

# Visual coverage and scanning behavior in two corvid species: American crow and Western scrub jay

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**Abstract** Inter-specific differences in the configuration of avian visual fields and degree of eye/head movements have been associated with foraging and anti-predator behaviors. Our goal was to study visual fields, eye movements, and head movements in two species of corvids: American crow (*Corvus brachyrhynchos*) and Western scrub jay (*Aphelocoma californica*). American crows had wider binocular overlap, longer vertical binocular fields, narrower blind areas, and higher amplitude of eye movement than Western scrub jays. American crows can converge their eyes and see their own bill tip, which may facilitate using different foraging techniques (e.g., pecking, probing) and manufacturing and handling rudimentary tools. Western scrub jays had a higher head movement rate than American crows while on the ground, and the opposite between-species difference was found when individuals were perching. Faster head movements may enhance the ability to scan the environment, which may be related to a higher perceived risk of predation of Western scrub jays when on the ground, and American crows when perching. The visual field configura-

tion of these species appears influenced mostly by foraging techniques while their scanning behavior, by predation risk.

**Keywords** Binocular vision · Head movements · Visual fields · Eye movements · Corvids

## Introduction

Animals gather information using different sensory modalities. For visually guided organisms like birds, the amount of information available around the head depends on (a) the visual coverage given by the relative position of eyes in the skull (Martin 1993; McFadden 1994; Iwaniuk et al. 2008), and (b) the behaviors that enhance visual coverage by monitoring the surroundings, such as eye, head, and body movements (Friedman 1975; Wallman and Letelier 1993; Land 1999a). Increasing visual coverage allows individuals to quickly detect stimuli (e.g., food, predators, conspecifics, etc.) that may affect fitness components (e.g., escaping a predator attack, joining a flock in a food-rich patch, etc.).

The extent of the visual field is a measure of visual coverage, when eyes and head do not move. Establishing the visual field configuration involves measuring the volume of space around the bird's head from which visual information can be retrieved (i.e., binocular and lateral areas as opposed to blind areas, Martin 1993). The relative width of the binocular, lateral, and blind areas differs substantially between species (Martin 2007), and this variability has been associated with differences in prey type, foraging techniques, chick-feeding tactics, and anti-predator behavior (Martin 2009).

Birds have eye movements of different amplitudes, frequency, duration, and speed that vary between visual contexts

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(e.g., fixation vs. exploratory, Martinez-Conde and Macknik 2008; Voss and Bischof 2009). When evoked with stimuli, eye movements in birds can vary from no movement (e.g., Ostrich *Struthio camelus*, Martin and Katzir 1995; Antarctic prion *Pachyptila desolata*, Martin and Prince 2001) to up to 36° of movement (Southern Ground Hornbill *Bucorvus leadbeateri*, Martin and Coetzee 2004). Eye movements are usually greater around and below the bill (Martin 1986a; Martin and Katzir 1994), and have been implicated in the manipulation of prey items when eyes converge (Martin 2009). However, the degree of eye movements in birds is relatively less than that of head movements (Gioanni 1988). Head movements consist of changes in head position in different planes (pitch, yaw, and roll axes, Bischoff 1988; Maldonado et al. 1988). From an ecological perspective, variations in head movement rate and duration have been associated with predator scanning (Jones et al. 2007), different foraging strategies (Land 1999b; Gall and Fernández-Juricic 2010), ambient light intensity (Gall and Fernández-Juricic 2009), and monitoring kin (Griesser 2003) and conspecifics (Dawkins 2002).

Studying between-species variation in visual field configuration and eye/head movement behaviors can enhance our understanding of the evolutionary divergence of avian visual systems, particularly in phylogenetically related species. However, relatively little attention has been devoted to between-species differences in visual coverage in Passeriformes despite their high degree of ecological diversity. Only five species of Passeriformes have had their visual fields described to date: European starlings, house sparrows, house finches, brown-headed cowbirds, and black phoebes (Martin 1986a, b; Fernández-Juricic et al. 2008; Blackwell et al. 2009; Gall and Fernández-Juricic 2010). Most of these species have a high degree of eye movement, medium-to-large binocular fields, and a relatively wide degree of visual coverage around their heads.

Our goal in this study was to determine the extent of the between-species differences in visual field configuration, eye movements, and head movements in two species of corvids: American crow (*Corvus brachyrhynchos*) and Western scrub jay (*Aphelocoma californica*). Corvids have been used as model species for understanding the evolution of various behaviors (caching, sociality, deception, tool use, Emery and Clayton 2004; Bluff et al. 2007; Clayton et al. 2007; Emery et al. 2007); however, we know little about how their visual systems gather information.

