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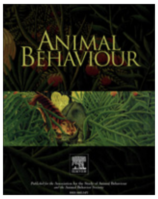

Visual systems and vigilance behaviour of two ground-foraging avian prey species: white-crowned sparrows and California towhees

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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.

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

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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 × 0.55 × 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 opthalmoscopic 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 (±0.5°) 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