



Sensory basis of vigilance behavior in birds: Synthesis and future prospects

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ABSTRACT

Birds gather visual information through scanning behavior to make decisions relevant for survival (e.g., detecting predators and finding food). The goal of this study was (a) to review some visual properties involved in scanning behavior (retinal specialization for visual resolution and motion detection, visual acuity, and size of the blind area), and (b) hypothesize how the inter-specific variability in these properties may lead to different scanning strategies. The avian visual system has a high degree of heterogeneity in visual performance across the visual field, with some sectors providing higher levels of visual resolution and motion detection (e.g., retinal specializations) than others (e.g., peripheral retina and blind area). Thus, information quality will vary in different parts of the visual field, which contradicts some theoretical assumptions on information gathering. Birds need to move their eyes and heads to align the retinal specializations to different sectors of visual space. The rates of eye and head movements can then be used as proxies for scanning strategies. I propose specific predictions as to how each of the visual properties studied can affect scanning strategies in the context of predator detection in different habitat types and with different levels of predation risk. Establishing the degree of association between sensory specializations and scanning strategies can enhance our understanding of the evolution of anti-predator behavior.

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1. Introduction

Animals are continuously gathering information through their sensory systems to make decisions that are relevant for their survival and reproduction. Avoiding predation is a key component of survival that hinges upon early detection of predators. In visually guided organisms like birds, scanning (also known as vigilance) is the behavioral process by which animals gather visual information (e.g., movement of leaves in a tree, a raptor flying around, and a group mate escaping) that could be indicative of a threat.

Behavioral ecologists have associated scanning with various aspects of anti-predator behavior from both theoretical and empirical perspectives, such as perceived predation risk, vigilance strategies, predator detection, and micro-habitat use (Lima, 1990, 1998; Lima and Dill, 1990; Krause and Ruxton, 2002; Caro, 2005; Cresswell, 2008). Scanning has been usually measured as changes in body position (Caro, 2005). For instance, in birds, it has been assumed that when individuals are head-up, they can obtain information through scanning, but when they are head-down (seeking food, pecking), they cannot obtain any visual information (Lima, 1987). This mutual exclusivity assumption between scanning and foraging has been challenged theoretically and empirically a few

times (reviewed in Fernández-Juricic et al., 2004a). The basic argument against this assumption is that many bird species have laterally placed eyes, which widen their fields of view (Martin, 2007; Fernández-Juricic et al., 2008) to the extent that they can gather information laterally even when their heads are down (Bednekoff and Lima, 2005; Fernández-Juricic et al., 2005). This has important fitness implications because predator detection probabilities when head-down have been estimated as approximately 30% (Lima and Bednekoff, 1999; Tisdale and Fernández-Juricic, 2009), but not 0% as proposed by the mutual exclusivity assumption.

However, what happens when birds are head-up scanning, supposedly gathering 100% information? Does the quality of head-up scanning vary? If so, what are the factors influencing scanning quality? At least theoretically, behavioral ecologists have assumed that animals gather high quality information all around their heads when in vigilance postures (Fernández-Juricic et al., 2004a). So, it is assumed that birds can see 360° around their heads and obtain high quality information throughout their visual fields. However, this assumption does not reflect the complexity and diversity of the sensory system (Dangles et al., 2009). To address these questions for birds, it is important to examine the configuration of the peripheral visual system, as it is the sensory window that is expected to affect scanning and thus the ability to detect predators.

The goal of this study is to review some sensory components of the avian visual system that are involved in scanning behavior,

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and hypothesize how the variability in these factors may affect scanning strategies when animals are in vigilant postures (e.g., head-up). I synthesize information on four visual properties: (1) area of high resolution in the visual field, (2) density and distribution of cells associated with motion detection, (3) visual acuity, and (4) size of the blind area at the rear of the head. I propose specific predictions as to how these visual properties can influence scanning strategies considering new proxies of scanning behavior (head movement rates), and discuss the potential effects of habitat complexity and predation risk on these vision–scanning relationships. Birds are excellent study species to assess the relationship between sensory systems and behavior at the comparative level because of their complex visual systems (Meyer, 1977; Cuthill, 2006; Martin and Osorio, 2008) and diverse antipredator strategies (Lima, 1993; Caro, 2005; Beauchamp, 2010).

2. Visual sensory properties in birds

In the context of anti-predator behavior, prey are expected to follow a series of steps to reduce the chances of mortality in the event of a predator attack: (1) scan the environment through *visual search*, (2) detect the predator, (3) identify the predator right after detection, (4) track it visually, and (5) change behavior to reduce visibility and/or escape (Lima and Dill, 1990; Cronin, 2005). These steps require gathering visual information over a short period of time to make quick decisions on strategies to avoid predation (Hemmi and Zeil, 2005). The visual information prey gather can be of a single type (e.g., motion) or multiple types (e.g., motion and variations in visual contrast). Antipredator behavior theory does not explicitly consider these *multiple* sources of visual information, which are generally associated with specific properties of the sensory system. In this study, I mostly focus on the first step, visual search when animals are in vigilant body postures (e.g., head-up), which is represented by monitoring the environment when no predator is visible in the visual field of the animal. Avian species

with laterally placed eyes have a relatively wide visual coverage due to the degree to which their lateral visual fields extend to the rear of the head (Fig. 1). The *limits* of the visual fields are determined by the projections of the edges of the retina of each eye into visual space (Fig. 1). Visual resolution within the wide avian visual field is influenced by the photoreceptors and retinal ganglion cells which occupy different layers in the retina. Phototransduction (the conversion of photons into electrical energy) takes place in the photoreceptors (cones and rods; McIlwain, 1996). This visual information is ultimately transferred from the retina to the visual centers of the brain through the retinal ganglion cells that form the optic axis (McIlwain, 1996). The retinal ganglion cells act as a visual information bottleneck, because they determine the upper levels of visual resolution of the visual system (Collin, 1999).

