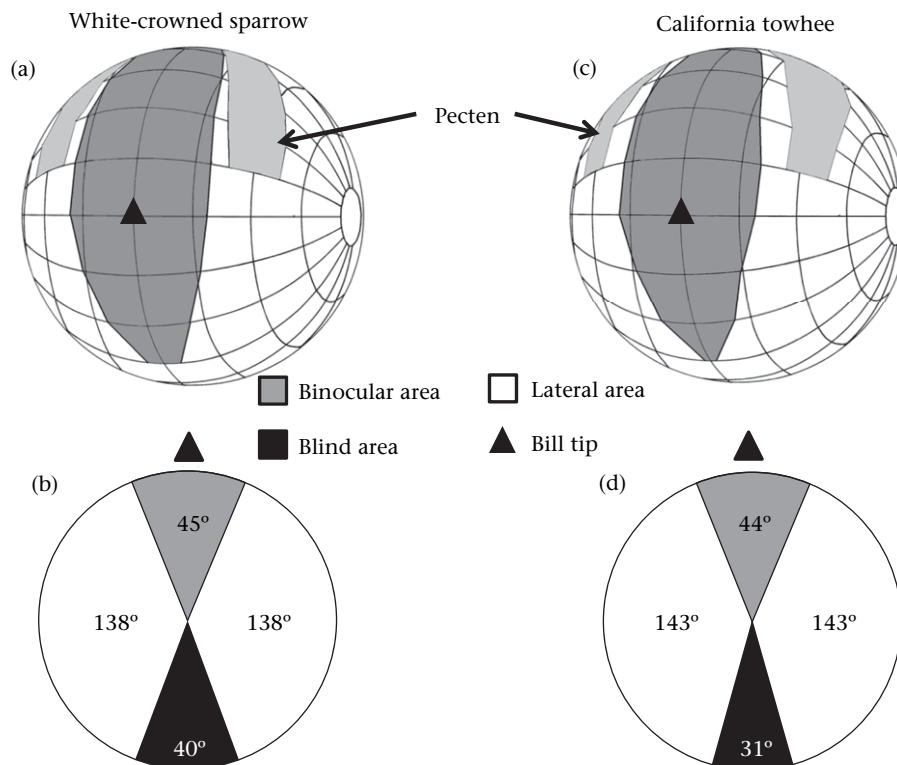


Figure 1. Orthographic projection of the boundaries of the retinal fields of the two eyes, along with projection of the pecten and bill tip, in white-crowned sparrows (a) and California towhees (c). A latitude and longitude coordinate system was used for the orthographic projections with the equator aligned vertically in the median sagittal plane. The bird's head is imagined to be at the centre of the globe (grid is at 20° intervals). Horizontal sections through the horizontal plane (90–270°) showing the visual field configuration of white-crowned sparrows (b) and California towhees (d). Charts represent the average retinal fields when the eyes were at rest.

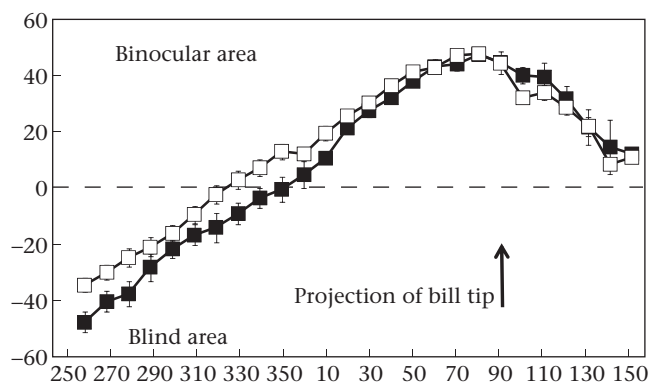


Figure 2. Average \pm SE angular separation of the retinal field margins as a function of elevation in the median sagittal plane in white-crowned sparrows (■) and California towhees (□). The width of the binocular area is indicated by positive values of overlap of the visual field margins; whereas the width of the blind area is indicated by negative values. The horizontal plane is represented by 90° (front of the head) to 270° (back of the head), with 0° indicating a position above the head. Arrow indicates projection of the bill tip.

