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The visual fields of two ground-foraging birds, House Finches and House Sparrows, allow for simultaneous foraging and anti-predator vigilance

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In birds, differences in the extent and position of the binocular visual field reflect adaptations to varying foraging strategies, and the extent of the lateral portion of the field may reflect anti-predator strategies. The goal of this study was to describe and compare the visual fields of two ground-foraging passerines, House Finch C*arpodacus mexicanus* and House Sparrow *Passer domesticus*. We found that both species have a binocular field type that is associated with the accurate control of bill position when pecking. Both species have eye movements of relatively large amplitude, which can produce substantial variations in the configuration of the binocular fields. We propose that in these ground foragers, their relatively wide binocular fields could function to increase foraging efficiency by locating multiple rather than single food items prior to pecking events. The lateral fields of both species are wide enough to facilitate the detection of predators or conspecifics while head-down foraging. This suggests that foraging and scanning are not mutually exclusive activities in these species, as previously assumed. Furthermore, we found some slight, but significant, differences between species: House Sparrow binocular fields are both wider and vertically taller, and the blind area is wider than in House Finches. These differences may be related to variations in the degree of eye movements and position of the orbits in the skull.

Keywords: binocular vision, C*arpodacus mexicanus*, lateral vision, mutual exclusivity assumption, orbit orientation, *Passer domesticus*, predation risk, scanning.

One of the most important assumptions that underlies the analysis of anti-predator vigilance in birds is that foraging and vigilance behaviours are mutually exclusive (Pulliam *et al.* 1982, Ward 1985, Bednekoff & Lima 2002). It is assumed that birds that are head-down foragers are not able simultaneously to detect predators and conspecifics (Fernández-Juricic *et al.* 2004a). However, recent evidence in two passerine species (Dark-eyed Juncos *Junco hyemalis*, Lima & Bednekoff 1999, Bednekoff & Lima 2005; Common Starling *Sturnus vulgaris*, Fernández-Juricic *et al.* 2005) argues against this assumption by showing empirically that birds allocate more time to head-up vigilance when head-down vision is blocked.

One of the factors influencing the allocation of time to anti-predator vigilance in birds could be the configuration of visual fields (Fernández-Juricic *et al.* 2004a), the portion of space that can be viewed instantaneously at any given head and body position (Martin 2007). For instance, a recent between-species comparison found that in ducks the species with a broader blind area behind the head spent more time vigilant during foraging (Guillemain *et al.* 2002). Anti-predator vigilance is particularly important in small- and medium-sized passerine birds, especially those that forage on the ground, as they are generally preyed upon by a wide variety of predators (e.g. Lima 1993, Suhonen 1993, Götmark & Post 1996). However, with the exception of Common Starlings (Martin 1986), there are no data on visual field configuration in ground-foraging passerines.

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Visual fields can be described by reference to the size of three main areas (Martin 2007): monocular (the area covered by each eye alone), binocular (the area in which the fields of both eyes overlap), and blind areas. The relative size of each of these areas has been shown to vary between species in relation to different foraging and anti-predator strategies (Martin 2007). In general, visually guided species that require accurate visual control of the bill while obtaining or manipulating items, or when feeding chicks (e.g. Eurasian Stone-curlew *Burhinus oedicnemus*, Lesser Flamingo *Phoeniconaias minor*, Rock Pigeon *Columba livia*) tend to have binocular areas centred on the bill and moderately sized blind areas (Martinoya *et al.* 1984, Martin 2007). However, in other species (e.g. Eurasian Woodcock *Scolopax rusticola*, Pink-eared Duck *Malacorhynchus membranaceus*), the bill falls outside or lies in the periphery of the binocular area, which is relatively narrower and the blind area is small or even not present (Martin 2007). Foraging in these species is based primarily upon tactile cues or filter feeding techniques, and the lack of a blind area has been associated with predator detection.

Our aim was to characterize visual fields in two ground-feeding passerine species, House Sparrows *Passer domesticus* and House Finches *Carpodacus mexicanus*. We compared different aspects of their visual fields: eye movements; width of binocular, monocular and blind areas; vertical extent of the binocular area; and, width of the projection of the pecten into the visual field. We also assessed morphological differences in the placement of the orbits in the skull, because they could affect the configuration of the visual fields (Heesy 2004, 2008).

We chose these species for two reasons. First, both are predominantly ground foragers that peck for small seeds and other plant material, although they also forage for invertebrates when provisioning young (Hill 1993, Lowther & Cink 2006). Secondly, House Sparrows (Barnard 1980, McVean & Haddlesey 1980, Elcavage & Caraco 1983, Elgar *et al.* 1984, Beveridge & Deag 1987, Elgar 1987, Harkin *et al.* 2000, Fernández-Juricic *et al.* 2001, Johnson *et al.* 2001, Liker & Barta 2002, Fernández-Juricic *et al.* 2004b), and to a lesser extent House Finches (Giesbrecht & Ankney 1998, Fernández-Juricic *et al.* 2006, Fernández-Juricic & Tran 2007), have been used frequently as models for studies of foraging and anti-predator behaviour. In most of these studies, it has been assumed explicitly or implicitly that head-up scanning and head-down foraging are mutually exclusive activities.