One measure of visual information quality is visual resolution: the sharper the image, the higher the quality of information. Within the retina, visual resolution is determined by the density of photoreceptors and retinal ganglion cells, which is not homogeneous across the retina (e.g., Querubin et al., 2009). In general, sectors within the retina with a higher density of photoreceptors and/or retinal ganglion cells have higher visual performance than sectors with lower cell density (Wyszecki and Stiles, 1982). Consequently, the quality of information gathered is expected to differ across the retina, and hence across the projection of the retina into the visual field (Fig. 1).

Most of the retina will provide relatively low quality information (i.e., low visual resolution) due to the relatively low density of photoreceptors and retinal ganglion cells (Fig. 1). The exception is the spot in the retina with the highest density of photoreceptors and ganglion cells, which will provide high quality information (i.e., high visual resolution; Fig. 1; Walls, 1942; Meyer, 1977). This high acuity spot is known as the *retinal specialization*. The projection of the retinal specialization is expected to take up a small portion of the whole visual field (Fig. 1).

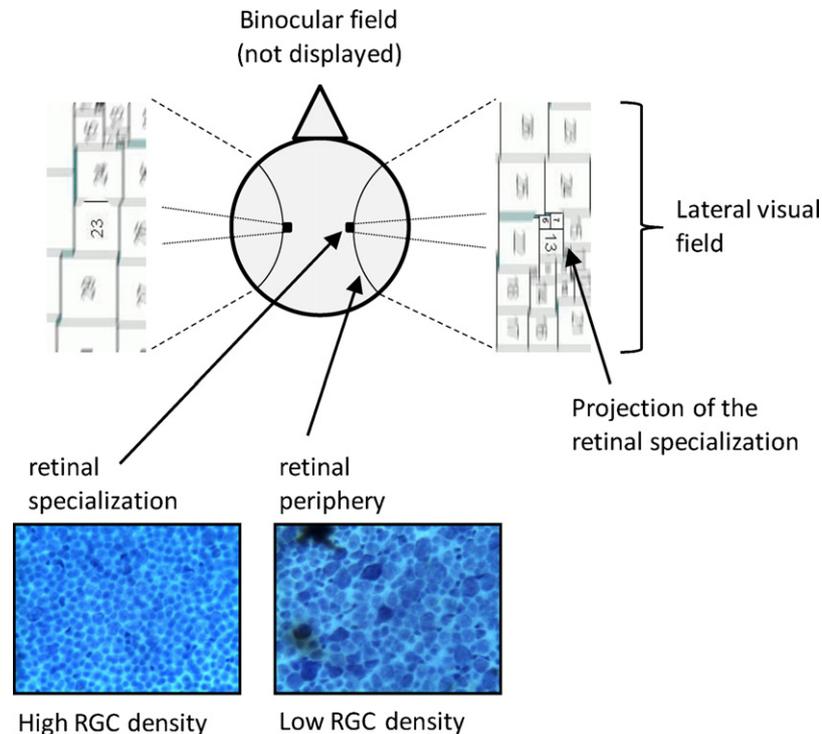


Fig. 1. Schematic representation of the projection of a central retinal specialization into the two lateral visual fields at a given head and eye position. The projection of the binocular field is not shown for clarity. The figures with numbers represent the visual scenes perceived by each eye. Visual resolution is the highest at the retinal specialization, but decreases towards the retinal periphery (e.g., blurred vision) due to lower density of photoreceptors and retinal ganglion cells (RGC).

Table 1

Some bird species whose retinal configurations have been described through topographic maps of the retinal ganglion cell layer. The type of retinal specialization is indicated as: F, fovea; VS, visual streak; Ar, area. Five species have been shown to have two specializations in their retinas. Most of the retinal topographic maps are available from the following database: <http://www.retinalmaps.com.au/> (Collin, 2008).