Retinal Density and Topography

Eye axial length differed significantly between species ($t_5 = 59.11, P < 0.001$), with California towhees (8.46 ± 0.02 mm) having larger eyes than white-crowned sparrows (6.91 ± 0.02 mm). Ganglion cell density in the area with the highest 25th percentile of density did not vary significantly between white-crowned sparrows ($23\,290.82 \pm 1180.28$ cells/mm²) and California towhees ($25\,673.87 \pm 3850.96$ cells/mm²; $t_5 = 0.68, P = 0.528$). Our estimates of spatial resolving power differed significantly between species ($t_5 = 3.18, P = 0.024$): California towhees (7.59 ± 1.01 cycles/degree) had higher levels of visual acuity than white-crowned sparrows (5.93 ± 0.15 cycles/degree).

Topographic maps represent retinal ganglion cell density variations across the retina (Fig. 3a, b). We found that both California towhees and white-crowned sparrows had one spot with the highest density of retinal ganglion cells, which can be considered to be a retinal specialization (Fig. 3a, b). Interestingly, this retinal specialization was located in the centro-temporal region. Given its position in the retina and the lateral position of the orbits in the skull, the retinal specialization would project partially into the nasal (or binocular) sector of the visual field in both species, particularly when the eyes converge.

We plotted the percentage of counts in different cell density ranges (Fig. 4), which can be considered a proxy of the proportional

area of the retina occupied by each cell density range, because we measured cell density with the same sampling effort across the retina. We found a significant interaction effect between species and cell density range, suggesting that the size of retinal areas with different cell density varied between species ($F_{3,20} = 4.23, P = 0.018$; Fig. 4). California towhees had a larger proportion of the retina in the lower cell density range (2000–12 000 cells/mm²); whereas white-crowned sparrows tended to have a larger proportion of the retina in the high-density range (22 000–32 000 cells/mm²). These results suggest that (1) California towhees may have a comparatively larger area of the retina with relatively lower visual resolution than the white-crowned sparrows (based solely on cell density) and (2) the drop in cell density from the highest cell density spot (32 000–42 000 cells/mm²) to the sector occupying the largest proportional area of the retina (12 000–22 000 cells/mm²) was more pronounced in the California towhee than in the white-crowned sparrow (Fig. 4).

Scanning and Movement Behaviour

Head movement rate differed significantly between species ($F_{1,59} = 9.05, P = 0.004$) but did not differ significantly with temperature ($F_{1,59} = 0.87, P = 0.355$). California towhees performed more head movements (89.65 ± 7.35 events/min) than white-crowned sparrows (63.05 ± 4.88 events/min). There was no significant difference between species in the traditional measure of vigilance behaviour (head-up rate: white-crowned sparrows, 9.52 ± 0.81 events/min; California towhees, 10.04 ± 1.22 ; $F_{1,59} = 0.13, P = 0.721$) and no significant effect of temperature ($F_{1,59} = 2.37, P = 0.129$).

Movements within the cage also differed significantly between species. White-crowned sparrows walked/hopped significantly more often (25.10 ± 2.83 events/min) than California towhees (2.17 ± 4.25 events/min; $F_{1,59} = 67.46, P < 0.001$), whereas California towhees jumped/flew significantly more often (17.96 ± 3.32 events/min) than white-crowned sparrows (9.32 ± 2.20 events/min; $F_{1,59} = 9.63, P = 0.003$). Temperature did not significantly affect movements within the cage (walk/hop rates: $F_{1,59} = 1.27, P = 0.263$; jump/fly rates: $F_{1,59} = 0.18, P = 0.674$).

DISCUSSION

Our main results show that both California towhees and white-crowned sparrows have large binocular visual fields, some degree of eye movement and a single retinal specialization that is located in the centro-temporal area of the retina. California towhees have larger eyes and hence higher overall visual acuity than white-crowned sparrows. However, outside of the retinal specialization, white-crowned sparrows had a greater proportion of high ganglion cell density areas compared to California towhees. Finally, California towhees displayed higher rates of head movements (hence, shorter intervals between consecutive head movements) than white-crowned sparrows.