METHODS

Visual fields

All visual field measurements were conducted at California State University Long Beach (CSULB) between November 2006 and March 2007. Individuals were captured in live traps from populations in Los Angeles County (House Sparrows) and Orange County (House Finches). Experimental protocols were approved by the CSULB Institutional Animal Care and Use Committee (Protocol #220).

We determined the retinal visual field using an ophthalmoscopic reflex technique (see detailed description of the visual field apparatus in Martin *et al.* 2007). An individual was secured on a foam cradle at the centre of the visual field apparatus using Velcro straps. The head was positioned with the eyes aligned with the pivot points (similar to the poles on a globe) of the perimeter arm. The bill was fixed at the position typically adopted in the wild (established from videos of both species recorded in semi-natural conditions) by taping it to a specially designed metal bill holder. We used a coordinate system in which 0° was directly above the bird's head, and 90° was at the horizontal plane. For measurements in elevations below the bill we replaced the bill holder with a thin metal wire because the bill holder obstructed our view of the retina. Nevertheless, we were not able to record the projections of the retinal margins from elevations 160° to 220° (70° to 130° below the bill tip) due to the feather, body, and tripod obstructions.

The position of the projection of the retinal margin of each eye was recorded using a Keeler Professional ophthalmoscope to an accuracy of ±0.5° at each elevation, which was varied in 10° increments in the median sagittal plane of the bird. We measured the maximum and minimum limits of the visual fields produced by eye movements and also the limits when the eyes were at rest. To do this we used two slightly different methods, which allowed us to better characterize the extent of the visual fields within each species and to collect a large enough sample to draw between-species comparisons.

Method one

Eye movements were elicited in four individuals of each species by producing slight sounds and flashes of a small light source presented to the side of the bird's head. We recorded the extreme positions of the retinal field margins produced by the movement of the eyes, and calculated the difference between these values as the maximum amplitude of eye movement at each elevation in the sagittal plane. We calculated the extent of the binocular and lateral visual fields, and the extent of the blind areas behind the head in the horizontal plane. We used the following assumptions: (1) the maximum binocular overlap is produced when eyes are converged (i.e. rotated maximally forward); and (2) the minimum binocular overlap is produced when eyes are diverged (i.e. rotated maximally backwards). To calculate the extent of the lateral field (monocular field – binocular field) for each eye, we used the following formula: (360 – (mean blind field + mean binocular field)/2), and represented graphically the configuration of all areas in the approximately horizontal plane (Martin & Katzir 1999). We also determined the average eye movement amplitude at all elevations.

Method two

We measured the retinal visual fields as a function of elevation when the eyes were at rest in 14 House Finches and 19 House Sparrows. At each elevation (changed in 10° increments), the position the eye adopted was observed with the ophthalmoscope three times in rapid succession. We only included measurements in which the eye did not exhibit movement. Therefore, with this procedure the number of individuals used to establish the extent of the visual fields at each elevation varied. We used the same technique to measure the position of the pecten – a highly pigmented vascular structure that appears as a black area when viewed through the ophthalmoscope and produces a blind portion within each lateral field. The vertical extent of the binocular field was calculated for each bird from the number of consecutive 10° elevations that had binocular overlap.

Skull parameters

We measured different morphological parameters on 10 skulls of each species from the Vertebrate Museum at CSULB (Fig. 1). On the frontal plane of the skull, we recorded rostrum width (widest part anterior to the cranium), cranium width (widest part of the cranium), cranium length (from the occipital to the base of the rostrum), eye socket width (the widest point in a plane parallel to the mandible), and the distance between the occipital and the centre of the eye socket (eye-centre-occipital-distance). The centre of the eye socket was determined as the point located halfway between the eye socket height and the eye socket width. On the transverse plane of the skull, we recorded cranium height (tallest part of the cranium, excluding the mandible). In the sagittal plane, we measured the nasal–temporal angle as the angle between the projection of the occipital to the bill tip and the projection of the occipital to the centre of the eye. With this information, we calculated different indices representing eye size and orbit position in the skull (see below).

Statistical analysis

We compared the average widths of the binocular field, blind area and pecten between species with general linear models, including the following categorical factors: species, elevation, bird identity (ID) and the interaction between species and elevation. All independent factors, except bird ID, were considered fixed. Bird ID was incorporated as a random factor to reduce potential biases due to individual differences in visual field configuration.

The average vertical extent of the binocular area was compared between species with a *t*-test for independent samples. Differences in average eye movement amplitude between species were analysed with a general linear model, including species, but controlling for the potential confounding effects of elevation.