Order	Scientific name	Common name	RS	References
Galliformes	<i>Pavo cristatus</i>	Peafowl	Ar	Hart (2002)
Ciconiiformes	<i>Coragyps atratus</i>	Black Vulture	F	Inzunza et al. (1991)
Ciconiiformes	<i>Gymnogyps californianus</i>	Condor	F	Inzunza et al. (1991)
Columbiformes	<i>Zenaidura macroura</i>	Mourning Dove	F	Dolan and Fernández-Juricic (2010)
Falconiformes	<i>Milvago chimango</i>	Chimango Caracara	F	Inzunza et al. (1991)
Passeriformes	<i>Molothrus ater</i>	Brown-headed Cowbird	F	Dolan and Fernández-Juricic (2010)
Passeriformes	<i>Pipilo crissalis</i>	California Towhee	F	Fernández-Juricic et al. (2011a)
Passeriformes	<i>Sturnus vulgaris</i>	European Starling	F	Dolan and Fernández-Juricic (2010)
Passeriformes	<i>Carpodacus mexicanus</i>	House Finch	F	Dolan and Fernández-Juricic (2010)
Passeriformes	<i>Passer domesticus</i>	House Sparrow	F	Dolan and Fernández-Juricic (2010)
Passeriformes	<i>Zonotrichia leucophrys</i>	White-crowned Sparrow	F	Fernández-Juricic et al. (2011a)
Falconiformes	<i>Falco sparverius</i>	American Kestrel	F/F	Inzunza et al. (1991)
Falconiformes	<i>Buteo fuscens australis</i>	Chilean Eagle	F/F	Inzunza et al. (1991)
Columbiformes	<i>Columba livia</i>	Rock Pigeon	F/Ar	Binggeli and Paule (1969)
Passeriformes	<i>Pitangus sulphuratus</i>	Great Kiskadee	F/Ar	Coimbra et al. (2006)
Passeriformes	<i>Myiozetetes cayanensis</i>	Rusty-margined Flycatcher	F/Ar	Coimbra et al. (2006)
Anseriformes	<i>Branta canadensis</i>	Canada Goose	VS	Fernández-Juricic et al. (2011c)
Procellariiformes	<i>Puffinus puffinus</i>	Manx Shearwater	VS	Hayes et al. (1991)
Strigiformes	<i>Tyto alba</i>	Barn Owl	VS	Bravo and Pettigrew (1981)

There are different types of retinal specializations, such as the fovea (pitted invagination of the retinal tissue), *area* (concentric increase in photoreceptor/retinal ganglion cell density without invagination of the retinal tissue), and visual streak (band-like *area* extending across the retina) (Meyer, 1977). Retinal specializations occur in different numbers and positions in the retina (Collin, 1999). In this study, I focus only on avian species with laterally placed eyes and a single centrally located fovea projecting into the lateral visual field (Fig. 1). This retinal configuration is relatively common in birds, particularly Passeriformes (Table 1). Of a sample of the bird species whose type of retinal specialization has been described through topographic maps of the retinal ganglion cell layer, approximately half have been found to possess a single fovea (Table 1). Species with this visual configuration detect predators and track their position and speed with high accuracy using their lateral rather than their binocular visual fields (Devereux et al., 2006). This is because the central visual axis of the fovea projects laterally due to the position of the orbits in the skull (Fig. 1).

Besides increasing visual resolution, the fovea has been proposed to be involved in reducing light scattering (Martin, 1986), facilitating image magnification (Walls, 1942) and image fixation and exaggeration of small movements (Pumphrey, 1948), and providing a directional focus indicator (Harkness and Bennet-Clark, 1978). At the center of the fovea, the ganglion cell, inner plexiform, and nuclear retinal layers may be displaced radially, giving rise to an invagination of the retinal tissue and a foveal pit (Fig. 2; Pumphrey, 1948; Meyer, 1977; Ruggeri et al., 2010). Foveae of different bird species differ in the depth of the foveal pit from shallow (concaviclivate fovea) to deep (convexiclivate fovea; Fig. 2; Walls, 1937; Pumphrey, 1948). From a morphological perspective, the deeper the foveal pit, the narrower its width (Fig. 2; Fite and Rosenfield-Wessels, 1975). This between-species difference in the depth and width of the foveal pit could potentially have important implications for scanning (see Section 4), because of differences in the area with the highest resolution in the visual field that can be covered per unit time as the animal moves its head and/or eyes (Fig. 2). Deep foveae have narrow foveal pits and thus are expected to have a relatively small area with the highest resolution in the visual field (Fig. 2). On the other hand, shallow foveae have wide foveal pits and are expected to have a relatively larger area with the highest resolution in the visual field (Fig. 2). The local visual resolution at the level of the retinal specialization is expected to be lower in species with shallow than those with deep foveae (Walls, 1942), assuming

similar eye size and cell packing. Nevertheless, the argument of the differences in the proportional area of the visual field with the highest visual resolution may still hold from the perceptual perspective of each species.

The ability to sense motion and variations in achromatic contrast in a scene can also influence scanning behavior (Cronin, 2005). Generally, predators increase the chances of successfully taking prey when attacking by surprise. Therefore, prey may benefit by having visual systems with high sensitivity to stimuli moving against the background that can be discriminated in a very short period of time (Levin, 1997; Jablonski and Strausfeld, 2000). Motion sensitive neurons can estimate the time remaining before collision with an object (Rind and Simmons, 1999; Xiao et al., 2006) based on a hierarchical system of cues, such as, changes in the rate of increase in size and complexity of the moving object (Carlike et al., 2006). Birds have a good ability to perceive motion (Dittrich and Lea, 2001), which is mostly an achromatic visual task (Osorio et al., 1999; Burton, 2000). Achromatic cues arise when visual targets vary in light intensity but not in spectral composition, whereas chromatic cues arise when visual targets vary in the spectra they reflect.

The detection of motion and achromatic cues in the avian retina has been associated with a type of photoreceptor called *double cone* through both physiological (von Campenhausen and Kirschfeld, 1998) and behavioral (Goldsmith and Butler, 2003, 2005) studies, although there is still debate about the ultimate function of double cones (Bennett and Théry, 2007). Double cones have principal and accessory members with broad spectral sensitivity (Bowmaker et al., 1997; Osorio and Vorobyev, 2005; Hart and Hunt, 2007). Double cones are abundant in the avian retina (25–50% of all cones), and interspecific variations in their *density* and *distribution* can be proxies of the ability to detect cues related to predator attacks (Hart, 2001).