Foraging behavior can affect substantially visual field configuration (Martin 2007). Our study species are omnivorous and feed on the ground and in trees/shrubs, but differ in mean body size (American crows, 506 g; Western scrub jays, 89 g). American crows show a broader variety of foraging techniques, even using rudimentary tools (Verbeek and Caffrey 2002), than Western scrub jays, which are scat-

ter-hoarders for most of the year (Curry et al. 2002). We predicted that American crows would have a wider binocular area and greater degree of eye movement than Western scrub jays to allow for more eye convergence to control bill position while manipulating different prey types or even tools (Martin 2009). We predicted that head movements would vary between species based on perceived risk of predation. A recent study found that chaffinches (*Fringilla coelebs*) increase their rate of sideways head movements after detecting a predator (Jones et al. 2007). Adult American crows are mainly preyed upon by aerial predators (Verbeek and Caffrey 2002), whereas Western scrub jays by both aerial and ground predators (Curry et al. 2002). Therefore, we predicted higher rate of head movement when Western scrub jays would be on the ground and when American crows would be perching on top of the canopy due to between-species differences in risk perception in different micro-habitats. Perceived predation risk may be lower for perching Western scrub jays, as they perch at middle or lower canopy levels which may increase their concealment. Perceived risk may be higher for American crows when perching on top of trees due to greater exposure.

First, we characterized the width and vertical extent of the binocular field, the width of the blind area at the rear of the head, and the degree of eye movement. Second, we compared the rate of head movements and the interval duration between consecutive head movements in two scanning contexts: individuals perching and individuals on the ground. The rate of head movement gives an indication of how frequently an individual shifts its visual fields to (a) enhance visual coverage and facilitate detection of an object (e.g., prey item, predator, Dunlap and Mowrer 1930), (b) estimate the distance of the object in relation to the observer (motion parallax, Kral 2003), and (c) explore an object with different eyes or parts of the retina which may differ in visual capacity (Dawkins 2002; Templeton and Gonzalez 2004). We also measured the interval duration between consecutive head movements, as it indicates the time a given head position is maintained, which may allow individuals to fixate the object on the fovea or *area centralis* to facilitate perceptual accuracy (Wallman and Pettigrew 1985; Maldonado et al. 1988).

## Methods

### Visual fields and eye movements

American crows and Western scrub jays were obtained with the cooperation of the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (USDA-APHIS) Wildlife Services. Agency personnel caught the individuals from a number of locations in Los Angeles County, CA

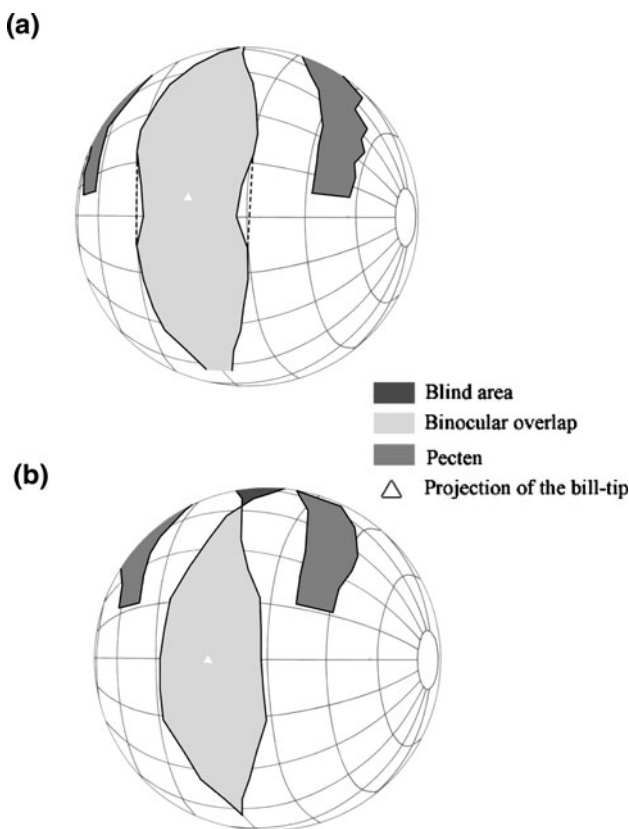
(Federal Fish and Wildlife Permit #MB004760-0). After capture, individuals were brought to the lab for less than 2 h to measure their visual fields in collaboration with USDA-APHIS personnel, and later transported to state-approved facilities for relocation.

Measurements were taken using a visual field apparatus (Martin 1984). Individuals were restrained in the center of the apparatus with their bodies in a horizontal position. Bills were positioned in wire-based beak holders and the head held at the angle birds naturally assume, based on pictures of perching individuals (American crows, 80°; Western scrub jays, 90°; the elevations at which the bill projected into the visual field can be seen in Figs. 1, 2, 3). We measured the retinal visual field using the ophthalmoscopic reflex technique (Martin 1984). We calculated the visual fields using an angular coordinate system. The head of the bird lay at the center of a space defined as a globe, and the horizontal axis of the globe projected through both eyes. The 0° elevation lay directly above the head of the bird, and elevations increased in 10° increments around the bird, such that 90° lay directly in front of the bird’s head,

and 270° lay directly behind the bird’s head at the horizontal plane (see example of this coordinate system in Fig. 4).

Using a Keeler Professional ophthalmoscope, we measured the projections of the retinal margins of each eye at each elevation in 10° increments, to an accuracy of ±0.5°. We were only able to obtain measurements on the retinal margins in elevations ranging from 150 to 270° (from below the bill to the back of the head, Fig. 4) due to obstructions of the apparatus or the animal’s body. We measured visual fields with two different methods: (1) when eyes were at rest, and (2) when eyes converged toward the bill tip and when eyes diverged so that they projected more laterally. Some individuals were exposed to a single method, but some to both; thus, sample size varied between methods.

