

Interspecific differences in the visual system and scanning behavior of three forest passerines that form heterospecific flocks

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Abstract Little is known as to how visual systems and visual behaviors vary within guilds in which species share the same micro-habitat types but use different foraging tactics. We studied different dimensions of the visual system and scanning behavior of Carolina chickadees, tufted titmice, and white-breasted nuthatches, which are tree foragers that form heterospecific flocks during the winter. All species had centro-temporally located foveae that project into the frontal part of the lateral visual field. Visual acuity was the highest in nuthatches, intermediate in titmice, and the lowest in chickadees. Chickadees and titmice had relatively wide binocular fields with a high degree of eye movement right *above* their short bills probably to converge their eyes while searching for food. Nuthatches had narrower binocular fields with a high degree of eye movement *below* their bills probably to orient the fovea toward the trunk while searching for food. Chickadees and titmice had higher scanning (e.g., head movement) rates than nuthatches probably due to their wider blind areas that limit visual coverage. The visual systems of these three species seem tuned to the visual challenges posed by the different foraging and scanning strategies that facilitate the partitioning of resources within this guild.

Keywords Foraging · Fovea · Vigilance · Visual acuity · Visual fields

Introduction

Birds are visually oriented animals (Schwab 2012) whose visual systems vary substantially between species in terms of the types of retinal specialization (e.g., fovea, visual streak, area; Meyer 1977; Collin 1999), the density of photoreceptors (Hart 2001), visual acuity (Kiltie 2000), the configuration of the visual fields (Martin 2007), etc. Variations in visual system configuration can also affect visual behaviors, such as scanning (Fernández-Juricic 2012). For instance, species with wider blind areas allocate more time to anti-predator vigilance to compensate for the lack of visual coverage (Guillemain et al. 2002).

This high degree of interspecific variability in the visual system has been linked to predation (Guillemain et al. 2002), foraging (Fernández-Juricic et al. 2011a), ability to feed the young (Martin 2009), and habitat type (Hart 2001). For instance, species living in closed habitats (e.g., tree foragers) have a higher density of photoreceptors associated with motion detection in areas of the retina pointing toward the ground, whereas species living in open habitats (e.g., ground foragers) have a higher density of these photoreceptors pointing toward the sky, reflecting the positions from which predators are more likely to attack (Hart 2001). Møller and Erritzøe (2010) presented evidence that birds living in open habitats have larger eyes, and thus higher overall visual acuity that might enhance the detection of predators from farther away, compared with those of species living in more complex habitats. Additionally, raptors living in open and closed habitats differ in the configuration of their visual fields, degree of eye movement, and scanning behavior in ways that would enhance their ability to detect prey in habitats with different degrees of visual obstruction (O'Rourke et al. 2010a, b).

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However, how both the visual system and scanning behavior vary within guilds (i.e., groups of species that exploit similar resources following similar strategies; Simberloff and Dayan 1991) in which species share the same micro-habitat types but use different foraging tactics has received less attention (but see Martin and Prince 2001). Characterizing these interspecific differences may enhance our understanding of not only sensory specializations to gather information about food and predators but also the potential role of the sensory system in partitioning resources within guilds (Siemers and Swift 2006). The guild of passerine tree foragers inhabiting North American temperate areas is a good model system to study the degree of interspecific variability in physiological and behavioral parameters because the foraging and anti-predator behaviors of its species have been extensively studied (reviewed in Grubb and Pravasudov 1994, 2008; Mostrom et al. 2002). Our goal was to characterize key dimensions of the visual system (visual acuity, position of the fovea, visual field configuration, degree of eye movements) and scanning behavior (head movement rates) of three members of this guild: Carolina chickadees (*Poecile carolinensis*; family Paridae; hereafter, chickadees), tufted titmice (*Baeolophus bicolor*; family Paridae; hereafter, titmice), and white-breasted nuthatches (*Sitta carolinensis*; family Sittidae; hereafter, nuthatches). These species differ in the substrates they use for foraging and for protective cover.

Chickadees primarily forage on smaller tree limbs and twigs (Mostrom et al. 2002). Titmice have a broader range of foraging substrates, including small branches, larger limbs, trunks, and the ground (Grubb and Pravasudov 1994). Finally, nuthatches forage on tree trunks and larger branches, and sometimes on the ground (Grubb and Pravasudov 2008). Because of these different foraging substrates, it can be proposed that chickadees and titmice have the visibility in their visual fields comparatively less obstructed by vegetation (e.g., tree canopy) than nuthatches (e.g., tree trunks), which can influence the probabilities of predator detection (e.g., Lima 1992). If a predator attacks, chickadees and titmice generally escape by flying toward another tree, whereas nuthatches generally escape by moving toward the opposite side of the tree trunk they were using for foraging (Lima 1993). Additionally, these three species vary in the orientation of their bodies and heads (in relation to the substrate) while foraging. Chickadees and titmice generally scan and search for food when their bodies and heads are at a steeper angle (i.e., closer to an upright position) in relation to the substrate (Grubb and Pravasudov 1994; Mostrom et al. 2002). Nuthatches tend to scan and search for food with their bodies and heads at a shallower angle (i.e., closer to a prone position) in relation to the substrate (Grubb and Pravasudov 2008). Additionally, these three species associate during the non-breeding

season to form heterospecific flocks, where chickadees and titmice are considered nuclear species (i.e., initiate flock movements and alarm-call upon detection of predators) and nuthatches are considered satellite species (i.e., eavesdrop on social information about predators; Sullivan 1984a, b; Dolby and Grubb 1998, 2000; Templeton and Greene 2007).

Based on the differences in their foraging and anti-predator behaviors, we made predictions about inter-specific differences in their visual systems taking into account hypotheses on visual acuity (Kiltie 2000), position of the fovea in the retina (Collin 1999), configuration of the visual field based on the position of the orbits (Heesy 2004), and degree of movement of the fovea through eye and head movements (Fernández-Juricic 2012). First, we predicted that visual acuity would be higher in titmice and nuthatches than in chickadees because they are bigger, and body mass (and eye size) is positively related to visual acuity (Kiltie 2000). Second, based on the preferred orientation of the bill when searching for food (Grubb and Pravasudov 1994, 2008; Mostrom et al. 2002), we predicted that the fovea of chickadees and titmice would be placed centro-temporally on the retina to enable high visual resolution in the region of the binocular field directly in front of the bill, as has been found in other Passeriformes (Blackwell et al. 2009; Dolan and Fernández-Juricic 2010; Fernández-Juricic et al. 2011a). Conversely, we predicted that nuthatches would have dorso-temporal fovea projecting ventro-nasally, hence providing high resolution below the bill and toward the tree trunks as the bill is usually held at a shallow angle in relation to the foraging substrate. Third, chickadee and titmouse have slightly more frontally placed eyes (Appendix) than nuthatches; thus, we predicted that these two species would have wider binocular fields (see also Iwaniuk et al. 2008). Fourth, as a result of the differences in the position of the eyes in the skull (Appendix), we predicted that chickadees and titmice would have wider blind areas behind their heads than nuthatches. Wider blind areas would limit visual coverage in chickadees and titmice (Guillemain et al. 2002), which could increase their degree of eye movements and their rate of head movements (Fernández-Juricic et al. 2010) to scan different parts of the environment with the fovea (Fernández-Juricic 2012), depending on the visual task (i.e., converging eyes to find food, diverging eyes to detect predators, etc.).

Methods

We determined between-species differences in eye size and retinal ganglion cell density (both parameters involved in visual acuity, Pettigrew et al. 1988), position of the fovea

(area with the highest visual resolution in the retina), visual field configuration (e.g., sizes of the binocular field, lateral field, and blind area), degree of eye movement, and scanning behavior (e.g., using head movement rates as proxies, Fernández-Juricic 2012).