Visual acuity, which is the ability to resolve fine details such as distinguishing between two closely spaced stimuli (McIlwain, 1996), is another visual property involved in predator detection. Inter-specific variation in prey's overall visual acuity (as opposed to the local visual resolution provided by the retinal specialization) can influence the distance at which predators are detected (Tisdale and Fernández-Juricic, 2009). In general, larger eyes project a larger image on the retina that is spread over a larger number of photoreceptors that transfer the information to the retinal ganglion cells (Land and Nilsson, 2002), ultimately increasing visual acuity. Larger bird species have larger eyes (Howland et al., 2004; Burton, 2008),

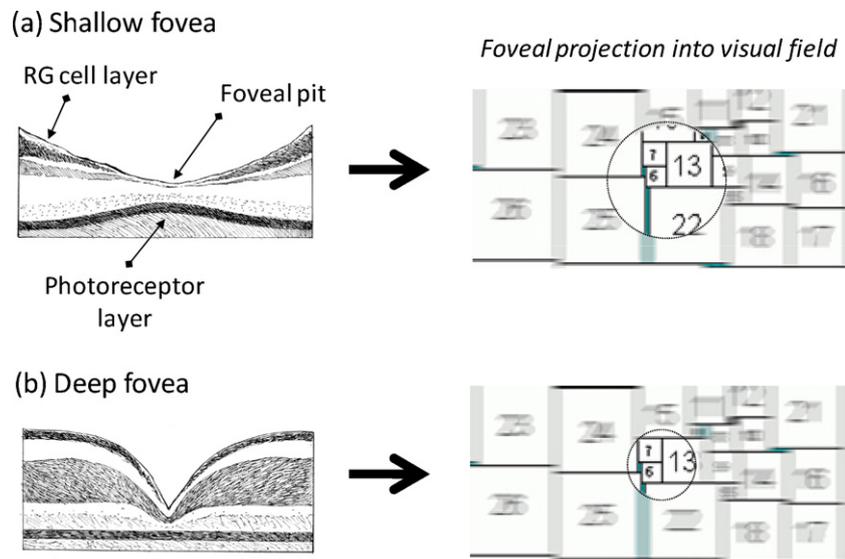


Fig. 2. Schematic representation of the cross section of the fovea, showing (a) shallow and (b) deep foveae, and their proposed projection into the visual field as areas of high visual resolution based on the width of the foveal pit (see text for details).

and thus higher visual acuity (Kiltie, 2000). Besides eye size, overall visual acuity also increases with the density of photoreceptors and ganglion cells in the retina (Land and Nilsson, 2002). There are other factors that can affect visual acuity (corneal diameter, aberration, diffraction, light intensity, etc.); however, they are not likely to vary much in diurnal birds as they are not limited by sensitivity to ambient light and have similar eye shapes (Martin, 1993; Hall and Ross, 2006).

The position of eyes in the skull can influence the width of the blind area at the rear of the head (Martin, 2007). Species with more frontally placed eyes tend to have wider blind areas, and consequently less visual coverage at any given head position (Iwaniuk et al., 2008). Species with wider blind areas spent more time in head-up positions probably to compensate for the lack of visual coverage (Guillemain et al., 2002). Additionally, predator detection is delayed when the attacker's approach is in the prey's blind area rather than in their lateral visual fields (Kaby and Lind, 2003; Devereux et al., 2006).

There is empirical evidence on the degree of interspecific variability in the type of retinal specialization (Meyer, 1977; Collin, 1999), density and distribution of double cones (Hart, 2001), visual acuity (Kiltie, 2000), and size of the blind area (Martin, 2007) in avian species living in different habitats. Other visual properties can also affect predator detection (e.g., contrast sensitivity and temporal visual resolution). For instance, temporal visual resolution, the speed with which visual stimuli are processed in the retina, may influence the delay in detecting predator attacks. However, we know relatively less about the degree of inter-specific variability in these other visual properties (e.g., Lisney et al., 2011). By focusing on the aforementioned four visual properties in anti-predator contexts, my intention is to provide a conceptual framework on how visual configuration can influence scanning behavior. This framework can be expanded in the future by including other visual components.

3. Scanning strategies

As mentioned above, behavioral ecologists have used the proportion of time individuals spent in head-up positions and the rate at which individuals interrupt foraging bouts to monitor the surroundings as proxies for scanning behavior (Caro, 2005). However,

these metrics have limited value to measure the quality of scanning while birds are in vigilant positions.

From the review on the four visual sensory components, it can be concluded that the theoretical assumptions described in Section 1 as to how birds gather visual information while head-up do not reflect the configuration of the avian visual system. First, most bird species cannot see 360° around their heads due to the presence of a blind area. Second, the visual field is heterogeneous in terms of visual performance. Some sectors of the visual field provide high visual performance (i.e., retinal specialization associated with high visual resolution, areas with high density of double cones associated with motion detection) and other sectors provide low visual performance (i.e., retinal periphery with low visual resolution, blind area at the rear of the head). Consequently, the areas of the visual field that provide high quality information are limited. Birds are expected to use these sectors of high visual performance to search for objects of interest (e.g., predators, food, and conspecifics) in the visual space and, once found, align these sectors to the objects and track them.