In the first method, we measured the visual fields of 10 American crows and 4 Western scrub jays when an individual’s eyes were not visibly tracking the motion of the ophthalmoscope. We also measured the projection of the pecten, a vascular structure in the retina that projects a blind region into the visual field (Meyer 1977). In the second method, we elicited eye movements with sounds and/or flashes of light directed at the front or rear of the individual’s head. When the eyes converged to the bill or diverged toward the rear of the head, we recorded the maximum and minimum positions of the retinal field margins of nine American crows and four Western scrub jays. The difference between maximum and minimum positions represented the amplitude of eye movement at a particular elevation. We also calculated the maximum and minimum width of the binocular, lateral, and blind areas. The lateral field (monocular field–binocular field) was calculated as:  $(360 - (\text{mean blind field} + \text{mean binocular field})/2)$  following Fernández-Juricic et al. (2008). We presented the information on the visual fields of these species based on the aforementioned assumptions (Figs. 1, 3) and on averages across individuals (Fig. 2) taking into account the degree of between-individual variability at each elevation. The latter data were used for statistical analyses.

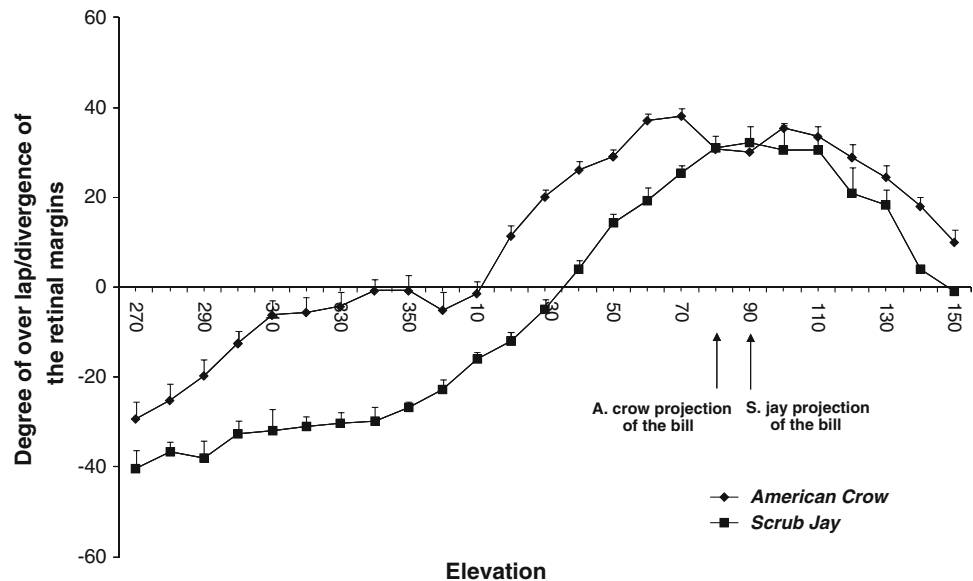


**Fig. 1** Orthographic projection of the boundaries of the retinal fields of the two eyes, along with projection of the pectens and bill-tips of **a** American crows and **b** scrub jays. A latitude and longitude coordinate system was used with the equator aligned vertically in the median sagittal plane. The bird’s head is imagined to be at the center of the globe (grid is at approximately 20° intervals)

### Head movements

We recorded videos of American crows and Western scrub jays in rural and suburban areas in Los Angeles and Orange Counties, California between June and August 2008 using a Sony Handycam DCR-HC36 between 0600 and 1500 hours in October to November 2008. We searched for individuals in their preferred habitats (Curry et al. 2002; Verbeek and Caffrey 2002). We avoided the possibility of re-sampling the same individual by moving at least 500 m in the opposite direction of the flying path of the bird that was videotaped. Directly after video recording had been completed, we measured ambient temperature, group size, distance

**Fig. 2** Average ( $\pm$ SE) angular separation of the retinal field margins as a function of elevation in the median sagittal plane in American crows and scrub jays. The width of the binocular area is indicated by positive values of overlap of the visual field margins; whereas the width of the blind area is indicated by negative values. The horizontal plane is represented by  $90^\circ$  (front of the head) to  $270^\circ$  (back of the head), with  $0^\circ$  indicating a position above the head. Arrows indicate projection of the bill-tips



between the observer and the bird, and between the bird and the nearest shrub/tree. We measured these variables because they are potential confounding factors that could influence vigilance behavior of individual birds (e.g., Fernández-Juricic et al. 2007; Gall and Fernández-Juricic 2009; Valcarcel and Fernández-Juricic 2009). Temperature was measured with a Fisher thermometer and distances with a meter tape.

We obtained additional videos from the Macaulay Library Sound and Video Catalog (<http://animalbehaviorarchive.org>). We selected videos for analysis based on overall quality (length > 30 s), ensuring that head movements could be accurately identified. When multiple videos from the same bird were available, we used only the longest video clip. Videos that showed aggressive interactions between individuals, preening events, or were recorded under extreme weather conditions were not included in the analysis. Overall, we analyzed 63 videos in two positions: on the ground (American crow, 10 videos; Western scrub jays, 9 videos) and perching (American crow, 18 videos; Western scrub jays, 26 videos). These videos corresponded to different individuals.