Carolina chickadees, tufted titmice, and white-breasted nuthatches used in this study were captured in several locations in Tippecanoe County, Indiana, USA. Birds were housed indoors in cages ($0.9 \times 0.7 \times 0.6$ m) with 1–4 individuals per cage, and were kept on a 14:10 h light:dark cycle at approximately 23 °C with food (sunflower seeds) and water ad libitum, supplemented with mealworms daily. Nine chickadees, seven titmice, and nine nuthatches were used for visual field and degree of eye movement measurements, of which five individuals of each species were used for retina extraction to measure eye size, retinal ganglion cell density, and to estimate the position of the fovea.

Eye size, ganglion cell density, and fovea position

After animals were euthanized using CO₂, we removed the eyes by cutting the conjunctiva and pulling the eye out by the optic nerve with forceps. We then measured three eye size parameters with digital calipers (Neiko Tools USA, 01407A; 0.01 mm accuracy): (1) eye axial length (anterior portion of the cornea to the most posterior portion of the back of the eye), (2) corneal diameter (inner diameter of the sclerotic ossicles), and (3) eye transverse diameter (outer diameter of the eyeball from side to side). The orientation of the retina (nasal, temporal, dorsal, ventral) was maintained by tracking the position of the pecten (i.e., a pigmented and vascular structure in the avian retina; Meyer 1977) in relation to the direction of the bill (Fernández-Juricic et al. 2011c). We hemisected the eye at the ora serrata using a razor blade and removed all vitreous humor and lens fragments using forceps and spring scissors. The retina was extracted following the whole-mount technique, which is described in Ullmann et al. (2012). We used cresyl violet to stain for retinal ganglion cells, which have axons that carry the visual information from the retina to the brain through the optic nerve (McIlwain 1996). The area of the retina with the highest density of retinal ganglion cells is the fovea and corresponds to the highest degree of visual resolution (Walls 1942; Meyer 1977).

Pictures of the retina (0.01 mm^2) were taken with a Panasonic Lumix FZ28 digital camera before and after staining to correct for tissue shrinkage. We used ImageJ (<http://rsb.info.nih.gov/ij/>) to measure the area of the retina before and after staining. We calculated the amount of shrinkage per picture by multiplying the area of the picture by the difference in the retinal area before and after staining (i.e., amount of shrinkage). Therefore, the correction factor

for tissue shrinkage was $0.01 + (0.01 \times \text{amount of shrinkage})$.

An Olympus BX51 microscope at $\times 100$ power was used to examine the retinal ganglion cell layer. Stereo Investigator (ver. 9.13; MBF Bioscience) was used to trace the perimeter of the retina with the SRS Image Series Acquire module, which uses a fractionator approach by which the program randomly and systematically places a grid onto the traced retina. We used average of 410 ± 2.09 grid sites per chickadee retina, 408 ± 3.76 grid sites per titmouse retina, and 407 ± 2.70 grid sites per nuthatch retina, although we could not measure cell density from all of them (see “Results”). A $50 \times 50 \mu\text{m}$ counting frame was placed in the upper left-hand corner of each grid site to avoid double counting, and the following parameters were estimated before counting: *asf* (area sampling fraction: the ratio of the area of the counting frame to the area of the grid) = 0.01751 ± 0.00054 per chickadee retina, 0.01139 ± 0.00056 per titmouse retina, and 0.01204 ± 0.00033 per nuthatch retina; *tsf* (thickness sampling factor: ratio of the height of the dissector to the mean measured tissue thickness) = 1 per retina, and ΣQ^- (sum of the total number of retinal ganglion cells) = $14,512 \pm 1,093$ per chickadee retina, $14,933 \pm 1,160$ per titmouse retina, and $18,018 \pm 1,021$ per nuthatch retina. On a given counting frame, we focused on the plane that would provide the highest resolution and contrast to identify the ganglion cells and obtained a photograph with an Olympus S97809 microscope camera. We captured the images using Snagit (www.techsmith.com/Snagit) and counted the retinal ganglion cells in each of the counting frame images with ImageJ to estimate cell density. Cell density (number of retinal ganglion cells/ mm^2) was calculated by dividing the number of cells in each picture by the tissue area corrected for shrinkage of each picture.

Retinal ganglion cells were differentiated from amacrine and glial cells based on cell shape, relatively large soma size, Nissl accumulation in the cytoplasm, and staining of the nucleus (Hughes 1977; Freeman and Tancred 1978; Ehrlich 1981; Stone 1981). The soma size of ganglion cells is small and contains a darkly staining nucleus in retinal regions with higher cell density, but it shows a prominent nucleus and heterogeneous distribution of Nissl granules in perifoveal and peripheral regions of the retina. Glial cells are generally oblong, narrow, and very elongated with deep Nissl accumulation, whereas amacrine cells are usually small teardrop-shaped cells with deep Nissl accumulation.

Based on the variations in the density of retinal ganglion cells across the retina, we followed Stone (1981) and Ullmann et al. (2012) in building retinal topographic maps. We plotted ganglion cell density values obtained from each counting frame onto a map of the sampling grids produced by Stereo Investigator using OpenOffice Draw (www.openoffice.org).

Within a given cell density range, we created isodensity lines by hand interpolating one or more adjacent density values (Moroney and Pettigrew 1987; Wathey and Pettigrew 1989).

Visual acuity was estimated based on the averaged eye size and retinal ganglion cell density of each species, assuming that all species have similar eye shapes and eye optical properties, which is expected due to their diurnal habits (Martin 1993). Visual acuity calculations followed the sampling theorem (Hughes 1977). Eye axial length was multiplied by 0.60 (based on Hughes 1977; Martin 1993) to estimate the posterior nodal distance (*PND*, length between the posterior part of the eye and the anterior surface of the retina, Reymond 1985). We then obtained the retinal magnification factor (*RMF*), which is the linear distance on the retina that subtends 1° (Pettigrew et al. 1988), as follows: $RMF = 2\pi PND/360$. We estimated visual acuity as the highest spatial frequency that can be detected: $(F_n) = \frac{RMF}{2} \sqrt{\frac{2D}{\sqrt{3}}}$, where *D* is the averaged retinal ganglion cell density (Williams and Coletta 1987). *F_n* is expressed in cycles per degree.

Visual field configuration and degree of eye movement

A visual field apparatus developed by Martin (1984) was used to measure the configuration of the visual field of chickadees, titmice, and nuthatches. Individuals were restrained by foam molds and straps within the apparatus with the bill placed in a fitted bill holder (preventing the head from moving; Appendix) such that the head was positioned at the center of a global space in three dimensions. Each species' head was held at the angle at which it is most frequently found based on pictures and videos taken in the wild. For the chickadee and titmouse, the head was positioned such that the dorsal portion of the lower mandible was parallel to the ground, and for the nuthatch, the dorsal portion of the lower mandible was inflected in a direction 10° above parallel to the ground. The configuration of the visual field was measured using a polar coordinate system, in which the 0° elevation lay directly above the head of each species, 90° in front, and 270° behind (see “Results”). Thus, the 90–270° plane was defined as the horizontal plane as it is parallel to the ground.

A Keeler professional ophthalmoscope was used to measure the retinal margins using an ophthalmoscopic reflex technique around the head to an accuracy of 0.5° (Martin 1984, 2007). We then mathematically corrected each value for close viewing following Martin (1984). At some elevations, the apparatus or the animal's body blocked our view of the retinal margins, limiting our measurements from 140° to 260° around the head. We took measurements on the visual fields at every 10° elevation increments within that range.