The means to obtain this high quality information with the retinal specializations in bird species with laterally placed eyes is to move the eyes and the head (Lemeignan et al., 1992; Dawkins and Woodington, 2000; Dawkins, 2002; Moinard et al., 2005; Fig. 3). In birds, head movements are usually more frequent and of greater amplitude than eye movements (Gioanni, 1988; Haque and Dickman, 2005), since the eyes fit tightly in the orbit, limiting their movement to a large degree (Jones et al., 2007a). However, it is necessary to consider the role of eye movements in information gathering because they can change the size of the blind areas substantially (i.e., when individuals converge and diverge their eyes towards and away from the bills, respectively; Fig. 3), thereby affecting visual coverage (Fernández-Juricic et al., 2008, 2010).

The study of scanning behavior in antipredator contexts using eye and head movements has been relatively limited in the behavioral ecology literature (but see Jones et al., 2007b, 2009). One of the reasons is methodological, as it is easier to record changes in body posture (head-up vs. head down) than changes in eye or head positions. Jones et al. (2007b) proposed the use of head movement rates (changes in head position per unit time while head-up) to study scanning behavior, but specific sensory hypotheses have yet to be put forward to make predictions about variations in head movement behavior in different contexts.

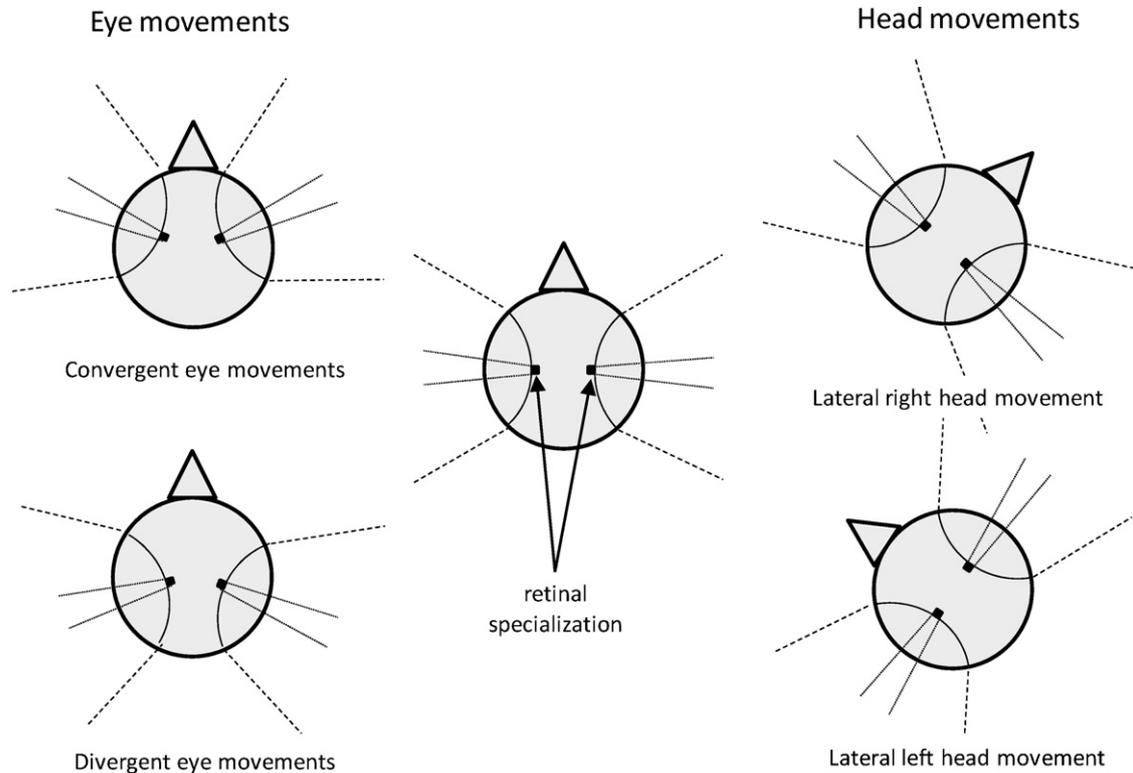


Fig. 3. Schematic representation of how the projections of the retinal specialization (foveae) into the lateral visual fields change as birds with laterally placed eyes move their heads laterally (to the right and left) and their eyes towards (convergent eye movements) and away (divergent eye movements) from the bill. The projection of the retinal specialization in visual space provides high quality information due to high visual resolution. The projection of the binocular field is not shown for clarity. This graphical representation follows the nomenclature of Fig. 1.

I propose that changes in both eye movements and head movements can be proxies for scanning strategies in birds. Individuals engage in two main visual tasks: visual search and visual tracking. In a visual search task, individuals vary the position of the retinal specialization to increase visual coverage with high visual resolution around visual space (Dunlap and Mowrer, 1930; Friedman, 1975; Fernández-Juricic et al., 2010). Scanning during visual search includes fast saccadic eye and/or head movements interspersed with short fixation periods (Land, 1999). In a visual tracking task, individuals expose the retinal specialization towards objects of interest that require to be sampled with high resolution (Bloch et al., 1984; Maldonado et al., 1988). Scanning during visual tracking includes saccadic eye and/or head movements combined with relatively longer fixation periods (Land, 1999). At least theoretically, during visual search animals do not focus for a long time on a given sector of the visual space; they literally scan their surroundings for the presence of objects of interest. During visual tracking, visual attention is focused on an object of interest (whether it moves or not) for a relatively longer period of time. Therefore, we can expect patterns of eye and head movement to be different between these two visual tasks.