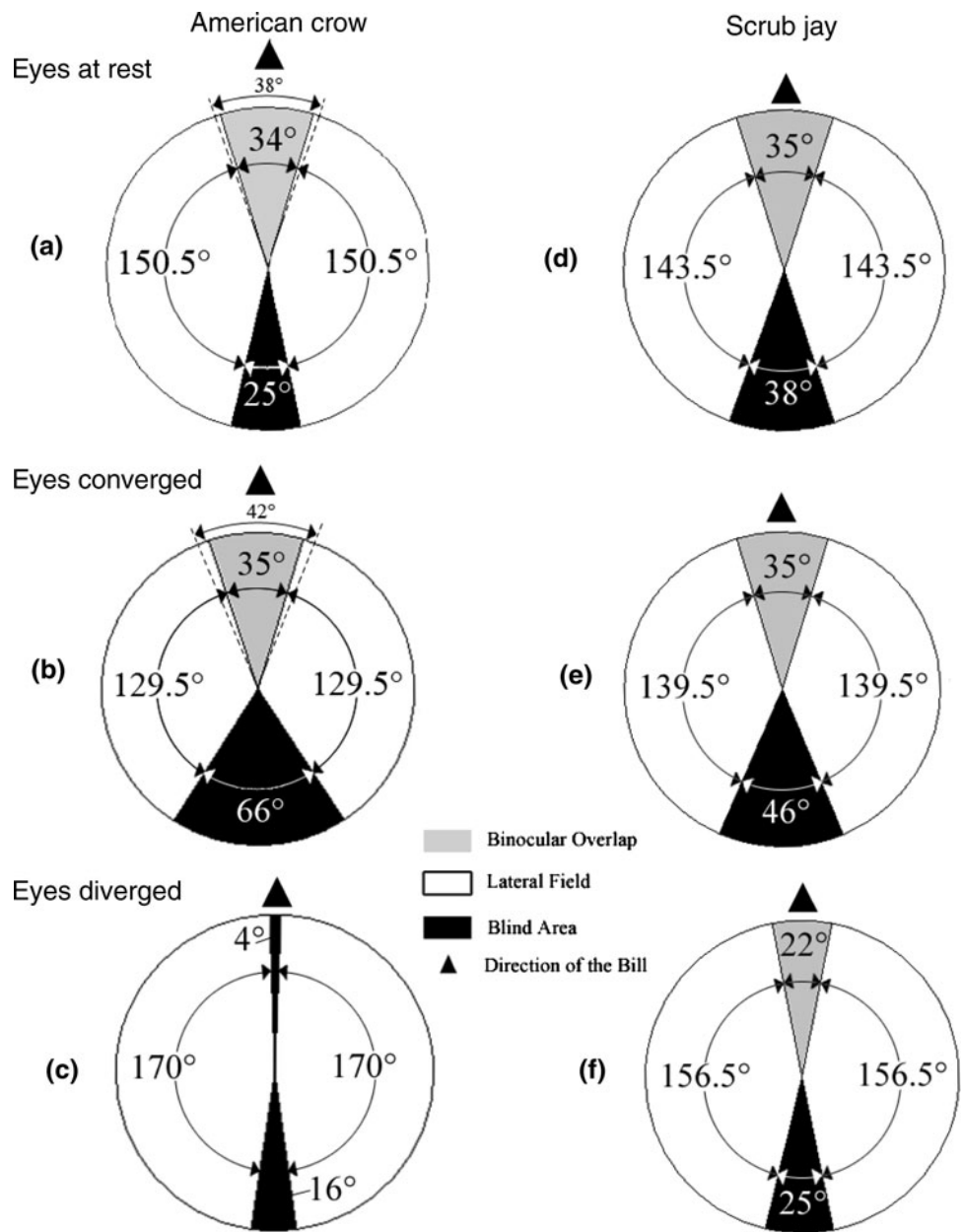
We recorded head movements with JWatcher (Blumstein and Daniel 2007) in two scenarios: when individuals were and were not walking/hopping. With this information, we calculated in each scenario the (a) rate of head movement (number of times the head moved about the pitch, yaw, and roll axes per min), and (b) interval duration between consecutive head movements (time in milliseconds that the head was stationary before the next head movement). We only obtained estimates of head movement rates and interval durations in the walking/hopping scenario when animals were on the ground.

#### Statistical analysis

We used general linear models to compare the width of the binocular field, blind area, and pecten, and the vertical extent of the binocular field, and degree of eye movements between species. Our models considered individual identity as a within-subject factor, and included species, elevation in the visual field, and the interaction between species and elevation. We only incorporated in the models those elevations from which we had data on either a positive (binocular area) or negative (blind area) overlap between eyes. Therefore, the averages presented did not include values from those elevations in which we did not record data.