Based on the skull measurements, we calculated different indices of eye size and orbit position in the skull. We used two indices of eye size: eye socket-width and eye socket-width : rostrum-width ratio. Rostrum-width : cranium-width ratio was calculated as an indicator of the proportion of the bill that occupies the frontal field of view. We also calculated eye-centre-occipital-distance : cranium-length ratio as an index of the relative position of the orbit on the frontal plane; a higher ratio indicates an orbit positioned towards the bill. The nasal–temporal angle was used as an indicator of the angle at which the orbit is set in the skull; high nasal–temporal angle values indicate that the orbit is tilted away from the bill. We compared these ratios and the nasal–temporal angle between species with general linear models, including species as a categorical factor. Eye socket-width was analysed in a similar way, but we also included a continuous factor controlling for cranium size. This factor was derived from a Principal Component Analysis considering cranium-length, cranium-height, and cranium-width. All cranium size variables were negatively correlated with a single PCA component (eigenvalue = 2.25, proportion of variability explained = 74.92%).

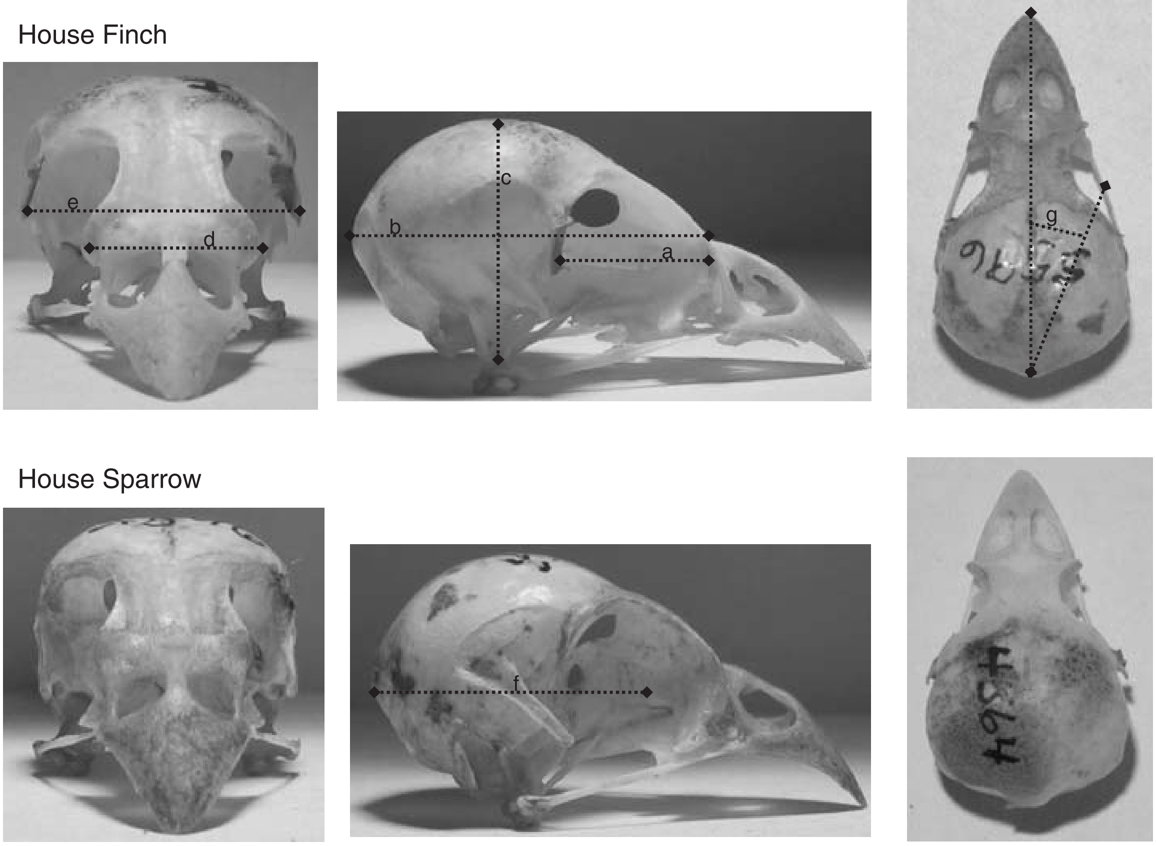

Figure 1. Frontal, lateral and top views of the skulls of House Finches and House Sparrows. Letters indicate different morphological measurements used to compare eye size and positioning in the skull: (a) eye socket width, (b) cranium length, (c) cranium height, (d) rostrum width, (e) cranium width, (f) distance between the occipital and the centre of the eye socket, and (g) nasal–temporal angle. All these parameters were measured in both species, but are shown in different pictures for the sake of clarity.

We checked for normality and homoscedasticity of the variables, but did not find major deviations. We also ran models with sex, but found no significant effects, so we do not report these results. Because the number of observations per combination of factors (e.g. elevation and species) was not balanced, all general linear models were conducted with Type III sums of squares. All means are presented ± se.