Visual search is expected to generate relatively quick changes in eye and head positions, whereas visual tracking is expected to generate comparatively fewer changes in eye and head positions to match the position of an object of interest. We can extend this argument to obtain a measurable proxy of scanning strategies through rates of eye and head movements. We can expect *high rates* and *low rates* of eye and/or head movements during visual search and visual tracking, respectively. Despite the sharp theoretical separation between these two visual tasks, in reality, animals switch from one to the other continuously. Several studies have been successful at distinguishing empirically between visual search and visual tracking bouts in chickens and pigeons (Andrew and

Dharmaretnam, 1993; Dawkins and Woodington, 2000; Dawkins, 2002).

From an evolutionary perspective, it is worth noting that there is a high degree of interspecific variability in the amplitude and patterns of eye and head movements that control visual search and visual tracking tasks in bird species other than chickens and pigeons (Wallman and Pettigrew, 1985; Wallman et al., 1994; Casperson, 1999; O'Rourke et al., 2010a,b; Fernández-Juricic et al., 2010). However, no attempt has been made to assess the potential relationship between the interspecific variability in the configuration of the visual system and the eye/head movement rates at the comparative level. This is a potential fruitful area of future research that can shed some light into the evolution of visual scanning strategies in predator–prey interactions.

4. Visual system configuration influencing scanning strategies: some predictions

Studying the relationship between visual system configuration and scanning behavior requires a comparative approach that reflects the levels of interspecific variability in visual physiology and eye/head movement behavior. Currently, there is not enough comparative information for species with different ecology and phylogenetic history to conduct the necessary analyses. What follows are some predictions for future testing on the potential role of the visual properties reviewed previously in scanning behavior (Fig. 4). I focus on head movements during visual search tasks because they are easier to record in birds with regular video devices than eye movements (but see Kjærsgaard et al., 2008). Nevertheless, some of the predictions may also hold for eye movements.

As described above, the width of the foveal pit could affect the size of the area with high resolution in the visual field. Narrower foveal pits are expected to have a smaller area of high resolution

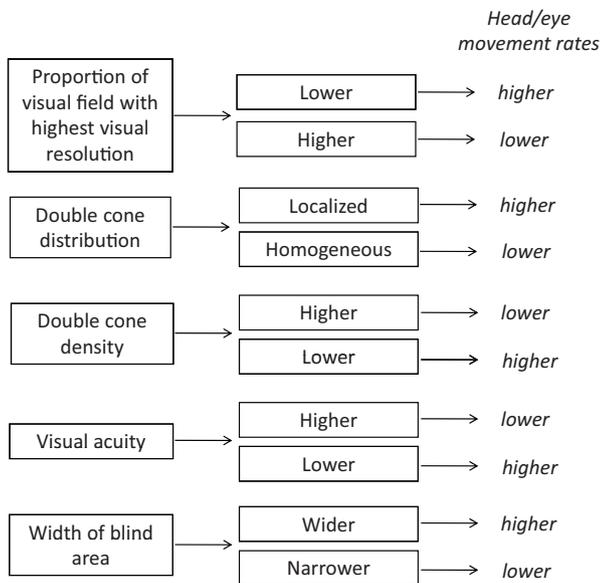


Fig. 4. Predicted effects of different visual properties (proportion of the visual field with the highest visual resolution, distribution and density of photoreceptors – double cones – associated with motion detection, overall visual acuity, and width of the blind area at the rear of the head) on scanning behavior (head movement rates) in a visual search context (see text for details). These predictions apply to bird species with laterally placed eyes with a single fovea located approximately centrally.

than wider foveal pits (Fig. 2). In a visual search context, I predict that as the width of foveal pit gets narrower, head movement rates would increase to enhance visual coverage with the smaller area of high resolution (i.e., projection of the retinal specialization; Fig. 4). In species with relatively wider foveal pits, I predict that head movement rates would be comparatively lower because of the greater visual coverage provided by the larger area of high resolution (i.e., projection of the retinal specialization; Fig. 4). There is some preliminary evidence supporting these predictions. In a comparison between two bird species belonging to the Emberizidae Family, Fernández-Juricic et al. (2011a) found that the species with a proportionally smaller area of high resolution in the retina showed higher head movement rates compared to the species with a larger area of high resolution. However, two-species comparisons do not have the necessary sample size to properly test these predictions (Garland and Adolph, 1994).

The density and distribution of double cones is expected to influence scanning strategies, given their role in motion detection and achromatic contrast perception (von Campenhausen and Kirschfeld, 1998; Goldsmith and Butler, 2005). In a visual search context, given similar overall densities of double cones, bird species with a higher density of double cones on one sector of the retina are expected to have higher head movements rates to expose this motion detection sector to as many different spots in the visual space as possible in relation to species with a less spatially restricted distribution of double cones (Fig. 4). Given a homogeneous distribution of double cones across the retina, in a visual search context I predict that species with proportionally higher overall density of double cones in relation to other photoreceptor types would have lower head movement rates due to their greater ability to resolve movement from different directions in the visual field (Fig. 4). These predictions consider the independent effects of the distribution and relative density of double cones; however, these parameters may be somewhat related (e.g., species with a more concentrated distribution may also have higher relative densities), although no study has addressed this type of relationship in birds from a comparative perspective. Depending on whether the relationship between double cone density and distribution is

positive or negative, different sets of predictions on scanning strategies could be made.