General linear models were also used to assess the effects of species (American crow, Western scrub jay) and position (perched, on the ground) on head movement rates and interval duration between consecutive head movements. We ran analysis when individuals were stationary and when they walked/hopped (this latter scenario only included animals on the ground). We tested for between-species differences in head movement rate within each position with planned comparisons. With the videos recorded by ourselves, we assessed the effects of confounding factors (temperature, distance to nearest shrub/tree, distance between observer and bird, and group size) on head movement rates and interval duration between consecutive head movements. This analysis was not intended to establish between-species differences in predation risk, but the effect of confounding factors on scanning behavior within each species. We present means  $\pm$  SE in the figures, and means  $\pm$  SE and SD in the text.

**Fig. 3** Horizontal sections through the horizontal plane (90°–270°) showing the visual field configuration of American crows (a–c) and scrub jays (d–f). Charts represent the average retinal fields when the eyes were at rest (a, d), fully converged (eyes rotated fully forward, b, e), which maximizes the width of the binocular and blind areas, and fully diverged (eye rotated fully backward, c, f), which minimizes the width of the binocular and blind areas. The similarity in values of the binocular field of American crows (a, b) when eyes converged in relation to eyes at rest was due to the bill blocking the projections of the retinal field margins



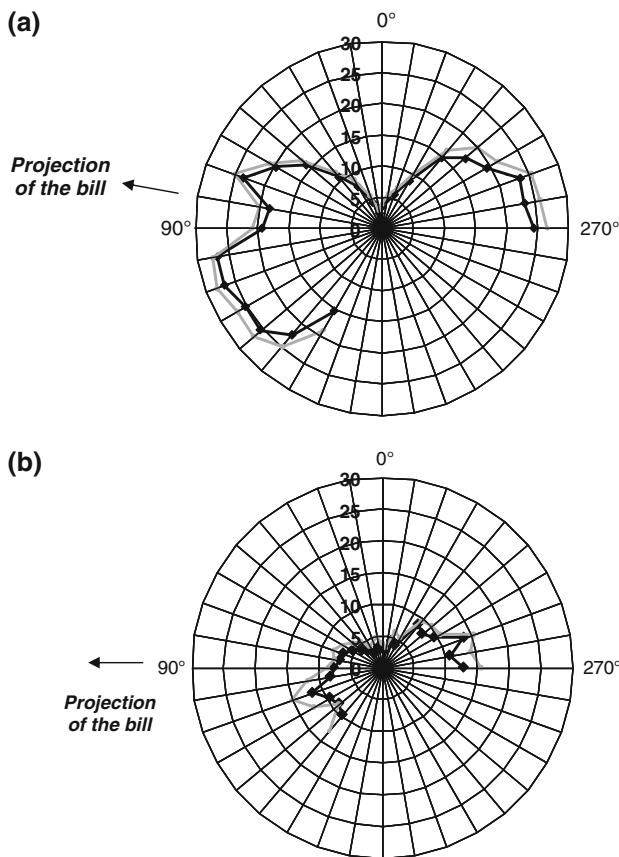
**Results**

At-rest visual fields

Three-dimensional representations of the at-rest visual fields show that both American crows and Western scrub jays had their bill-tips projecting within the binocular field (Fig. 1). The bill of the Western scrub jay projected into the visual field around the horizontal plane (90°), whereas that of the American crow projected slightly higher vertically (80°). The binocular field occupied a larger area in the American crow than in the Western scrub jay (Figs. 1, 2). The vertical extent of the binocular field differed significantly between species ( $F_{1,12} = 26.30, P < 0.001$ ; Figs. 1, 2),

being larger in the American crow (169.00, SE = 6.93°, SD = 24.69°) than in the Western scrub jay (102.50, SE = 10.96°, SD = 9.57°).

The maximum width of the binocular field occurred at elevation 70° (e.g., above the bill) in the American crow and at elevation 90° (e.g., in the eye-bill tip plane) in the Western scrub jay (Fig. 2). At elevation 90° with the eyes at rest, the width of the binocular field was similar in both species (Fig. 3a, d). However, in the American crow the bill intruded enough in the binocular area to block our view of the retinal margin, which suggests that individuals can observe their bill-tips (see also Martin and Coetzee 2004). The extrapolated width of the binocular field at elevation 90° at rest was estimated as 38° for American crows,



**Fig. 4** Average amplitude of eye movements (black line) as a function of elevation in the median sagittal plane in the **a** American crows (based on nine individuals), and **b** scrub jays (based on four individuals). The grey line indicates the SE of the average values in each elevation

assuming that the retinal margin follows a circular projection (Martin and Coetzee 2004).

Across all recorded elevations, the average width of the binocular field differed significantly between species ( $F_{1,12} = 86.20$ ,  $P < 0.001$ ), with American crows (22.69, SE = 0.54°, SD = 13.32°) having larger binocular fields than Western scrub jays (11.16, SE = 1.85°, SD = 11.75°). Besides a significant elevation effect ( $F_{21,170} = 31.78$ ,  $P < 0.001$ ), we also found that the width of the binocular field varied in different ways between species depending on elevation ( $F_{12,170} = 3.60$ ,  $P < 0.001$ ; Fig. 2).