RESULTS

Overall, House Finches and House Sparrows have similar configurations of their visual fields, with a well-defined blind area behind the head and a binocular area that includes the projection of the bill (Figs 2 & 3). In the approximately horizontal plane, the average binocular field widths of both species were similar when the eyes were converged maximally (Fig. 3). The amplitude of eye movements in both species was sufficient almost to abolish binocularity when the eyes were diverged maximally (Fig. 3). Eye movements changed the size of the blind area behind the head by 45% in House Finches and 38% in House Sparrows (Fig. 3). The lateral fields in both species were large, between 130° and 140°, which represents about 90% of the total visual field (Fig. 3). This result suggests that it is likely that both species can obtain information from their lateral fields while head-down searching for food.

The maximum width of the binocular field occurred at an elevation 30° below the projection of the bill in House Sparrows and 40° below the bill in House Finches (Fig. 4). Across all recorded elevations, the average *width* of the binocular field was significantly larger in House Sparrows (29.48 ± 1.05°) than in House Finches (26.96 ± 1.37°; Table 1, Fig. 4). Furthermore, the average *vertical extent* of the binocular field was significantly larger ($t_{12} = 2.84$, $P = 0.015$) in House Sparrows (200.00 ± 4.47°) than in House Finches (178.75 ± 5.49°). The averaged maximum

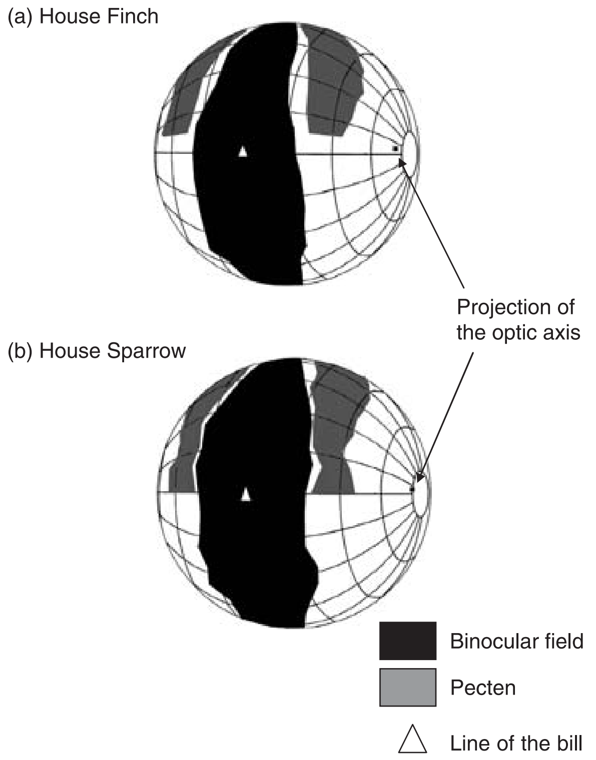

Figure 2. Visual fields of (a) House Finches and (b) House Sparrows. Perspective views of an orthographic projection of the averaged boundaries of the retinal fields when both eyes are at rest. The head is imagined to be at the centre of the sphere with the bill tip projecting towards the point shown (triangle) and the fields projected onto the surface of the sphere (grid at 20° intervals).

Table 1. Differences in the average width of the binocular field, blind area and pecten between House Sparrows and House Finches. Results from general linear models with two fixed factors (elevation and species), one random factor (bird ID), and the interaction between elevation and species. Significant effects are marked in bold.

	F	df	*P*
Binocular field			
Intercept	668.89	1,222	< **0.001**
Elevation	52.44	17,222	< **0.001**
Bird ID	7.10	20,222	< **0.001**
Species	25.19	1,222	< **0.001**
Elevation × species	1.32	16,222	0.188
Blind area			
Intercept	236.96	1,222	< **0.001**
Elevation	94.89	11,222	< **0.001**
Bird ID	8.65	20,222	< **0.001**
Species	48.74	1,222	< **0.001**
Elevation × species	0.84	11,222	0.605
Pecten			
Intercept	1243.93	1,132	< **0.001**
Elevation	38.58	7,132	< **0.001**
Bird ID	4.51	20,132	< **0.001**
Species	0.01	1,132	0.916
Elevation × species	2.96	7,132	**0.006**

width of the blind area occurred at the elevation of 230° for both species (Fig. 4). Across all recorded elevations, the average width of the blind area was significantly larger in House Finches (28.93 ± 2.13°) than in House Sparrows (25.03 ± 2.04°; Table 1, Fig. 4).

The average width of the pecten did not vary between House Sparrows (21.68 ± 0.64°) and House Finches (21.82 ± 0.81°) across elevations (Table 1). However, we found a significant interaction effect between species and elevation (Table 1), by which the House Finch pecten was significantly wider than that of the House Sparrow at the elevation of 20° (House Finch, 29.51 ± 1.38°; House Sparrow, 22.87 ± 1.64°; $F_{1,132} = 5.44$, $P = 0.021$), and marginally non-significant at 30° (House Finch, 29.52 ± 1.47°; House Sparrow, 24.20 ± 0.83°; $F_{1,132} = 3.27$, $P = 0.073$).