The degree of eye movements can vary substantially between species (e.g., Martin 2007; Fernández-Juricic et al. 2008; Blackwell et al. 2009), which can change the configuration of the visual field (e.g., size of binocular and blind areas) when animals converge or diverge their eyes from their eye-resting position. Therefore, the visual fields of all three species were measured when (1) the eyes were at rest, (2) the eyes were converged, and (3) the eyes were diverged. Resting measurements were taken when the animal visibly relaxed its eyes (i.e., the animal was not tracking the observer), which happened right away or after a quick series of pursuit eye movements due to apparent fatigue of the extraocular muscles. During these eye-resting measurements, we were careful to note that the eyes did not move by tracking the eyes and taking several measurements of the retinal margins in succession, which are the ultimate indicator of variations in retinal position. With the eyes at rest, we also measured the projection of the pecten which creates a blind spot within the dorso-frontal visual space. For converge/diverge measurements, we elicited maximum levels of eye movements by presenting objects and/or sounds around the bird's head. Therefore, the animal exhibited two types of eye movement: saccadic, when we first drew the attention of the individual to the position of the objects/sounds, and pursuit, when the individual then tracked objects/sounds. Eye movement was elicited in the direction of the elevation being measured. The degree of eye movement was measured at each 10° elevation interval from 140° below the bill to 270° behind the head. All the measurements on the degree of eye movement reported in this study considered both eyes. The degree of eye movement in a particular direction (elevation) was calculated by the difference between the maximum (converged) and minimum (diverged) values. Finally, we calculated the extent of the lateral field as $[360 - (\text{mean blind field} + \text{mean binocular field})/2]$ (Fernández-Juricic et al. 2008). In Fig. 4, eye movement values are presented as the averaged degree of eye movement per elevation across individuals.

Head movements

Recent studies have proposed that head movement rates are a good proxy of scanning behavior in birds (O'Rourke et al. 2010b; Fernández-Juricic et al. 2011a, b) because they indicate the speed with which the foveae gather high-quality visual information from different parts of their surroundings (Fernández-Juricic 2012). Higher head movement rates are indicative of a faster visual sampling rate (e.g., for predators or food), which could be the result of higher perceived predation risk and higher visual obstruction in the environment (Fernández-Juricic et al. 2011c). Regular head movements (head moving along a single axis where the direction of the eye-bill tip vector

follows the head movement; O'Rourke et al. 2010b) were measured when the bird was in head-up (vigilance) posture from videos recorded in the field and videos obtained from the Macaulay library sound and video catalog (<http://animalbehaviorarchive.org>). All videos included in the analysis came from habitats characteristic of each of the studied species, which we evaluated based on the background vegetation.

We only used videos of individuals moving throughout the foraging substrate where head movements could be accurately measured; we did not include videos of individuals flying or videos showing inter- or intra- specific interactions (e.g., aggression) or preening events. Videos at the Macaulay Library Sound and Video Catalog listed information on the month and location the video was taken, and the observer who recorded the video. This information was used to avoid including videos from the same individual. If several videos from the same individual were available, we used the longest video.

We recorded videos in Tippecanoe County (Indiana, USA) during the 2010 and 2012 non-breeding seasons (January–March). Videos were recorded with a JVC Everio GZ-MG330-HU camcorder mostly in the mornings and early afternoons. The chances of resampling the same individual was reduced by keeping track of the individual recorded on a given session or by moving at least 50 m in the opposite direction of the last individual recorded. After recording a given individual, we measured ambient temperature, group size, perching height, and distance between the observer and the bird as previous studies found that these variables could influence vigilance behavior (e.g., Beauchamp 2003; Gall and Fernández-Juricic 2009; Carr and Lima 2012). Temperature was measured with a Kestrel portable weather station. Perching height was estimated by visually rotating the location of the bird in the tree onto the ground and then measuring the ground distance with a meter tape (± 0.05 m; Fernández-Juricic et al. 2006). Distance between the observer and the bird was also measured with a meter tape.

Overall, sample sizes per species were as follows: chickadee (3 video catalog, 11 recorded by authors), titmouse (10 video catalog, 10 recorded by authors), and nuthatch (6 video catalog, 8 recorded by authors). The averaged length of all videos was 68.86 ± 12.02 s. Head movements were recorded with JWatcher (Blumstein and Daniel 2007). We calculated the head movement rate as changes in head position per second while the animal was head-up (i.e., the head was above the shoulder). We did not measure the amplitude or direction of the head movements, nor did we measure head bobbing as our studied species do not engage in this behavior. Additionally, we did not record the degree of eye movements while animals were moving their heads because we used videos obtained in the field

and we lacked the technology (e.g., eye-tracker) to obtain that information. It is likely that birds were actually moving their eyes while moving their heads (e.g., Gioanni 1988). Therefore, any interpretation we make in relation to the functional properties of eye and head movements should be taken with care due to the constraints of our measurements.

Statistical analysis

General linear mixed models were used to compare among species the overall and peak density of retinal ganglion cells, width of the binocular field, blind area, and pecten, and the degree of eye movements. In all these models, we included individual identity as a within-subject factor. Models on density of retinal ganglion cells included species as the between-subject factor. Models on the visual field configuration and degree of eye movement included species, elevation in the visual field, and the interaction between species and elevation as the between-subject factors. In the models on visual field configuration and degree of eye movement, we only used those elevations from which we had data on positive (binocular area) or negative (blind area) overlap between eyes. Consequently, the means (\pm SE) presented did not include values from those elevations in which data were not recorded. Pair-wise comparisons (*t*-tests) were used to determine differences between pairs of species. General linear mixed models were run in SAS 9.2 (Cary, NC, USA).

General linear models were used to establish differences among species in corneal diameter, eye transverse diameter, eye axial length, and head movement rates. Additionally, we also established the effects of potential confounding factors (flock size, temperature, perching height, distance between observer) on head movement rates with the videos we recorded using a general linear model. We excluded the Macaulay library sound and video catalog videos as they did not report any of these potential confounding factors. Tukey HSD tests were used to assess differences between pairs of species. General linear models were run in Statistica 10 (Tulsa, OK, USA). Throughout the text we present least squares means (\pm SE).

Results

Eye size, ganglion cell density, and fovea position

We successfully processed and counted retinal ganglion cells from five chickadees (three left and two right eyes), four titmice (two left and two right eyes), and five

nuthatches (three right and two left eyes). With the exception of one nuthatch retina that had a tear in its center, we were also able to determine the position of the potential fovea in each of these retinas (see below).

The differences in body mass among species (Carolina chickadee, 10 g; tufted titmouse, 21.6 g; white-breasted nuthatch, 21 g; Dunning 2008) were reflected in eye size. The three parameters related to eye size varied significantly between species: corneal diameter ($F_{2,11} = 26.09$, $P < 0.001$), transverse diameter ($F_{2,11} = 102.78$, $P < 0.001$), and axial length ($F_{2,11} = 45.82$, $P < 0.001$). Corneal diameter and eye axial length were significantly smaller in chickadees (corneal diameter 4.13 ± 0.12 mm, axial length 5.19 ± 0.11 mm) than in titmice (corneal diameter 5.22 ± 0.13 mm, axial length 6.60 ± 0.13 mm) and nuthatches (corneal diameter 5.21 ± 0.12 mm, axial length 6.41 ± 0.11 mm, Tukey tests, $P < 0.001$), without significant differences in these traits between the latter two species (Tukey tests, $P > 0.488$). Eye transverse diameter varied significantly between species in all-pair-wise comparisons (Tukey tests, $P < 0.006$), with titmice having the highest values (8.80 ± 0.10 mm), nuthatches, intermediate values (8.27 ± 0.09 mm), and chickadees, the lowest values (6.95 ± 0.09 mm).