At the 270° elevation (i.e., to rear of the head) with the eyes at rest, we found that the blind area was 13° wider in the Western scrub jay than in the American crow (Fig. 3a, d). Across all recorded elevations, the average width of the blind area varied significantly between species ( $F_{1,12} = 111.10$ ,  $P < 0.001$ ), with Western scrub jays (24.47, SE = 1.14°, SD = 10.89°) having a wider blind area than American crows (7.75, SE = 1.11°, SD = 11.05°). Additionally, we found significant differences in the width of the blind area at different elevations ( $F_{12,89} = 8.45$ ,  $P < 0.001$ ;

Fig. 2), but without a significant interaction between species and elevation ( $F_{10,89} = 1.05$ ,  $P = 0.407$ ). Across all elevations, Western scrub jays had a longer vertical extent of the blind area (from elevation 270 to 35°, including elevation 150°; Fig. 2) than American crows (from elevation 270 to 10°; Fig. 2).

The projection of the pecten extended longer vertically in the American crow than in the Western scrub jay (Fig. 1). Across elevations, the width of the pecten was significantly larger in the American crow (17.140, SE = 0.57°, SD = 5.21°) than in the Western scrub jay (12.07, SE = 1.06°, SD = 4.47°;  $F_{1,10} = 23.66$ ,  $P < 0.001$ ; Fig. 1). In both species, the width of the pecten varied significantly across elevations ( $F_{8,52} = 8.09$ ,  $P < 0.001$ ), with the highest averaged width at 10° in the American crow, and at 20° in the Western scrub jay. We did not find a significant interaction between species and elevation ( $F_{6,52} = 1.41$ ,  $P = 0.227$ ).

#### Degree of eye movement and visual fields

The average maximum amplitude of eye movement was recorded at elevation 110° in both species, being 56.6% lower in the Western scrub jay than in the American crow at that elevation (Fig. 4). Across elevations, the degree of eye movement was significantly higher in American crows (16.42, SE = 0.34°, SD = 9.23°) than in Western scrub jays (7.31, SE = 0.55°, SD = 4.56°;  $F_{1,11} = 262.63$ ,  $P < 0.001$ ). In both species, eye movements varied significantly across elevations ( $F_{24,250} = 15.51$ ,  $P < 0.001$ ; Fig. 4). Additionally, we found a significant interaction between species and elevation ( $F_{23,250} = 4.08$ ,  $P < 0.001$ ). In both species, the degree of eye movement was higher in the horizontal plane than above their head, particularly below the bill and at the back of the head (Fig. 4). However, eye movements were higher at elevation 70° (i.e., right above the bill) in American crows than in Western scrub jays (Fig. 4).

At the horizontal plane, eye movements modified the configuration of the visual fields in both species. When we elicited eye movements toward the front of the head (see “Methods”), American crows increased the width of the blind area by 164% in relation to the eyes-at-rest position (Fig. 3a, b); however, the binocular field did not change much (1°) in relation to the eyes-at-rest position because the bill blocked our view of the retinal margin (see above). The extrapolated width of the binocular field with converged eyes for American crows was estimated as 42°, assuming that the retinal margin follows a circular projection (Martin and Coetzee 2004). Western scrub jays did not vary substantially the width of binocular overlap at 90° when we elicited eye movements toward the front of the head in relation to the eyes-at-rest position (Fig. 3d, e). However, the width of the blind area increased by 21% in relation to the eyes-at-rest position (Fig. 3d, e).

When American crows diverged their eyes, the width of the binocular and blind areas decreased by 88 and 36%, respectively, compared to the eyes-at-rest position (Fig. 3a, c). Interestingly, American crows abolished the area of binocular overlap, generating a blind area of 4° in front of the bill when their eyes diverged (Fig. 3c). When Western scrub jays diverged their eyes, the width of the binocular and blind areas decreased by 37 and 34%, respectively, compared to the eyes-at-rest position (Fig. 3d, f).

### Head movement

With the video data we recorded in the field, we assessed the effects of potential confounding factors on head movement behavior within each species. We found that temperature, distance between the observer and the bird, distance to the nearest shrub/tree, and group size did not affect head movement rates (American crow,  $r$  varied from  $-0.31$  to  $0.23$ ; Western scrub jay,  $r$  varied from  $-0.22$  to  $0.32$ ;  $P > 0.05$ ) or the interval duration between consecutive head movements in these species (American crow,  $r$  varied from  $-0.29$  to  $-0.06$ ; Western scrub jay,  $r$  varied from  $-0.02$  to  $0.16$ ;  $P > 0.05$ ).

Head movement rate varied significantly between perched and on-ground positions ( $F_{1,59} = 46.94$ ,  $P < 0.001$ ), with no significant species effect ( $F_{1,59} = 0.43$ ,  $P = 0.516$ ). However, we found a significant interaction between position and species ( $F_{1,59} = 11.06$ ,  $P = 0.002$ ). When individuals were on the ground, Western scrub jays moved their heads at a significantly faster rate than American crows ( $F_{1,59} = 5.72$ ,  $P = 0.020$ ; Fig. 5). However, we found the opposite effect when animals were perching: head movement rate was significantly faster in American crows than in Western scrub jays ( $F_{1,59} = 5.80$ ,  $P = 0.019$ ; Fig. 5).