The average maximum eye movement amplitude of both species was recorded at the elevation 10° below the horizontal (Fig. 5). Eye movements in House Sparrows (16.36 ± 1.23°) were on average greater than in House Finches (11.16 ± 1.15°, $F_{1,39} = 11.94$, $P = 0.001$), controlling for the effects of elevation ($F_{1,39} = 11.30$, $P = 0.002$; Fig. 5).

We found a number of differences in the size and positioning of the orbit in the skull between species. Eye socket width was significantly larger in House Sparrows (8.83 ± 0.06 mm) than in House Finches (8.18 ± 0.07 mm; $F_{1,17} = 12.69$, $P = 0.002$), controlling for cranium size ($F_{1,17} = 0.22$, $P = 0.642$). Additionally, eye socket-width : rostrum-width ratio was larger in House Sparrows (1.12 ± 0.03) than in House Finches (1.04 ± 0.03), but the difference was marginally non-significant ($F_{1,18} = 4.14$, $P = 0.057$). These results suggest that House Sparrows have relatively larger eyes than House Finches. Rostrum-width : cranium-width ratio was larger in House Finches (0.56 ± 0.02) than in House Sparrows (0.51 ± 0.01; $F_{1,18} = 7.71$, $P = 0.012$), indicating that the House Finch bill occupies a proportionally larger area of their frontal field of view. The lateral positioning of the eyes differed between species: the eye-centre-occipital-distance : cranium-length ratio was significantly larger in House Finches (0.810 ± 0.004) than in House Sparrows (0.779 ± 0.005; $F_{1,18} = 22.70$, $P < 0.001$), indicating that House

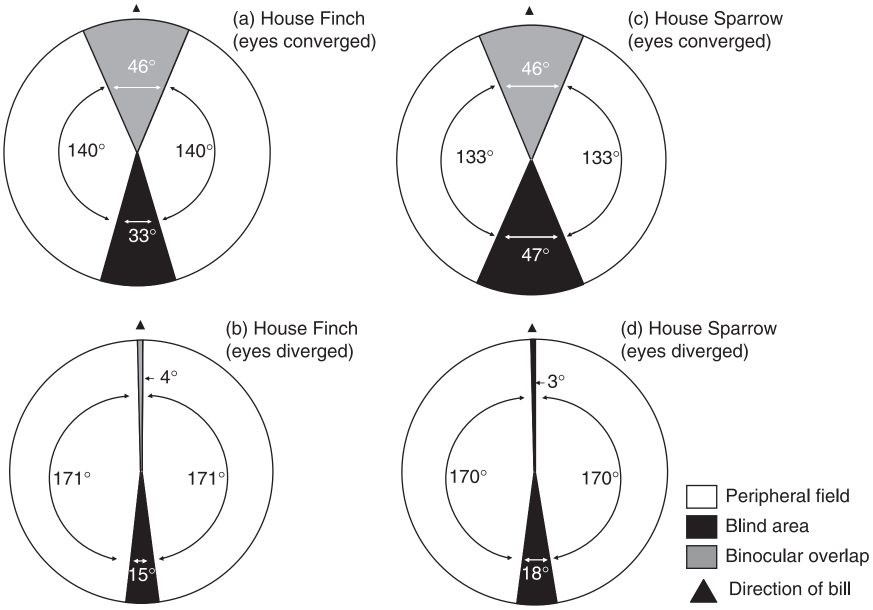

Figure 3. Horizontal sections through the retinal visual fields of House Finch (a,b) and House Sparrow (c,d) at the approximately horizontal plane. For each species, we present average retinal fields when the eyes were fully converged (eyes rotated fully forward), which maximizes the size of the binocular and blind areas (a,c) and fully diverged (eye rotated fully backward), which minimizes the size of the binocular and blind areas (b,d).

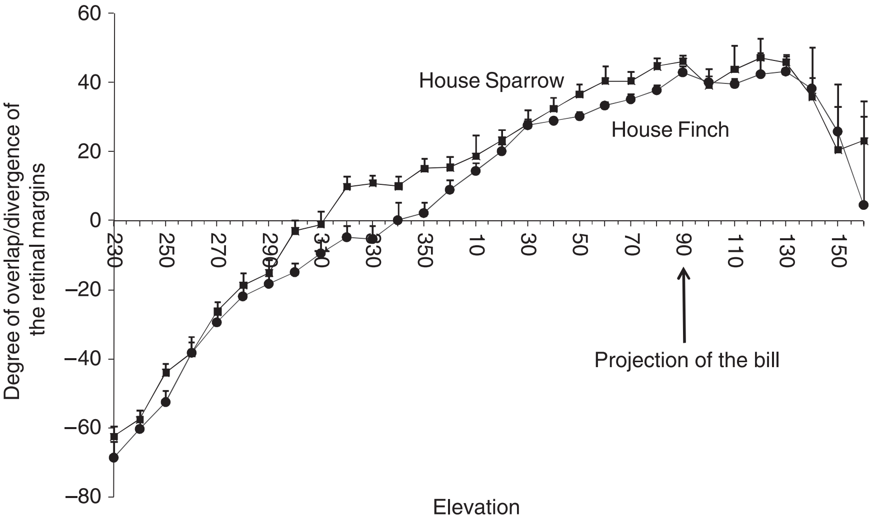

Figure 4. Average width (± se) of binocular overlap and width of the blind area in House Finches and House Sparrows as a function of elevation in the median sagittal plane. Positive values represent the degree of binocular overlap, negative values the width of the blind area.