We quantified the density of retinal ganglion cells using 372.60 ± 6.11 grid sites per retina in the chickadee, 385.75 ± 6.83 grid sites per retina in the titmouse, and 385 ± 6.83 grid sites per retina in the nuthatch. The mean overall density of retinal ganglion cells differed significantly among species ($F_{2,10} = 66.57$, $P < 0.001$). Nuthatches ($18,660 \pm 239$ cells/mm²) had significantly higher ganglion cell densities than chickadees ($15,467 \pm 218$ cells/mm²; $t_{10} = 9.87$, $P < 0.001$) and titmice ($15,189 \pm 240$ cells/mm²; $t_{10} = 10.25$, $P < 0.001$), without significant differences between the latter two species ($t_{10} = 0.86$, $P = 0.410$). The peak retinal ganglion cell density (density in the peri-foveal grid sites around the fovea) also varied significantly among species ($F_{2,10} = 9.04$, $P = 0.006$). Nuthatches ($35,850 \pm 1,201$ cells/mm²) had significantly higher peak ganglion cell densities than titmice ($31,339 \pm 1,241$ cells/mm²; $t_{10} = 2.61$, $P = 0.026$) and chickadees ($28,969 \pm 1,102$ cells/mm²; $t_{10} = 4.22$, $P = 0.002$), without significant differences between the latter two species ($t_{10} = 1.43$, $P = 0.184$). Based on the averaged peak density of retinal ganglion cells and averaged eye size values per species, we estimated that nuthatches had the highest visual acuity of the three species (6.83 cycles/degree), followed by titmice (6.57 cycles/degree), and chickadees (4.97 cycles/degree).

The retinal ganglion cell topographic maps of the three species revealed a concentric increase in retinal ganglion cell density toward the central part of the retina (Fig. 1 shows a representative map of each species). Based on

morphological features on the whole mount, we determined that each of the three species had a fovea (i.e., a pitted structure with sloping walls descending concentrically from the plane of view; black dot in each topographic map in Fig. 1) located centro-temporally from the center of the retina. However, our results differ from those of Fite and Rosenfield-Wessels (1975) who reported that white-breasted nuthatches had a fovea located ventrally from the center of the retina instead of the centro-temporal position found in our study. Although we did not perform cross-sections to determine the morphology of different retinal layers, we did not find any foveal pit in the ventral part of the nuthatch retina. We also hemisected the eye of a white-breasted nuthatch while still in the skull and confirmed the centro-temporal orientation reported here.

Visual fields with eyes at rest

Three-dimensional representations of the at-rest visual fields show that the three species (chickadees, titmice, nuthatches) had the projections of their bill-tips toward the binocular field (Fig. 2a–c). The bill tip of nuthatches projected toward the binocular field around the horizontal plane (90°; Fig. 2c), whereas those of chickadees and titmice projected at a slightly lower elevation (100°; Fig. 2a, b). We could not measure the total vertical extent of the binocular field as in some elevations below the bill because the visual field apparatus obstructed our measurements. Consequently, our estimates of the minimum vertical extent of the binocular field were the same (130°) across species.

At 90° elevation with the eyes at rest, the width of the binocular field was similar in the titmice (53°) and chickadee (51°), but narrower in the nuthatch (37°) (Fig. 2d–f). However, in the nuthatch the bill intruded in the binocular area to the extent that it blocked our view of the retinal margins (Fig. 2f). This suggests that nuthatches could observe their bill tips (see also Martin and Coetzee 2004). Thus, the extrapolated width of the binocular field at 90° elevation with the eyes at rest was estimated as 45° for nuthatches (Fig. 2f), assuming that the retinal margin follows a circular projection (Martin and Coetzee 2004).

Across all recorded elevations, the averaged width of the binocular field differed significantly among species ($F_{2,18} = 20.81$, $P < 0.001$). Chickadees ($32.82 \pm 0.78^\circ$; $t_{18} = 7.02$, $P < 0.001$) and titmice ($32.70 \pm 0.96^\circ$; $t_{18} = 6.06$, $P < 0.001$) had significantly wider binocular fields across the recorded elevations than nuthatches ($26.38 \pm 0.85^\circ$), but without significant differences between the two parids ($t_{18} = 0.13$, $P = 0.899$; Fig. 3). Pooling all species, we found that the averaged width of the binocular field varied across elevations ($F_{16,199} = 56.12$,

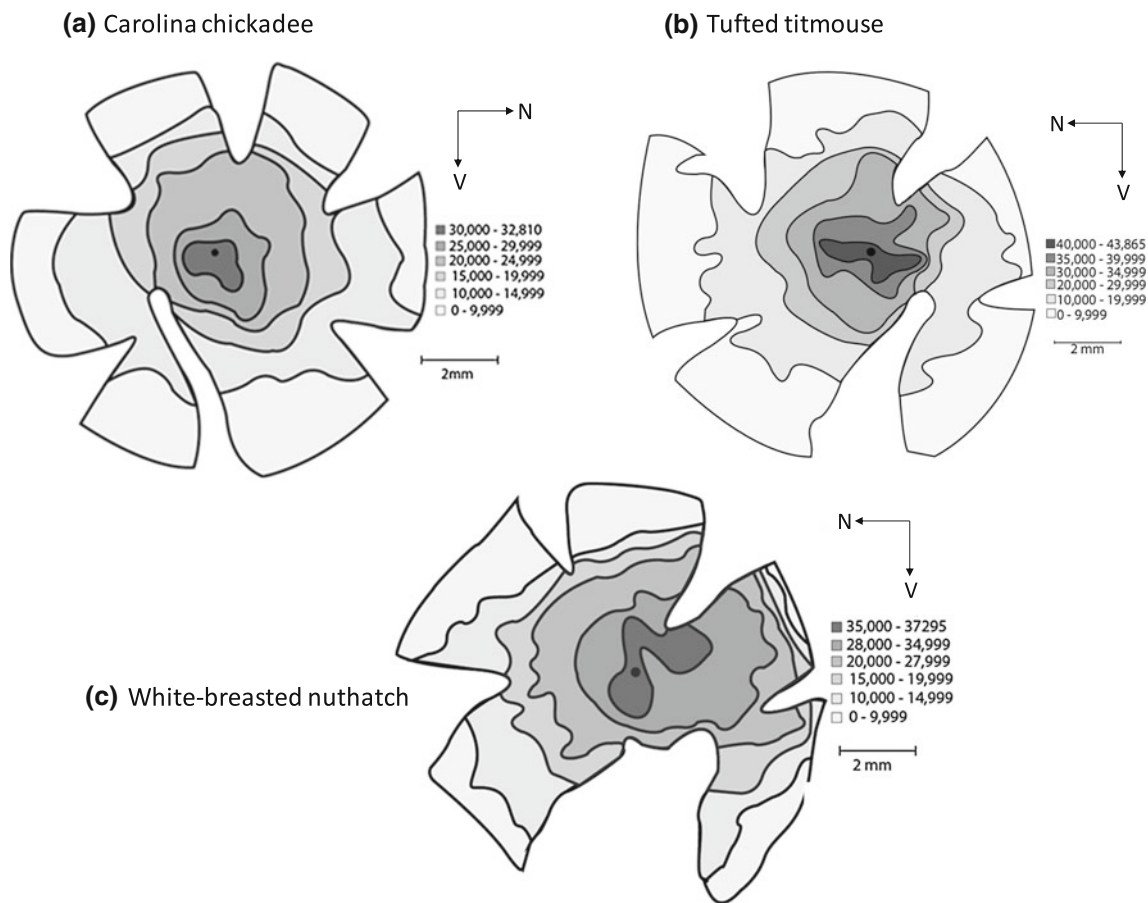


Fig. 1 Representative examples of the retinal topographic maps of **a** Carolina chickadees, **b** tufted titmice, and **c** white-breasted nuthatches. Numbers represent ranges of retinal ganglion cell density

(cell/mm²). V ventral, N nasal. The presence of a potential fovea is indicated by a black dot toward the central part of the retina. These maps are based on a single individual from each species

$P < 0.001$); however, there was no significant interaction between species and elevation ($F_{27,199} = 1.28$, $P = 0.656$; Fig. 3).