Visual acuity can play an important role in predator detection. In a visual search context, species with higher overall visual acuity are expected to have lower head movement rates because they can resolve objects to a greater degree at a given distance within the limits of visual resolution than species with lower overall acuity (Fig. 4). A recent study found decrease in the rate of head movement in species with bigger eyes (and thus higher visual acuity; Fernández-Juricic et al., 2011c). However, this comparison only included five species from different families (Falconidae, Accipitridae, Anatidae, Emberizidae) and was probably influenced by between-species differences in the type and number of retinal specializations (Fernández-Juricic et al., 2011c).

The width of the blind area at the rear of the animal's head is expected to limit the area covered by the visual field. In a visual search context, I predict that species with wider blind areas would have higher head movement rates than species with narrower blind areas to compensate for the lack of visual information (Fig. 4). Some two-species comparison studies have shown that the species with the wider blind area allocates more time to head-up scanning than the species with the narrower blind area (Guillemain et al., 2002; Tisdale and Fernández-Juricic, 2009), but no study has tested these effects on head movement rates.

The predictions presented above consider the *independent* effects of each visual property on scanning strategies. But these visual properties are likely to have some degree of association between them. More importantly, different bird species are likely to have different combinations of visual properties that may lead to different scanning strategies. Yet, very little is known as to how the *combined* effects of all these visual properties would affect scanning behavior. This is a fruitful area for future research that should start by characterizing the associations between different elements in the avian visual system at the comparative level before studying their effects on scanning strategies.

There are some studies that are indicative of potential associations. Martin and Katzir (2000) and Martin and Coetsee (2004) found a positive relationship between eye size (a proxy of visual acuity) and the size of the blind area at the rear of the bird's head. They interpreted this finding as evidence of species with larger eyes reducing glare effects due to sunlight through larger blind areas. However, the authors had information on only one species of Passeriformes (the most ecologically diverse avian order) and did not control for phylogenetic effects. Dolan and Fernández-Juricic (2010) suggested a negative relationship between eye size and the peak retinal ganglion cell density in the retinal specialization based on a comparison of five bird species without controlling for phylogenetic relatedness. The argument is that species with smaller eyes (and thus lower visual acuity) could compensate by increasing resolution within the retinal specialization with higher number of sensory neurons. Additionally, a recent study found that both achromatic and chromatic vision may complement each other to enhance visual acuity (Lind and Kelber, 2011). How these relationships (and others) could influence scanning strategies is yet to be determined.

5. Effects of habitat type and predation risk

In the previous sections, I presented a framework to establish the relationship between visual system configuration and scanning behavior in birds using head movement rates. This can be used to make more specific predictions about the role of habitat type, predation risk, etc. in the evolution of visual systems and scanning strategies that would enhance predator detection in different environmental conditions. I provide some examples below.

Assuming similar levels of predation risk across habitats, visual conditions differ between open (i.e., low vegetation complexity) and closed (i.e., high vegetation complexity) habitats in terms of ambient light intensity, spectral properties of the light, and degree of visual obstruction (Endler, 1993; Altshuler, 2001; Denno et al., 2005). Predators have been reported to change their attack strategies with changes in vegetation complexity (Denno et al., 2005; Michel and Adams, 2009). Consequently, prey may be exposed to predators to different degrees depending on habitat complexity (Boinski et al., 2003; Shepard, 2007). Consider, for instance, the effects of aerial predation, which is an important source of mortality for Passeriformes (e.g., Gotmark and Post, 1996; Roth and Lima, 2003; Roth et al., 2006), on species that specialize in foraging in closed and open habitats. When prey forage in closed habitats (e.g., in trees), predators approach from multiple directions (e.g., above and below) and have shorter exposure times; whereas when prey forage in open habitats (e.g., on the ground), predators approach from specific directions (e.g., above) and have comparatively longer exposure times (Boinski et al., 2003).

Considering species with a single centrally located fovea, species specialized in foraging in closed habitats would be constrained mainly by *visual coverage* to detect close predator attacks from any direction. These species are expected to have comparatively narrow blind areas, a large proportion of the visual field with high visual resolution (wider foveal pits; Fig. 2), and a more homogeneous distribution of double cones, which can increase the probabilities of predator detection from different directions in complex visual environments. On the other hand, species specialized in foraging in more open habitats are expected to be constrained mainly by *visual acuity* to visually resolve predators approaching at a distance from specific directions in the visual field (e.g., above the ground). These species would have high overall visual acuity, high degree of retinal specialization (narrow foveal pits; Fig. 2), and a more localized distribution of double cones, which can increase the probabilities of detecting aerial predators above the ground. These visual configurations are also likely to be associated with variations in scanning strategies (e.g., head movement rates; Fig. 4) in open and closed habitats.

Although these predictions make numerous assumptions, many of which may be unrealistic (e.g., predation risk and mortality is similar between habitat types), they provide some directions for future comparative research on vision–behavior relationships. At this moment empirical evidence is scant. In a study of three congeneric species of squirrel monkeys living in habitats with different degrees of vegetation complexity, Boinski et al. (2003) corroborated that aerial predators are more exposed to prey before an attack in open compared to closed habitats. Consequently, squirrel monkeys living in open areas invest more time in directional scanning to spot predators early, whereas species living in closed areas engage in scanning mostly after detecting visual and auditory clues that may be indicative of a predator (Boinski et al., 2003). Møller and Erritzøe (2010) found that bird species living in open habitats have larger eyes and thus higher visual acuity than species living in more complex habitats. Finally, Hart (2002) found that some species of avian ground foragers have higher densities of double cones concentrated in the ventral part of the retina, which projects upwards, coinciding with the usual direction of attacks from aerial predators.