Finch orbits are positioned farther forward in the skull (e.g. towards the bill). Finally, the nasal–temporal angle was greater in House Finches (19.60 ± 0.34°) than in House Sparrows (16.21 ± 0.29°; $F_{1,18} = 57.90$, $P < 0.001$), suggesting that House Finch orbits are pointed more outward from the bill (e.g. diverge more from the sagittal plane). The position of the orbit in the skull is consistent with the larger binocular areas of House Sparrows and larger blind areas of House Finches.

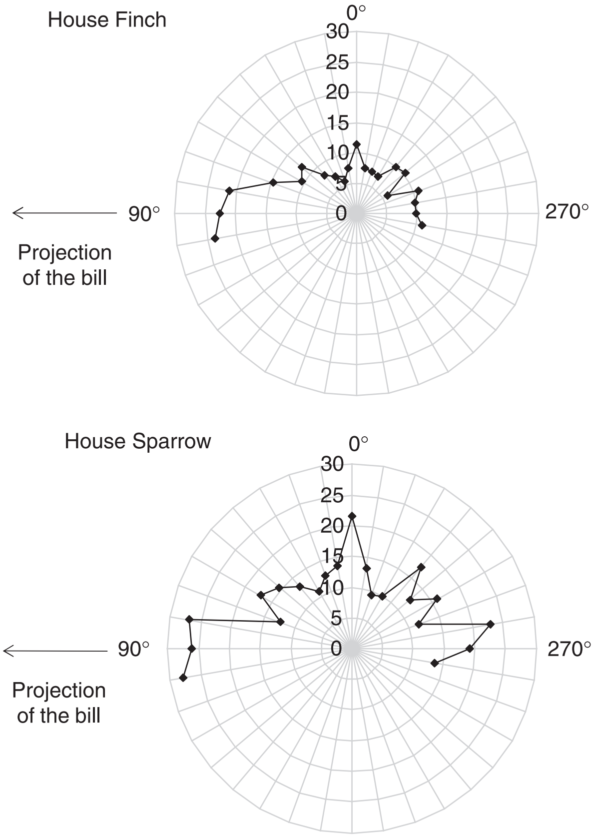

Figure 5. Average amplitude of eye movements as a function of elevation in the median sagittal plane in House Finches and House Sparrows.

DISCUSSION

House Finches and House Sparrows are both ground foragers that inhabit open and semi-open areas, exploiting primarily seed material. The projection of the bill tip in both species falls in the central region of the binocular field, which extends vertically more than 180°, even to 70° below the plane of projection of the bill. This suggests that these birds can potentially observe food items using binocular vision while head-up (e.g. standing with the bill held horizontal). These visual field configurations, when the eyes are in the resting position, are characteristic of species that appear to use visual information for the accurate control of bill position (Martin 2007).

Eye movements, binocular fields and foraging

The degree of eye movement in these two passerines indicates that they may temporarily switch between different visual field configurations. For example, both species can switch between having a wide region of binocular overlap to almost complete abolition of frontal binocularity. The degree of maximum binocular overlap was slightly greater in House Finches and House Sparrows than for the other passerine species described so far, the Common Starling (Martin 1986). This may be associated with locating small multiple food items that are dispersed over a relatively large angular distance (Friedman 1975). Common Starlings mainly forage for single items using an open-billed probing technique rather than searching for items scattered across a surface (Feare 1984).

Visual fields and vigilance

Common Starlings have wide lateral visual fields (Martin 1986), which can explain their ability to gather visual information about the behaviour of conspecifics and predators when head-down (Fernández-Juricic *et al.* 2005). We found that House Sparrows and House Finches can move their eyes to increase visual coverage in such a way that their overall visual fields extend above (large vertical extent of the binocular field) and behind (wide lateral fields) their heads. This suggests that both species can detect visual stimuli while head-down. This finding violates the assumption of mutual exclusivity between foraging and scanning behaviour that is prevalent in studies using these species as models. For instance, Fernández-Juricic *et al.* (2001) assumed that House Sparrows detected an observer approaching only when head-up, a bias that could have underestimated alert distances.