At the 270° elevation (i.e., rear of the head along the plane of the bill) with the eyes at rest, we found that the blind area was the widest in the chickadee (57°), intermediate in the nuthatch (46°), and the smallest in the titmouse (41°) (Fig. 3). Across all recorded elevations, the average width of the blind area varied significantly between species ($F_{2,18} = 8.18$, $P = 0.003$). Chickadees ($32.91 \pm 1.51^\circ$) had significantly wider blind areas than titmice ($27.74 \pm 1.81^\circ$; $t_{18} = 3.20$, $P = 0.005$) and nuthatches ($27.55 \pm 1.50^\circ$; $t_{18} = 3.62$, $P = 0.002$), without significant differences between the latter species ($t_{18} = 0.11$, $P = 0.913$). Pooling all species, the width of the blind area differed across elevations ($F_{17,144} = 29.12$, $P < 0.001$; Fig. 3), but without a significant interaction between species and elevation ($F_{17,144} = 0.83$, $P = 0.656$).

The projection of the pecten extended vertically 70° in all species (from 0° to 70° above the bill) (Fig. 2a–c).

Across elevations, the width of the pecten varied significantly among species ($F_{2,11} = 14.34$, $P < 0.001$). All pairwise differences were significant (t_{11} varied from 2.27 to 5.34, $P < 0.044$): nuthatches had the widest pecten ($25.74^\circ \pm 0.82^\circ$), titmice had an intermediate sized pecten ($22.95^\circ \pm 0.92^\circ$), and chickadees had the narrowest pecten ($19.72^\circ \pm 0.76^\circ$). Pooling all species, the width of the pecten varied significantly across elevations ($F_{7,58} = 39.38$, $P < 0.001$), without a significant interaction between species and elevation ($F_{14,58} = 0.97$, $P = 0.489$).

Degree of eye movement and visual fields

Across elevations, the degree of eye movement varied among species significantly ($F_{2,21} = 29.35$, $P < 0.001$; Fig. 4). Titmice ($76.33^\circ \pm 1.41^\circ$) had the highest degree of eye movement, followed by chickadees ($71.24^\circ \pm 1.23^\circ$), and nuthatches ($61.58^\circ \pm 1.37^\circ$), with all pair-wise comparisons being significant (t_{21} varied from 2.72 to 5.25, $P < 0.020$). Pooling all species, the degree of eye movement varied significantly across elevations ($F_{22,221} = 4.79$,

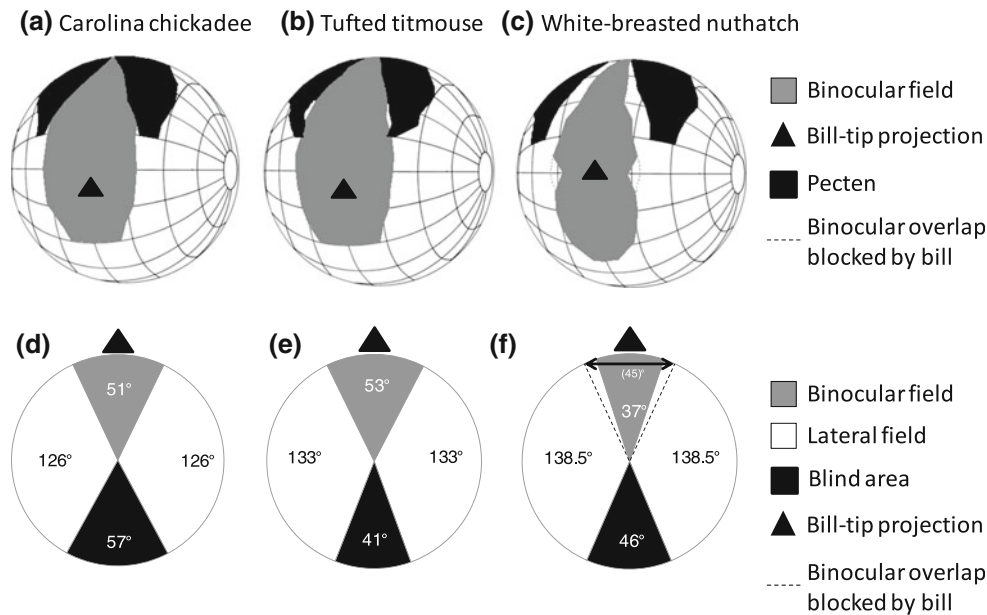
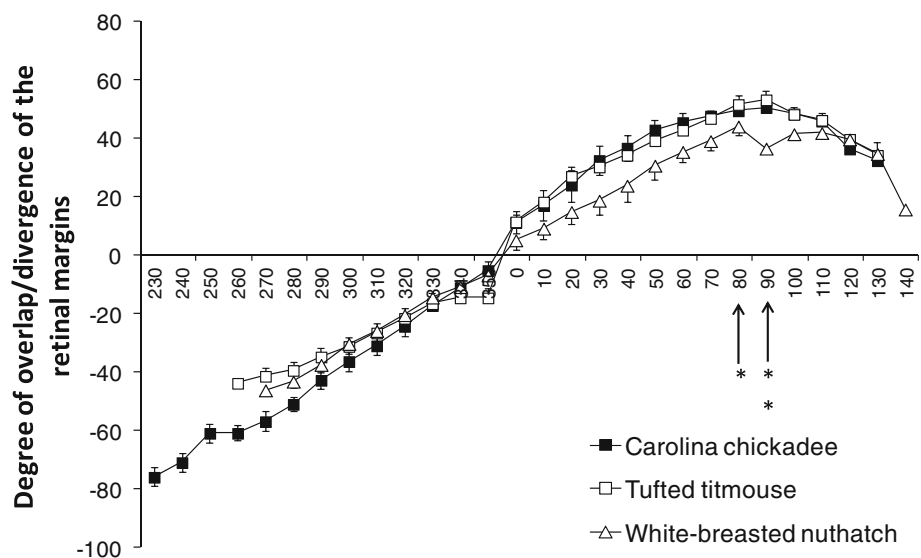


Fig. 2 Different views of the visual field configuration with the eyes at rest of Carolina chickadees (**a, d**), tufted titmice (**b, e**), and white-breasted nuthatches (**c, f**). (**a–c**) Orthographic projection of the boundaries of the retinal fields of the two eyes, along with projection of the pectens and bill tips. A latitude and longitude coordinate system was used with the equator aligned vertically in the median

sagittal plane. The head of the animal is at the center of the globe (grid is at approximately 20° intervals). (**d–f**) Visual field sections through the horizontal plane (90°–270°). The dotted lines in (**b, e**) represent extrapolated binocular field widths assuming that the retinal margin follows a circular projection (see text for details)

Fig. 3 Mean (\pm SE) angular separation of the retinal field margins in relation to elevation around the head in the median sagittal plane of Carolina chickadees, tufted titmice, and white-breasted nuthatches. Binocular fields are indicated by positive values of overlap of the visual field margins, whereas blind areas are indicated by negative values. Orientation landmarks are at 90° (*front of the head*), 270° (*back of the head*), and 0° (*above the head*). Arrows indicate projection of the bill-tip in relation to the ground (*Carolina chickadee, tufted titmouse; *white-breasted nuthatch)