The interval duration between consecutive head movements varied significantly between positions ( $F_{1,59} = 17.84$ ,

$P < 0.001$ ), but without significant differences between species (American crow,  $807.10$ ,  $SE = 64.03$ ,  $SD = 280.58$  ms; Western scrub jay,  $852.86$ ,  $SE = 62.78$ ,  $SD = 425.37$  ms;  $F_{1,59} = 0.26$ ,  $P = 0.612$ ). The interaction between position and species was not significant ( $F_{1,59} = 1.46$ ,  $P = 0.231$ ).

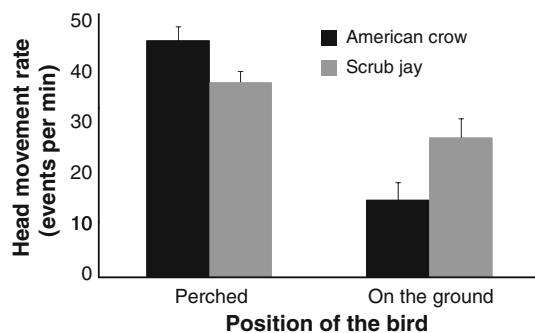
Finally, while individuals walked/hopped, we did not find significant differences between species in head movement rate (American crow,  $23.72$ ,  $SE = 4.22$ ,  $SD = 17.38$  events/min; Western scrub jay,  $19.91$ ,  $SE = 4.86$ ,  $SD = 9.51$  events/min;  $F_{1,19} = 0.35$ ,  $P = 0.561$ ) and in the interval duration between consecutive head movements (American crow,  $943.68$ ,  $SE = 156.09$ ,  $SD = 690.94$  millisecond; Western scrub jay,  $831.01$ ,  $SE = 180.23$ ,  $SD = 194.76$  millisecond;  $F_{1,19} = 0.23$ ,  $P = 0.642$ ).

### Discussion

We found differences in visual coverage and scanning behavior in two Passeriformes within the Corvidae family. Our results can be summarized as follows. American crows have wider and vertically longer binocular fields, narrower blind areas, and a greater degree of eye movement than Western scrub jays. Additionally, while head-up on the ground, Western scrub jays scanned with a higher rate of head movements than American crows. However, while head-up perching, American crows scanned with a higher rate of head movements than Western scrub jays.

Inter-specific differences in multiple behaviors have been reported within the Corvidae family; and some of these behaviors have been associated with variations in brain structure (e.g., food-caching behavior, Kamil et al. 1994; Basil et al. 1996; Lucas et al. 2004; episodic-like memory, Clayton and Dickinson 1998; Pravosudov and de Kort 2006). Additionally, Kulemeyer et al. (2009) studied variations in skull morphology in European corvids, and suggested a relationship between foraging behavior and size of the binocular fields. Based on the assumption that orbit convergence can be an indicator of the width of the binocular field (Iwaniuk et al. 2008), inter-specific differences in corvid foraging techniques were associated with changes in the width and vertical length of the binocular field and even the ability of some species to see their bill tips (Kulemeyer et al. 2009). Our findings provide physiological and behavioral evidence that at least two species of corvids vary in visual field configuration (including the parameters suggested by Kulemeyer et al. 2009) and strategies to gather visual information through head movements. We discuss the potential reasons behind these between-species differences in the following paragraphs.

In a recent paper, Martin (2009) proposed that binocular fields in birds are functionally different from those in mammals. Avian binocular fields may primarily provide



**Fig. 5** Variations in head movement rates (in different axes) between American crows and scrub jays when perched and when on the ground. This analysis was restricted to individuals that did not walk or hop when perched and while standing on the ground. All differences are significant (see text for details)

information to control bill position and timing of final approach to a visual target during foraging. The American crow may fit this profile, with an overall wider binocular field compared to the Western scrub jay. American crows obtain various food items (seeds, fruits, terrestrial and marine invertebrates, amphibians, reptiles, birds, mammals, eggs, refuse, carcasses, etc.) from the ground, trees, bushes, and water by both pecking and probing (Verbeek and Caffrey 2002). The combination of wider binocular fields and higher eye movement amplitude may provide a greater ability to gather visual information in front of the head in a broad variety of foraging substrates as well as handle food types with different shapes, sizes, and accessibility. This may ultimately enhance the foraging opportunities for American crows. On the other hand, Western scrub jays have a lower diversity of prey items in their diets (Curry et al. 2002), which may reduce visual demands. Interestingly, the between-species differences in the width of the binocular field were lower (around 3°) at 90° elevation. This suggests that Western scrub jays could enhance binocular overlap by placing objects right in front of the bill to fixate on them, whereas American crows would have greater flexibility in terms of bill placement in relation to a target object due to their wider binocular fields at other elevations.

American crows are able to observe their own bill-tips, which may be valuable for two reasons. First, they probe into the ground, much in the same way as the European starling *Sturnus vulgaris* does (Martin 1986a). Both species have large eye movement amplitude that allows for eye convergence and wider binocular areas (European starling, 36°, Martin 1986a; American crow, 42°, this study). Individuals that probe benefit from these visual properties because the bill pokes into the ground, opens up, and then eyes are swung forward to look for prey items between the mandibles (Martin 1986a). Second, American crows have been reported to use rudimentary tools and other natural objects for different purposes (Caffrey 2000, 2001). For instance, an individual was observed grabbing a piece of wood with its feet and then hammering it with its beak into a triangular shape to access a hole in a wooden post with a spider in it (Caffrey 2000). Convergent eye movements may allow American crows to bring central portions of the retina forward and inspect visually an object to manufacture a tool and manipulate it to target another object in the environment. It would be interesting to test this idea in other corvids that are known for tool use (e.g., New Caledonian crow *Corvus moneduloides*, Hunt 1996; Weir et al. 2002).