Nevertheless, the detection of visual stimuli while head-down may not be as effective as when head-up (Lima & Bednekoff 1999), and it may primarily employ motion detection rather than high acuity, which allows identification of the alerting stimulus. A recent study (Hart 2001) showed that the concentration of double cones, which are associated with motion detection (Campenhausen & Kirschfeld 1998), is higher in the ventral part of the retina (which looks upwards) in ground-foraging birds compared with those that forage in trees. This head-down detection may be enough to generate a timely response to a relevant stimulus (e.g. predator attack). For instance, if flock mates flush, individuals that are foraging head-down would stop to scan the surroundings with their head up and then make a decision as to whether or not to flee (e.g. Cresswell *et al.* 2000).

Between-species differences in visual fields

Despite the general similarities between House Sparrows and House Finches in relation to previously described visual field types in birds (Martin 2007), we found significant differences in some parameters between these two species. The average width of the binocular field across elevations was about 2.5° larger in House Sparrows than in House Finches. It is unclear whether this statistically significant difference is biologically relevant. We calculated the degree of binocular coverage of the substrate based on this difference. House Sparrows would have a 1.5-mm and a 3.01-mm increase in binocular coverage from head-down and head-up positions, respectively, in relation to House Finches. This difference could modify the speed with which seeds scattered on the ground are located. This explanation is speculative and requires testing. However, recent evidence indicates that House Sparrows forage more efficiently than House Finches (Shochat *et al.* 2004).

The vertical extent of the binocular field determines where the blind area begins in the sagittal plane. A larger blind area could restrict the ability of birds to detect potential predators (Fernández-Juricic *et al.* 2004a). The upper vertical limit of the blind area of House Sparrows was lower than in House Finches, which could be related to micro-habitat preferences and predation risk. House Sparrows may benefit from vertically shorter blind areas because they increase the chances of predator detection while head-down, and this may be of particular importance in this species, which naturally inhabits open areas (Lowther & Cink 2006). On the other hand, House Finches, which occupy mainly open forests or edge habitats and prefer foraging patches that are closer to high perches (Hill 1993), may have a reduced need to detect predators from above the head.

Between-species differences in the width of the binocular and blind areas could be caused by three non-mutually exclusive anatomical factors, which may not necessarily be related to functional explanations. First, House Sparrows have larger eyes, which could increase the spatial extent of their visual coverage. Secondly, House Sparrows have larger eye movement amplitudes, allowing them to increase eye convergence and divergence, and consequently the sizes of the binocular and blind areas. Thirdly, House Sparrows have more forward-pointing eye sockets, such that the bill occupies a proportionally smaller area of the frontal field of view, thereby increasing the retinal margin overlap in front of the head, and consequently the size of the binocular field.

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REFERENCES

Barnard, C.J. 1980. Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Anim. Behav.* **28**: 295–309.

Bednekoff, P.A. & Lima, S.L. 2002. Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance. *J. Avian Biol.* **33**: 143–149.

Bednekoff, P.A. & Lima, S.L. 2005. Testing for peripheral vigilance: do birds value what they see when not overtly vigilant? *Anim. Behav.* **69**: 1165–1171.

Beveridge, F.M. & Deag, J. M. 1987. The effects of sex, temperature and companions on looking up and feeding in single and mixed species flocks of House Sparrows (*Passer domesticus*), Chaffinches (*Fringilla coelebs*) and Starlings (*Sturnus vulgaris*). *Behaviour* **100**: 303–320.

Campenhausen, M.V. & Kirschfeld, K. 1998. Spectral sensitivity of the accessory optic system of the pigeon. *J. Comp. Physiol. A* **18**: 1–6.

Cresswell, W., Hilton, G.M. & Ruxton, G.D. 2000. Evidence for a rule governing the avoidance of superfluous escape flights. *Proc. R. Soc. Lond. B* **267**: 733–737.

Elcavage, P. & Caraco, T. 1983. Vigilance behavior in house sparrow flocks. *Anim. Behav.* **31**: 303–304.

Elgar, M.A. 1987. Food intake rate and resource availability: flocking decisions in House Sparrows. *Anim. Behav.* **35**: 1168–1176.

Elgar, M.A., Burren, P.J. & Posen, M. 1984. Vigilance and perception of flock size in foraging House Sparrows (*Passer domesticus* L.). *Behaviour* **90**: 215–223.

Feare, C. 1984. *The Starling*. Oxford: Oxford University Press.

Fernández-Juricic, E. & Tran, E. 2007. Changes in vigilance and foraging behaviour with light intensity and their effects on food intake and predator detection in house finches. *Anim. Behav.* **74**: 1381–1390.

Fernández-Juricic, E., Jimenez, M.D. & Lucas, E. 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environ. Cons.* **28**: 263–269.

Fernández-Juricic, E., Erichsen, J.T. & Kacelnik, A. 2004a. Visual perception and social foraging in birds. *Trends Ecol. Evol.* **19**: 25–31.

Fernández-Juricic, E., Jokimäki, J., McDonald, J., Melado, F., Toledano, A., Mayo, C., Martín, B., Fresneda, I. & Martín, V. 2004b. Effects of opportunistic predation on anti-predator behavioral responses in a guild of ground foragers. *Oecologia* **140**: 183–190.