$P < 0.001$; Fig. 4). Additionally, the interaction between species and elevation was significant ($F_{44,221} = 3.64$, $P < 0.001$). Therefore, we ran another model to establish whether eye movement amplitude would vary above and below the bill across species. For this model, we considered up to three elevations above and below the bill (if available) without considering the elevation where the tip of the bill projected. We found significant species ($F_{2,17} = 11.73$, $P < 0.001$) and elevation ($F_{1,9} = 36.36$,

$P < 0.001$) effects, and a significant interaction between species and elevation ($F_{2,9} = 45.36$, $P < 0.001$). The degree of eye movement was higher above than below the bill in chickadees ($82.90^\circ \pm 2.64^\circ$ vs. $35.36^\circ \pm 3.86^\circ$, respectively) and titmice ($82.20 \pm 3.11^\circ$ vs. $66.52 \pm 4.02^\circ$, respectively; Fig. 4a–b). However, the degree of eye movement was higher below than above the bill in nuthatches ($73.69^\circ \pm 4.23^\circ$ vs. $58.96^\circ \pm 2.70^\circ$, respectively; Fig. 4c).

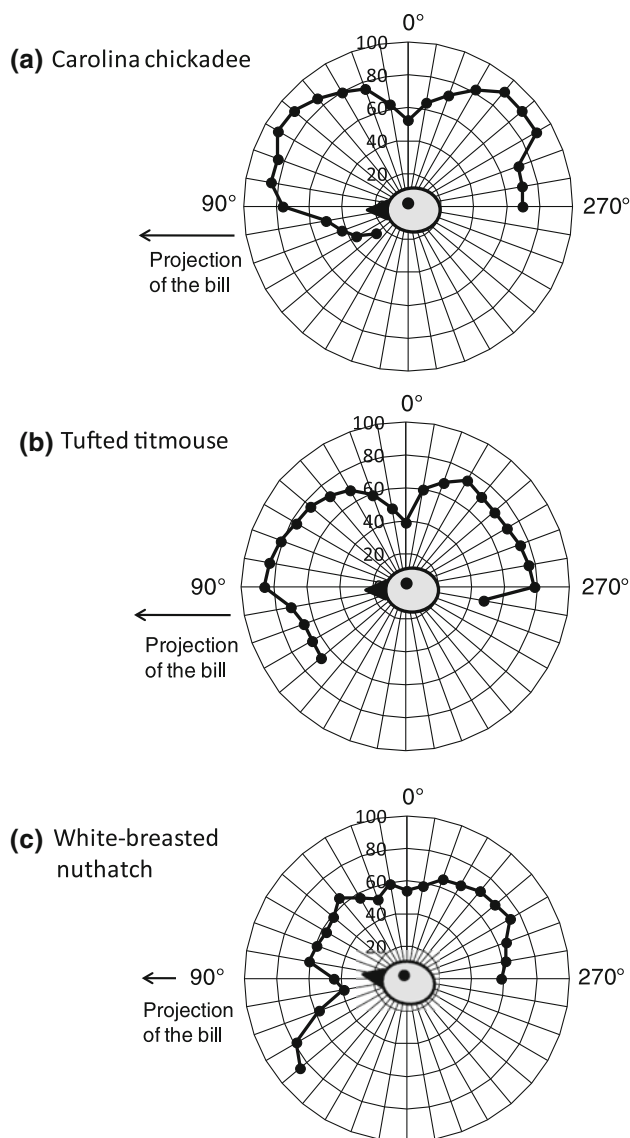


Fig. 4 Mean degree of eye movements in relation to elevation in the median sagittal plane in (a) Carolina chickadees, (b) tufted titmice, and (c) white-breasted nuthatches. Degree of eye movement is shown in the same scale (0°–100°) in all species while viewing the bird's head from the left side. The projection of the bill is in relation to the eye

In the horizontal plane, eye movements modified the relative size of the binocular, lateral, and blind areas in all the species (Fig. 5). When we elicited eye convergence (see “Methods”), chickadees increased the binocular overlap by 49 % and the blind area by 60 % in relation to the eyes-at-rest position (Fig. 5a), and titmice, by 47 and 100 %, respectively (Fig. 5b). The increase in the binocular field of nuthatches with the eyes converged was lower (22 %) compared with the eyes-at-rest position because the bill blocked our view of the retinal margins (see above; Fig. 5c). The extrapolated width of the nuthatch binocular field with eyes converged was estimated as 55° (Fig. 5c), assuming that the retinal margin

follows a circular projection (Martin and Coetzee 2004). The blind area of nuthatches with the eyes converged increased by 52 % in relation to the eyes-at-rest position (Fig. 5c).

In the horizontal plane, when individuals diverged their eyes, the width of the binocular and blind areas decreased by 102 and 63 %, respectively, in chickadees, and by 117 and 49 %, respectively, in titmice compared with the eyes-at-rest positions (Fig. 5d, e). Chickadees and titmice could actually abolish the area of binocular overlap, giving rise to a blind area of 1° and 9°, respectively, in front of the bill when the eyes diverged (Fig. 5d, e). When nuthatches diverged their eyes, the width of the binocular and blind areas decreased by 97 and 80 %, respectively, in relation to the eyes-at-rest position (Fig. 5f).

Head movements

Head-movement rate varied significantly among species ($F_{2,45} = 24.09$, $P < 0.001$). Chickadees had the highest head movement rates (2.05 ± 0.12 events/s), titmice had intermediate values (1.56 ± 0.10 events/s), and nuthatches had the lowest head movement rates (0.90 ± 0.12 events/s). All pair-wise differences between species were significant (Tukey tests, $P < 0.01$). We repeated the analysis excluding the catalog videos and including the videos we recorded to assess the effects of the potential confounding factors. None of these factors significantly influenced head movement rates (flock size, $F_{1,22} = 3.38$, $P = 0.079$; temperature, $F_{1,22} = 0$, $P = 1$; perch height, $F_{1,22} = 0.69$, $P = 0.693$; distance between observer and bird, $F_{1,22} = 0.01$, $P = 0.976$). After controlling statistically for these factors, we still found significant differences between species ($F_{2,22} = 26.97$, $P < 0.001$) following the same patterns described above.