Western scrub jays neither probe nor use tools, which may reduce the need for binocular fields as wide as those of American crows. However, the binocular fields of Western scrub jays are indeed wider than those in other species that

do not use visually guided strategies in the pursuit of prey (e.g., mallard duck, *Anas platyrhynchos*, Martin 1986b; woodcocks *Scolopax rusticola*, Martin 1994). Thus, Western scrub jays are expected to use their binocular fields to visually manipulate food items (Terhune 1977; Langen and Gibson 1998) or the substrate used to cache food (Stulp et al. 2009).

On the other hand, Western scrub jays may not require as much eye movement amplitude as American crows do to manipulate their main passive food types (e.g., seeds). This interpretation assumes that differences in eye movement amplitude between species have implications for the use of visual cues while foraging. Actually, the Western scrub jay is the Passeriform with the lowest degree of eye movement (average 7°) reported to date, compared with American crows (average 16°, this study), European starlings (range 11°–32°, Martin 1986a), house sparrows (average 16°, Fernández-Juricic et al. 2008), house finches (average 11°, Fernández-Juricic et al. 2008), brown-headed cowbirds (average 19°, Blackwell et al. 2009), and black phoebes (average 11°, Gall and Fernández-Juricic 2010). Martin (2009) suggested that the reduced amplitude of eye movements in birds may be associated with relatively large eyes in relation to the size of the orbits. Whether the same proximate mechanism may account for variations in the degree of eye movement in Passeriformes needs to be further explored.

American crows and Western scrub jays also differed in the behavioral strategies to gather visual information through head movements. Western scrub jays had a higher head movement rate while on the ground than American crows. Western scrub jays live in dry wooded areas with oaks or piñon pines (Curry et al. 2002). Both ground (bobcat *Felis rufum*, house cat) and aerial (Cooper's hawk *Accipiter cooperii*, sharp-shinned hawk *Accipiter striatus*, great horned owl *Bubo virginianus*) predators attack adult scrub jays (Curry et al. 2002). Furthermore, Western scrub jays mob particularly ground predators (bobcats, house cats, squirrels, snakes, and humans; Curry et al. 2002). This evidence suggests that jays may perceive a slightly higher risk of predation on the ground than while perching in middle or lower canopy levels, leading to higher head movement rates, as found in chaffinches when exposed to a ground predator (Jones et al. 2007). Visual coverage is more constrained in Western scrub jays (e.g., wider blind area, shorter vertical extent of the binocular field, reduced eye movements), which may increase the need to compensate by moving the head more to scan the visual space in risky scenarios.

While perching, American crows had higher head movement rates than Western scrub jays. American crows have been described as “very alert and observant”, and they perch on top of the canopy in open habitats with scattered



trees (Verbeek and Caffrey 2002). Their wide visual coverage (long vertical binocular fields, narrow blind areas) may facilitate scanning for conspecifics from these exposed positions, as they show some levels of cooperative breeding, gather in pre-roosting aggregations before forming large roosting areas, and display sentinel behavior (Conner et al. 1975; Dagostino et al. 1981; Stouffer and Caccamise 1991; Moore and Switzer 1998; Verbeek and Caffrey 2002). However, exposure to predators increases while perching. For instance, adult American crows fall prey of mostly aerial predators (golden eagle *Aquila chrysaetos*, bald eagle *Haliaeetus leucocephalus*, Northern goshawk *Accipiter gentilis*, great horned owl, red-tailed hawk *Buteo jamaicensis*, sharp-shinned hawk, etc. Verbeek and Caffrey 2002). American crows also mob aerial predators (red-tailed hawk, common raven *Corvus corax*; Verbeek and Caffrey 2002). Therefore, American crows may have a higher perceived risk of predation while perching, leading to an increase in head movement rates.

In birds with laterally placed eyes, rapid head movements allow individuals to view an object with the right and left foveae in a short period of time, which may facilitate the detection of location and depth cues. For instance, black phoebes (*Sayornis nigricans*) increase their head movement rates when tracking a prey item from a perch right before launching an attack. Additionally, hens (*Gallus domesticus*) tend to move their heads at a faster pace when exposed to novel visual stimuli (Dawkins 2002). It is possible that American crows and Western scrub jays increased their head movements in risky scenarios to scan as many spots as possible in their visual space with their high acuity retinal areas. This could facilitate the early detection of and escape from predators (Tisdale and Fernández-Juricic 2009).

Comparing phylogenetically related species allows us to reduce the number of confounding factors that influence between-species differences in physiology and behavior; however, conclusions about the evolution of visual information gathering need to be taken with care because our sample size in this study consists of only two species. Future studies should assess whether there are different visual strategies related to foraging and anti-predator behaviors in corvids using several species and controlling for phylogenetic effects.

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