Fernández-Juricic, E., Smith, R. & Kacelnik, A. 2005. Increasing the costs of conspecific scanning in socially foraging starlings affects vigilance and foraging behaviour. *Anim. Behav.* **69**: 73–81.

Fernández-Juricic, E., Gilak, N., McDonald, J.C., Pithia, P. & Valcarcel, A. 2006. A dynamic method to study the transmission of social foraging information in flocks using robots. *Anim. Behav.* **71**: 901–911.

Friedman, M.B. 1975. How birds use their eyes. In Wright, P., Caryl, P.G. & Vowles, D.M. (eds) *Neural and Endocrine Aspects of Behavior in Birds*: 181–204. Amsterdam: Elsevier.

Giesbrecht, D.S. & Ankney, C.D. 1998. Predation risk and foraging behaviour: an experimental study of birds at feeders. *Can. Field Nat.* **112**: 668–675.

Götmark, F. & Post, P. 1996. Prey selection by Sparrowhawks, *Accipiter nisus*: relative predation risk for breeding passerine birds in relation to their size, ecology, and behavior. *Philos. Trans. R. Soc. Lond. B* **351**: 1559–1577.

Guillemain, M., Martin, G.R. & Fritz, H. 2002. Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). *Funct. Ecol.* **16**: 522–529.

Harkin, E.L., van Dongen, W.F.D., Herberstein, M.E. & Elgar, M.A. 2000. The influence of visual obstructions on the vigilance and escape behaviour of House Sparrows, *Passer domesticus*. *Aust. J. Zool.* **48**: 259–263.

Hart, N. 2001. Variation in cone photoreceptor abundance and the visual ecology of birds. *J. Comp. Physiol. A* **187**: 685–698.

Heesy, C.P. 2004. On the relationship between orbit orientation and binocular visual field overlap in mammals. *Anat. Rec. Part A* **281A**: 1104–1110.

Heesy, C.P. 2008. Ecomorphology of orbit orientation and the adaptive significance of binocular vision in primates and other mammals. *Brain Behav. Evol.* **71**: 54–67.

Hill, G.E. 1993. House Finch (*Carpodacus mexicanus*). In Poole, A. & Gill, F. (eds) *The Birds of North America*, No. 46. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Johnson, C.A., Giraldeau, L.-A. & Grant, J.W.A. 2001. The effect of handling time on interference among House Sparrows foraging at different seed densities. *Behaviour* **138**: 597–614.

Liker, A. & Barta, Z. 2002. The effects of dominance on social foraging tactic use in House Sparrows. *Behaviour* **139**: 1061–1076.

Lima, S.L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bull.* **105**: 1–47.

Lima, S.L. & Bednekoff, P.A. 1999. Back to the basis of anti-predatory vigilance: can nonvigilant animals detect attack? *Anim. Behav.* **58**: 537–543.

Lowther, P.E. & Cink, C.L. 2006. House Sparrow (*Passer domesticus*). In Poole, A. (ed.) *The Birds of North America Online*. Ithaca: Cornell Laboratory of Ornithology; Retrieved from The Birds of North American Online database: http://bna.birds.cornell.edu/BNA/account/House_Sparrow/

Martin, G.R. 1986. The eye of a passeriform bird, the European Starling *Sturnus vulgaris*: eye movement amplitude, visual fields and schematic optics. *J. Comp. Physiol.* **159**: 545–547.

Martin, G.R. 2007. Visual fields and their functions in birds. *J. Ornithol.* **148**: S547–562.

Martin, G.R. & Katzir, G. 1999. Visual fields in Short-toed Eagles *Circaetus gallicus* and the function of binocularity in birds. *Brain Behav. Evol.* **53**: 55–66.

Martin, G.R., Jarrett, N. & Williams, M. 2007. Visual fields in Blue Ducks and Pink-eared Ducks: visual and tactile foraging. *Ibis* **149**: 112–120.

Martinoya, C., Le Houezec, J. & Bloch, S. 1984. Pigeon's eyes converge during feeding: evidence for frontal binocular fixation in a lateral-eyed bird. *Neurosci. Lett.* **45**: 335–339.

McVean, A. & Haddlesey, P. 1980. Vigilance schedules among House Sparrows *Passer domesticus*. *Ibis* **122**: 533–536.

Pulliam, H.R., Pyke, G.H. & Caraco, T. 1982. The scanning behaviour of Juncos: a game-theoretical approach. *J. Theor. Biol.* **95**: 89–103.

Shochat, E., Lerman, S.B., Katti, M. & Lewis, D.B. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artifical food patches. *Am. Nat.* **164**: 232–243.

Suhonen, J. 1993. Predation risk influences the use of foraging sites by tits. *Ecology* **74**: 1197–1203.

Ward, P. 1985. Why birds in flocks do not coordinate their vigilance periods. *J. Theor. Biol.* **114**: 383–385.

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