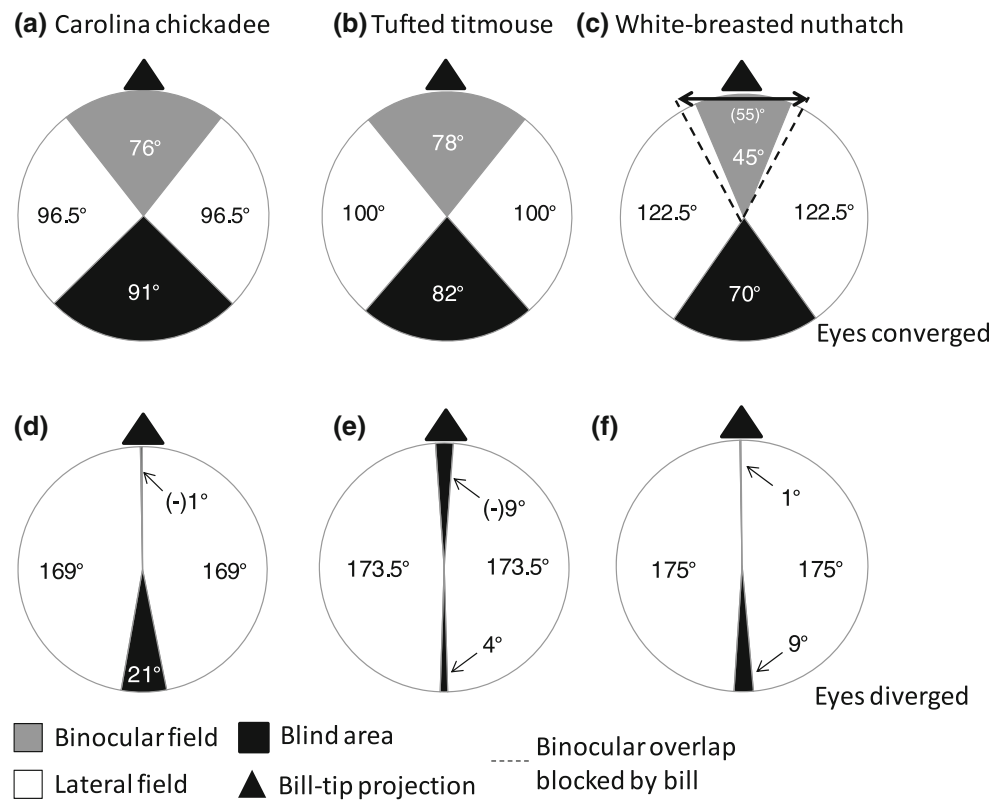
Discussion

Our results suggest that the visual system and scanning behavior of chickadees, titmice, and nuthatches have not only some similarities, but also many differences. We found support for some of our predictions (e.g., interspecific variation in visual acuity, width of the binocular fields, degree of eye movement, and head movement rates; position of the fovea in titmice and chickadees; width of the blind area in chickadees) but not for others (e.g., position of the fovea in nuthatches; width of blind areas in titmice and nuthatches). We discuss these findings in light of the foraging and anti-predator strategies of these three tree foragers.

Visual acuity

The inter-specific differences in visual acuity followed variations in body mass, as found previously (Kiltie 2000).

Fig. 5 Visual field sections through the horizontal plane (90°–270°) of (a, b) Carolina chickadees, (c, d) tufted titmice, and (e, f) white-breasted nuthatches. Charts represent the average retinal field when the eyes were converged (eyes rotated fully forward; a, c, e), which maximizes the size of the binocular and blind areas, and when the eyes were diverged (eyes rotated fully backward; b, d, f), which minimizes the size of the binocular and blind areas. The dotted lines in the white-breasted nuthatch (c) chart represent the extrapolated binocular field assuming that the retinal margin follows a circular projection (see text for details)



Visual acuity is influenced by eye size (which is associated with body mass; Garamszegi et al. 2002; Howland et al. 2004) and retinal ganglion cell density (Pettigrew et al. 1988). The highest visual acuity of nuthatches was likely affected by having the highest peak ganglion cell density of the three species. Titmice had intermediate values of visual acuity, followed by chickadees, which had the smallest eye size and lowest ganglion cell density. The implication is that nuthatches would be able to perceive visual stimuli (e.g., predators, conspecifics) from farther away than titmice and specially chickadees.

Contrary to our prediction, all three studied species had a single fovea, located centro-temporally in the retina, and thus projecting into the frontal side of the lateral field close to the edges of the binocular field. The peak retinal ganglion cell density around the fovea was slightly higher in these tree foragers compared with other avian ground foragers (house finch 25,256 cells/mm², house sparrow 23,920 cells/mm², brown-headed cowbird 21,665 cells/mm², European starling 25,317 cells/mm², Dolan and Fernández-Juricic 2010). This relatively higher retinal ganglion density would lead to higher localized visual resolution (given similar eye sizes). Species with a single fovea would tend to move their eyes (hence, their foveae) around substantially to scan for predators and search visually for food. Overall, tree foragers are expected to have visual demands that are different from those of

ground foragers due to the higher complexity of their visual environments (Hughes 1977; Hart 2001; Møller and Erritzøe 2010).

Binocular fields

As predicted, chickadees and titmice had wider binocular fields compared with those of nuthatches (Fig. 6a, b), which may be associated with the position of the eyes in the skull (Appendix). Actually, the binocular widths of titmice with the eyes at rest (53°) and converged (78°) were higher than that of any previously studied bird species (Martin 1984, 2004, 2007; Fernández-Juricic et al. 2010, a). Such wide binocular fields are not necessary to navigate complex environments (Martin 2009), like the closed habitats these species occupy. One possibility is that wide binocular fields may facilitate sampling the foraging substrate at relatively short distances by increasing light sensitivity and contrast discrimination (reviewed in Heesy 2009), which would enhance the detection of food in closed habitats with relatively low ambient light levels. Another possibility is that wide binocular fields are associated with arboreal habits, potentially providing depth perception from stereoscopic cues as the animal moves through the foliage (Changizi and Shimojo 2008). However, Martin (2009) argued that stereoscopic depth perception may be absent in most bird species and that birds rely primarily

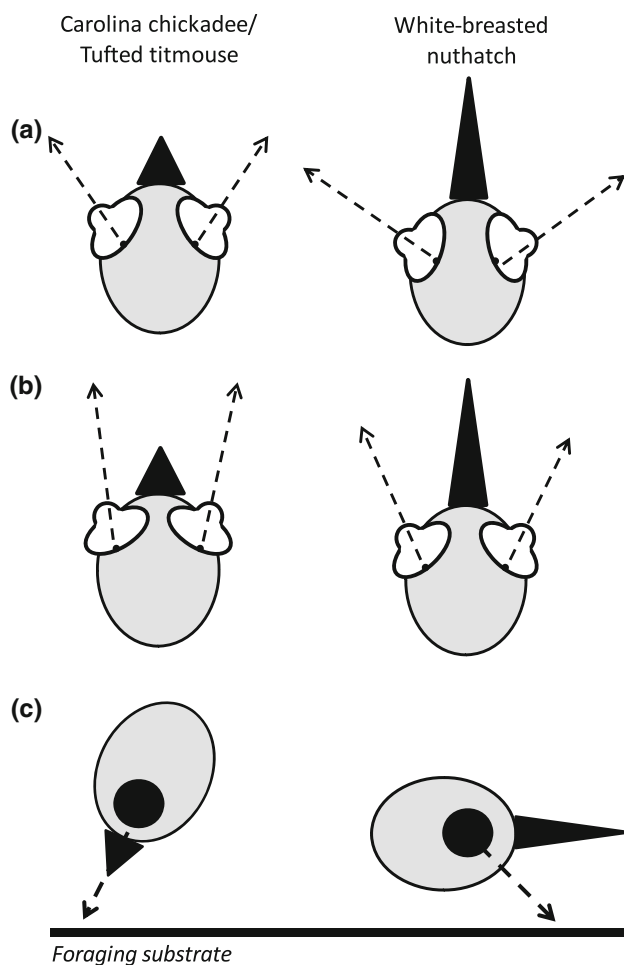


Fig. 6 **a, b** Top-views showing the approximate projection of the fovea into the visual fields of Carolina chickadees/tufted titmice and white-breasted nuthatches with the eyes **(a)** at rest and **(b)** converged. The more frontally placed eyes of the chickadees/titmice would result in the fovea projecting more frontally, whereas the more laterally placed eyes of the nuthatches would result in the fovea projecting slightly more laterally. **(c)** Side-view representation of the approximate projection of the fovea of Carolina chickadees/tufted titmice and white-breasted nuthatches while seeking food, taking into account the convergence of the eyes in the direction of the foraging substrate. The arrows do not provide any reference to binocularity or the ability to visualize the bill-tip

upon direction of travel and time to contact cues derived from optic flow-field information. More information on the function of the binocular fields of these species should be gathered in the future to test these hypotheses.