The width of the blind area of white-crowned sparrows and California towhees is smaller than that of some of their aerial predators (e.g. red-tailed hawks, Cooper's hawks, American kestrels; O'Rourke et al. 2010a). This finding supports the view that increasing visual coverage in prey species may actually enhance the detection of potential predators (Hughes 1977). However, the binocular visual fields of our study species are actually wider than those of some of their avian predators (O'Rourke et al. 2010a), contrary to the view that predators have wider binocular fields than prey (Hughes 1977). Binocular vision in birds may be functionally different from that in mammals (Martin 2009): birds appear to use only 5–10° of their binocular visual field during flight; wider

Table 1

Differences in the average width of the binocular field and the blind area, and in the average eye movement between white-crowned sparrows and California towhees, considering the effects of elevation around the head

	F	df	P
Average width of the binocular area			
Species	2.75	1, 19	0.113
Elevation	39.11	22, 279	<0.001
Species*elevation	1.35	18, 279	0.159
Average width of the blind area			
Species	11.47	1, 19	0.003
Elevation	17.44	13, 114	<0.001
Species*elevation	0.83	10, 114	0.598
Average eye movement			
Species	7.85	1, 18	0.0118
Elevation	20.76	19, 302	<0.0001
Species*elevation	0.96	18, 302	0.5051

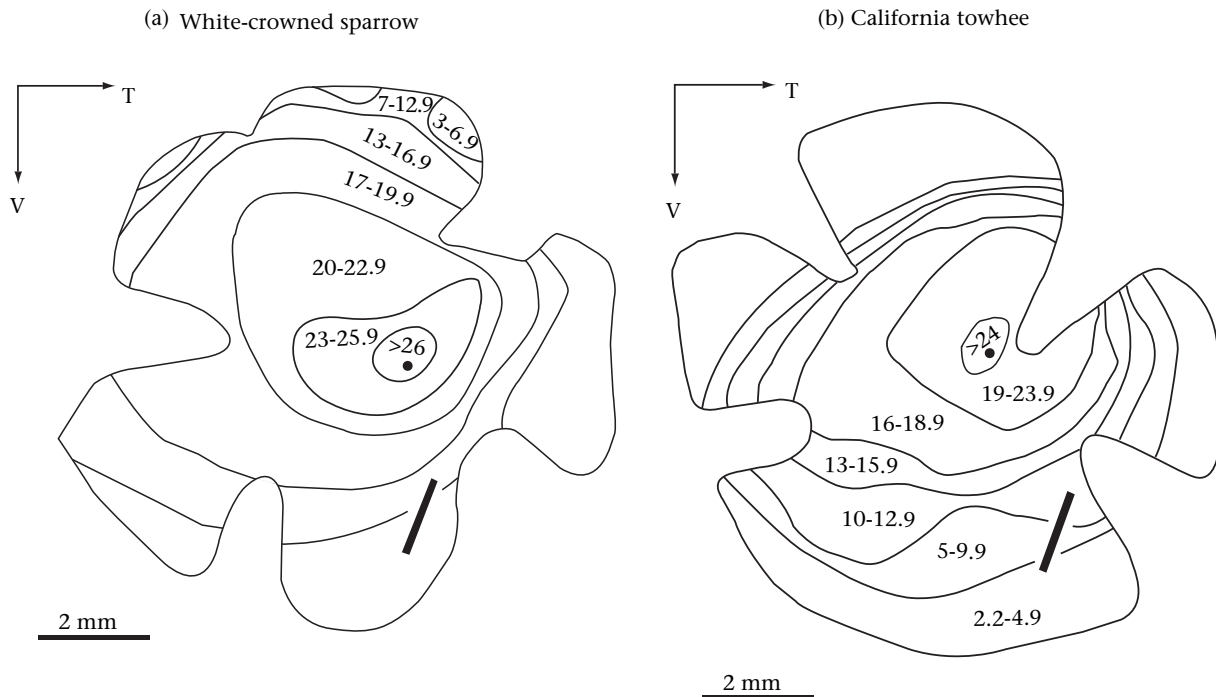


Figure 3. Examples of retinal topographic maps of (a) white-crowned sparrows and (b) California towhees. Numbers represent ranges of retinal ganglion cell density (cells/mm² × 10³). The pecten is indicated by the black line in the lower half of each diagram. Shown are the left eyes of both species. V = ventral region; T = temporal region.