Predation pressure varies between prey species (Gotmark and Post, 1996; Tornberg, 1997), which could lead to different levels of perceived predation risk (Cresswell, 2011). The visual morphology of species with higher levels of predation risk may reflect specializations to increase the chances of predator detection under certain ecological conditions. For instance, species subject to higher predation risk may have comparatively higher density of double cones and/or narrower blind areas than species subject to lower predation risk, but without changes in rates of eye/head movements

necessarily. Alternatively, between-species variation in predation risk may be associated mostly with changes in scanning behavior. For instance, American crows and Western scrub jays increase their head movement rates to increase visual coverage in the micro-habitats in which they are under higher risk of predation, perching and on the ground, respectively (Fernández-Juricic et al., 2010). Additionally, in some species with single centrally located foveae, individuals adjust their rate of head movements depending on the levels of risk. For example, brown-headed cowbirds increase head movement rates at the periphery of the group probably to enhance visual coverage to detect predators early, and reduce head movement rate when group mates are farther apart and when foraging in small groups likely to fixate on neighbors and benefit from collective detection (Fernández-Juricic et al., 2011b).

6. Conclusions

The configuration of the avian visual system has a high degree of heterogeneity in visual performance around the animal's head. This means that, at least in bird species with laterally placed eyes and centrally placed retinal specializations, there are some sectors of the visual field that provide high levels of visual resolution and motion detection in comparison with other sectors (e.g., peripheral retina and blind area). The implication is that when birds are monitoring for predators while head-up, the quality of scanning will vary in different parts of the visual field. Therefore, the theoretical assumption that birds can gather high quality information all around their heads while head-up can be considered unrealistic. From a theoretical perspective, violations of this assumption can affect the vigilance strategies of social birds. For instance, Fernández-Juricic et al. (2004b) found that the coordination of vigilance behavior (i.e., group mates taking turns scanning for predators) can be a beneficial strategy only in species with a visual system that prevents individuals from gathering information in head-down body postures (e.g., large blind areas and narrow visual fields).

As a direct consequence of the heterogeneity in visual performance, birds need to move their eyes and heads to cover with high resolution their surroundings. The rates of eye and head movements can be used as proxies of scanning strategies in future studies. Measuring head movement rates should be relatively easy to do in birds with the current video technology and behavior recording software. Recent studies have found that changes in head movement rates are associated with changes in the degree of visual obstruction in the environment (Franklin and Lima, 2001), changes in the levels of perceived predation risk before and after a predator is detected (Jones et al., 2007b, 2009), and risk perception in groups (Fernández-Juricic et al., 2011b). Measuring eye movements can be more challenging because birds (a) do not move their eyes as much as their heads (Gioanni, 1988; Haque and Dickman, 2005), (b) the degree of eye movement varies substantially between species (Blackwell et al., 2009; Fernández-Juricic et al., 2010; O'Rourke et al., 2010a), and (c) birds can vary eye position while simultaneously changing head position (Wallman and Letelier, 1993). The maximum amplitude of eye movements (Fernández-Juricic et al., 2008) as well as the patterns of eye movements (Voss and Bischof, 2009) can be measured with the animal's head restrained. However, these measurements lack ecological relevance. A novel alternative is to use eye trackers, which have been tested preliminary in birds (Kjærsgaard et al., 2008). Basically, an eye tracker consists of close-up cameras recording the eye under infra-red illumination, which allows the tracking of the pupil and corneal reflections. Another set of cameras point towards the visual scene that each eye can perceive. The images are then synchronized digitally allowing to determine the position of the projection of the retinal specialization

in the visual space. Eye trackers can then record eye movement rates along with the patterns of eye movement (e.g., convergent and divergent). The technology to record the movements of both eyes when birds can move their heads freely is still under development.

I presented a group of novel predictions that link visual physiology with scanning behavior that can be tested empirically using a comparative approach. These predictions only consider bird species with laterally placed eyes and centrally located retinal specializations. Head and eye movement patterns are expected to vary with the position of the eyes in the orbits (e.g., more or less frontal) as well as the position and type of the retinal specialization, and hence the projection of the area with high resolution in the visual field. Additionally, I focused the predictions on anti-predator behavior when animals are in vigilant postures. However, it is likely that animals use other components of their visual systems simultaneously (binocular visual field) for foraging purposes, which could potentially influence head movement rates besides the effects described above in terms of detecting predators.

From an evolutionary perspective, studying the relationship between the inter-specific variability in avian visual systems and scanning behavior can help establish the degree to which the sensory system co-evolved with information gathering strategies. From a theoretical perspective, animals are expected to optimize their vigilance strategy depending on the perceived risk of predation by gathering information that will enhance the chances of spotting a predator on time to escape. But the mismatch between model assumptions and the sensory basis of gathering visual information creates a gap that limits our ability to test empirically the hypotheses and predictions of many predator–prey interaction models. Future studies integrating visual physiology and anti-predator behavior will be necessary to develop models with more realistic assumptions on information gathering that will lead to more refined predictions.

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