Previous studies have suggested that some avian species can see their bill tips (Martin 2009), which was associated with relatively wide binocular fields (e.g., American crow, Fernández-Juricic et al. 2010; New Caledonian crow, Troscianko et al. 2012). However, our results show that the nuthatch is able to see its bill-tip with a relatively narrower binocular field than that of the chickadee and titmouse. This may be explained by the nuthatch's longer bill

(20.55 mm) that protrudes into the binocular field, compared with those of chickadees (7.83 mm) and titmice (10.65 mm) (Frens 2010). Visualizing the bill tip may facilitate probing and manipulating food items by wedging them into bark crevices (Grubb and Pravasudov 2008). Our results suggest that the ability of species to visually inspect their bills may be the result of a trade-off between the width of the binocular field and the length of the bill.

Eye and head movements

Our prediction of wider blind areas in species with more frontally placed eyes was met when individuals converged their eyes. However, contrary to our expectation, we found that nuthatches had wider blind areas than titmice with the eyes at rest. This difference could be attributed to eye movement amplitude. All studied species had high degrees of eye movement (with both eyes $>60^\circ$ across all elevations) compared with that of previously studied species (Martin 1998; Martin and Coetzee 2004; Fernández-Juricic et al. 2008, 2010). However, they differed in their eye movement strategies around the bill, which may be associated with their foraging strategies.

Chickadees and titmice had slightly more frontally positioned eyes (Appendix) and the highest degree of eye movement occurred slightly above the plane of the bill. This may allow these two species to converge their eyes toward the bill and change the position of the foveae, which would project into the binocular field slightly above the bill when head-down searching for food at steep angles in relation to the foraging substrate (Fig. 6). Nuthatches, on the other hand, had relatively more laterally placed eyes (Appendix) with a high degree of eye movement mostly below the bill. This would allow nuthatches to converge their eyes and change the position of the fovea, which would project into the binocular field slightly below the bill toward the foraging substrate when the bill is held at a shallow angle in relation to the tree trunk during food searching (Fig. 6). These morphological and sensory features may enhance the ability of these species to detect food through different foraging tactics while exploiting the same micro-habitats.

Moving the head is another strategy (besides eye movements) to move the fovea around and obtain high visual resolution information on objects of interest (Dunlap and Mowrer 1930; Friedman 1975; Fernández-Juricic 2012). Generally, quicker head movement rates should translate into more regions of the visual space that can be updated per unit time with high-quality information through inspection with the foveae. The nuthatch had the lowest head movement rate of all three species. This may be the result of a lower need to scan the environment because of its higher visual acuity to detect stimuli at

farther distances, smaller blind areas, and more laterally placed eyes increasing visual coverage. Conversely, chickadees and titmice had higher head movement rates, probably because they often seek food in a head-down posture with the bill oriented at steep angles in relation to the substrate, and therefore have to raise their heads frequently to monitor for potential predators. Additionally, chickadees showed higher head movement rates than titmice. Titmice had higher visual acuity and narrower blind areas than chickadees, potentially decreasing the need to scan as frequently through head movements. An alternative explanation based on Newton's second law is that it would require more force (i.e., greater energetic costs) for titmice to move their heads as often as chickadees due to their larger body mass.

Implications for heterospecific flocking behavior

Our results have some implications for the behavioral interactions among these species when they form heterospecific flocks during the non-breeding season. A common assumption is that satellite species eavesdrop on the alarm calls of nuclear species (Templeton and Greene 2007; Bartmess-LeVasseur et al. 2010). There is evidence in the guild of tree foragers we studied that some of its satellite species (e.g., white-breasted nuthatch, downy woodpecker *Picoides pubescens*) decrease their investment in vigilance (Sullivan 1984a, b; Dolby and Grubb 1998) and increase foraging efforts and risk-taking behaviors (Dolby and Grubb 2000) when associated with nuclear species (tufted titmouse, Carolina chickadee). However, our results suggest that the visual system of at least one of these satellite species, the nuthatch, may enable them to have a good ability to detect predators visually from far away (i.e., higher visual acuity) and from different parts of the environment (i.e., narrower blind areas, larger lateral fields). Additionally, the auditory system of nuthatches does not have high sensitivity for the high-frequency alarm calls of chickadees and titmice (Henry and Lucas 2008). All this sensory evidence in principle challenges the idea that the nuthatch eavesdrops on the alarm calls of the titmouse and chickadee because of potential limitations of its sensory system.

One possibility is that nuthatches actually rely on social *visual* information from the nuclear species by tracking visually their foraging and anti-predator behaviors.

Alternatively, nuthatches may use both sources of information (auditory and visual) depending upon their main behavioral activity. When nuthatches engage in non-foraging activities, they may rely to a greater extent on visual cues from the nuclear species. However, when foraging, they may use some vocalizations of the nuclear species as cues to engage in visual monitoring for predators. This is because foraging nuthatches tend to have a very large portion of their visual field blocked by the tree trunk as they move quickly in search of food and appear to have their visual attention focused away from the areas where predators would generally attack (Fig. 6). As a result of this compromised foraging technique, nuthatches may compensate for the reduced availability of visual information with auditory information. Future studies manipulating both visual and auditory cues simultaneously could provide an opportunity to assess the attention targets of nuthatches in heterospecific flocks.

Conclusions

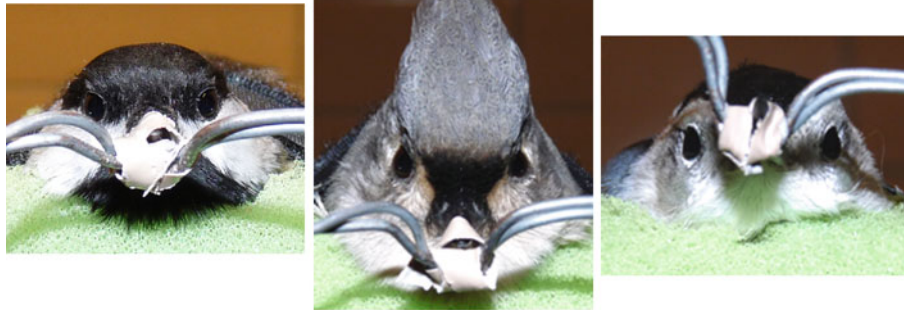
Overall, we found that chickadees, titmice, and nuthatches differ in some key components of their visual system and scanning behavior. These differences may be the result of phylogenetic relatedness (chickadees and titmice belong to the family Paridae; nuthatches to the family Sittidae) and/or specializations to the visual challenges posed by the different foraging and scanning strategies that facilitate the partitioning of resources within this guild.

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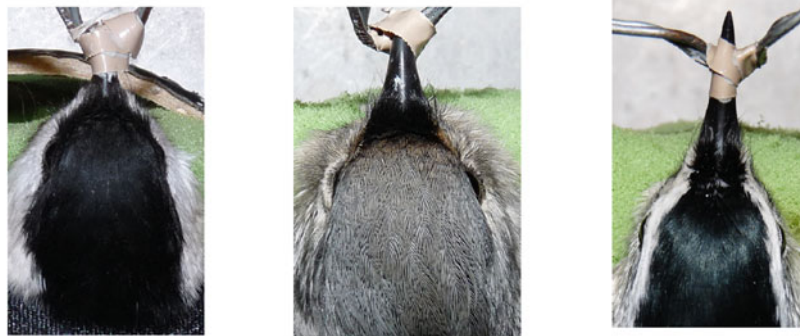
Appendix

Eye positioning in the skull of (a) Carolina chickadees, (b) tufted titmice, and (c) white-breasted nuthatches while in the visual field apparatus. Chickadees and titmice have their orbits positioned slightly more toward the bill than nuthatches.

Front-views



Top-views



(a) Carolina chickadee

(b) Tufted titmouse

(c) White-breasted nuthatch

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