binocular areas may thus be subject to other selective pressures, such as foraging. Our results suggest that passerines foraging mostly on passive prey (e.g. seeds) on the ground appear to have larger binocular areas (see also Fernández-Juricic et al. 2008) and a single retinal specialization compared to birds that specialize on catching active prey (invertebrates, vertebrates) through sit-and-wait strategies, which have narrower binocular areas and two retinal specializations (Tucker 2000; Coimbra et al. 2006; Gall & Fernández-Juricic 2010; O'Rourke et al. 2010a). The difference may be related to the distance at which individuals detect food items visually before pursuing them. California towhees and white-crowned sparrows detect prey at close distances from the ground. Their wide binocular fields (45°) may help them widen the sampling area over which prey can be seen. Additionally, wide binocular areas can enhance contrast discrimination, by which minor changes in luminance between adjacent objects or different parts of the same object can be easier to distinguish through

summation of the visual images extracted from each eye (Campbell & Green 1965; Blake et al. 1981). This binocular contrast could make food items more salient against the visual background, increasing visual performance in the binocular field in relation to the lateral fields (Templeton & Christensen-Dykema 2008). The width of the binocular field of California towhees and white-crowned sparrows is actually similar in size to those of ground foragers belonging to other families, like house sparrows (Passeridae) and house finches (Fringillidae) (Fernández-Juricic et al. 2008).

The centro-temporal location of the area with the highest retinal ganglion cell density in white-crowned sparrows and California towhees suggests that it projects partially into the frontal part of the visual field, which is expected to increase visual resolution in the binocular field, especially when the eyes converge. Temporal retinal specializations have generally been described in birds that pursue moving prey (raptors, swallows, terns) and hummingbirds, which need a fine tuning of the distance and relative speed between the bill and the food item (Pumphrey 1948). These species generally have a deep fovea (pitted retinal areas with relatively higher visual resolution). White-crowned sparrows and California towhees appear to have a shallow fovea, with lower visual resolution. The difference may stem from the fact that our study species may not need the extra acuity provided by a deep fovea because their passive prey are found relatively close to their bills. Nevertheless, Pettigrew (1991) proposed that the presence of a retinal specialization in the temporal part of the retina could be even more relevant to binocular vision than orbit convergence because animals need high acuity to establish differences between the two retinal images. Overall, the combination of wide binocular fields, positioning of the retinal specialization and eye movements may not only increase binocular contrast but also achieve high visual acuity towards the direction of the bill. These visual specializations in these two ground foragers have implications for their foraging behaviour, as they would help fixate prey binocularly and visually guide the bill towards prey (e.g. individual seeds; Fernández-Juricic et al. 2008; Martin 2009).

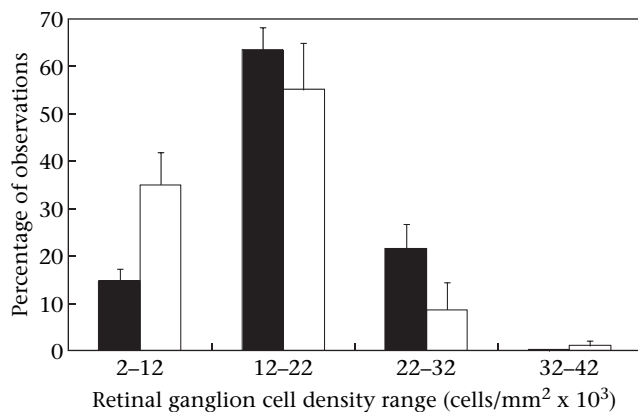


Figure 4. Average percentage of retinal ganglion cell density counts in different cell density ranges for white-crowned sparrows (■) and California towhees (□).

Head movement rates were higher in white-crowned sparrows and California towhees than in some of their predators (O'Rourke et al. 2010b). These two ground foragers have lower visual acuity than their predators because their eyes are smaller. Therefore, they may need to move their heads faster to check the visual space with the high resolution of the retinal specialization. For example, Jones et al. (2007) found that chaffinches, *Fringilla coelebs*, increased their head movement rates after detecting a predator, suggesting that they were visually tracking the predator's location.

We predicted that white-crowned sparrows would have higher scanning rates than California towhees also because of differences in visual acuity. With the traditional measure of vigilance behaviour, we found no variation between species. However, using head movement rates, we found that California towhees actually moved their heads at a faster rate than white-crowned sparrows when scanning the mostly featureless visual space of the cage. Scanning patterns were not affected by differences in microhabitat structure, as we controlled for the visual background, nor were they related to body movement patterns, as both species moved within the enclosure, but they followed different strategies to do so (white-crowned sparrows hopped/walked more frequently, whereas California towhees flew/jumped more often). We can only provide post hoc explanations of this result based on differences in retinal topography and social organization.

We found differences in the topography of the retina of white-crowned sparrows and California towhees that could potentially influence the mechanisms by which these species acquire visual information. Peak retinal ganglion cell density in the retinal specialization of both species was similar. If the drop in cell density (and thus visual resolution) from the retinal specialization to the periphery of the retina is gradual, we would expect to find a large area of the visual field with high acuity (Dolan & Fernández-Juricic 2010). On the other hand, if the drop in cell density from the retinal specialization to the periphery of the retina is more abrupt, we would expect to find a proportionally smaller area of the visual field with high acuity (Dolan & Fernández-Juricic 2010). The latter scenario (e.g. higher proportion of the retina with lower acuity) can lead to a greater reliance on the retinal specialization to monitor with high acuity the surroundings, which could increase the rate of head movements. Although California towhees had higher overall visual acuity (due to larger eyes; Kiltie 2000), their ganglion cell density distribution was shifted towards a greater proportion of the retina with lower visual resolution, which could account for their quicker head movement rates. White-crowned sparrows had a greater proportion of the retina with comparatively higher visual resolution, which may have reduced the need for quick head movements to scan the visual space. The retinal topography pattern of the white-crowned sparrow may actually compensate for its relatively smaller eye.

An alternative explanation for the between-species differences in scanning patterns may be related to variations in social behaviour. The California towhee is considered a solitary species, and the white-crowned sparrow, a social species (Chilton et al. 1995; Kunzmann et al. 2002). The strategy to monitor visually could be related to how each species processes information in the brain. Recent studies in birds have shown that certain neuroendocrine circuits get activated in response to social stimuli that elicit affiliation, but they get suppressed or produce no response to social stimuli that elicit aversion or aggression (Goodson 2008). These circuits are more developed in social avian species than they are in less social species (Goodson et al. 2006). This pathway may be mediated by hormones (e.g. testosterone) promoting higher levels of motivation and aggression (Soma et al. 2008; Goymann 2009), which may lead to a higher level of visual 'awareness' and vigilance

behaviour in solitary species (Favreau et al. 2009), and thus faster head movements to scan the environment for potential risks. Actually, a recent study found that California towhees are more vigilant (e.g. spend more time in head-up postures) in social conditions than in solitary conditions to avoid the risk of conspecific aggression, a behaviour opposite that of more social species (Fernández-Juricic et al. 2009). Therefore, California towhees may need to scan more for potential threats because they do not live in groups in which collective detection may reduce the need for vigilance. Nevertheless, given that we only studied two species within the same family, we cannot reach conclusions about the evolution of visual strategies based on social organization.

We also found other between-species differences in the configuration of the visual fields. We speculate about these differences to derive some post hoc hypotheses on the relationship between visual systems and ecology of emberizids that can be tested in the future. Specifically, California towhees have greater visual coverage above and behind their heads than do white-crowned sparrows, which could be related to variation in foraging strategies as well as microhabitat use. White-crowned sparrows leaf-scratch the ground to find food. However, California towhees use a double-scratching technique, by which they position their eyes above the area to be scratched, hop forward and then sweep backwards with their feet removing debris while maintaining the body and head relatively stationary (Sibley et al. 2001). During double-scratching, California towhees assume a head-down position, reducing visual coverage; consequently, having vertically longer binocular fields and narrower blind areas may allow individuals to detect aerial predators in this body position. California towhee's greater visual coverage may be particularly relevant as this species forages in dense shrubby areas that block the view of the surroundings (Kunzmann et al. 2002). Enhancing predator detection opportunities may be beneficial for California towhees because their shorter, rounder wings make them less agile flyers than white-crowned sparrows (Sibley et al. 2001), which could compromise their escape when attacked by a predator. White-crowned sparrows can increase visual coverage through their greater degree of eye movements given their wider blind area; however, the selective pressure for visual coverage may be lower as they rely on collective detection to escape from predator attacks when foraging in open areas (Chilton et al. 1995; Sibley et al. 2001).

Our findings have interesting implications for the study of the mechanistic basis of information-gathering behaviours in birds. The visual systems of these two ground foragers combine traits to enhance predator detection through greater visual coverage and head movements, but also to increase the chances of food detection at close distances (both species have wide binocular fields). Retinal configuration and social organization may affect baseline scanning patterns through changes in head movement rates necessary to monitor visual space with high acuity. Future studies integrating visual physiology and different parameters of scanning behaviour would allow us to test the relative role of retinal and visual field configuration in predator detection. Ultimately, taking a mechanistic approach can help us elucidate whether the configuration of the visual system or other ecological factors act as a constraint on foraging and antipredator strategies.

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Supplementary Material

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