

Vigilance and predator detection vary between avian species with different visual acuity and coverage

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Interspecific variations in avian visual systems have been suggested to influence antipredator strategies, yet little empirical evidence exists on how morphological and ecological factors associated with visual properties can constraint predator detection. We investigated antipredator responses (predator detection probabilities and vigilance behavior) in 2 species with different visual properties (European starlings, *Sturus vulgaris*, have higher acuity and wider blind areas at the rear of their heads than house sparrows, *Passer domesticus*) in relation to distance to the predator, body posture, and head orientation. Visual acuity may affect the distance at which a predator is detected; while the size of the blind area may influence the body postures and head orientation with the highest predator detection probabilities. Distance to the decreased predator detection probabilities of house sparrows (lower acuity) but not those of European starlings. Certain body postures and head orientations, influenced both species despite the interspecific differences in visual field configuration. Times allocated to scanning were similar, but European starlings had longer head-up scan bouts likely to enhance scanning coverage, whereas house sparrows had higher head-up scan rates probably to reduce the length of interscan intervals. We discuss alternative interpretations; however, our findings suggest that sensory configurations may limit the effectiveness of some antipredator strategies under certain ecological conditions, which has implications for understanding the evolution of different behavioral mechanisms that reduce predation risk. *Key words*: predator detection, vigilance, visual acuity, visual ecology, visual fields. [*Behav Ecol* 20:936–945 (2009)]

Animals need information to reduce environmental uncertainty and make decisions that enhance their fitness (Phelps 2007). Scanning behavior while animals are foraging has usually been studied in relation to gathering information about potential predators (Elgar 1989; Bednekoff and Lima 1998a; but see Valone 2007). Gathering information can be costly (Watson et al. 2007), either through direct energy expenditure or through a reallocation of efforts (e.g., increased vigilance time could reduce foraging time). Animals are therefore expected to engage in information gathering when the benefits exceed the costs (Dall et al. 2005).

The configuration of the sensory systems has been implicated in influencing the costs of information gathering (Fernández-Juricic et al. 2004; Phelps 2007). For instance, in visually oriented animals like birds, foraging with part of the visual field blocked can affect the availability of public information to make foraging decisions (Templeton and Giraldeau 1995), increase vigilance efforts to compensate for the scarcity of information (Fernández-Juricic et al. 2005), and switch feeding methods to increase foraging efficiency (Guillemain et al. 2001). However, there is a high degree of interspecific variability in visual properties (Kiltie 2000; Hart 2001; Martin 2007), which could constraint information gathering in different ways and thus lead to different behavioral strategies.

For instance, at a proximate level, Guillemain et al. (2002) attributed between-species variations in vigilance effort to between-species differences in the configuration of the visual

fields (e.g., limits of the space around an animal's head from which information can be obtained). At the comparative level, Kiltie (2000) suggested that differences in the optimal viewing distance to detect predators may be associated with interspecific variations in visual acuity (e.g., visual resolution). These studies indicate that the combination of visual properties of different species could potentially enhance predator detection under a certain range of social and environmental conditions (Fernández-Juricic et al. 2004). Assessing between-species differences in antipredator performance at the extremes of the range of visual field configuration and visual acuity may allow us to make associations between visual properties and factors limiting the gathering of information, which can ultimately improve our understanding of the evolution of antipredator strategies.

The goal of this study was to quantify variations in antipredator strategies (probability of detecting a predator and vigilance behavior) in 2 social ground foraging species: the European starling *Sturnus vulgaris* and the house sparrow *Passer domesticus*. Although previous research has focused on the latency to detect a predator (Lima 1995; Kaby and Lind 2003; Whittingham et al. 2004; Fernández-Juricic and Tran 2007), quantifying the probability of detection is important because it is the currency of many theoretical models (e.g., Bednekoff and Lima 1998b). Our approach was to conduct seminatural experiments in which foraging individuals from both species were presented with a model predator flying by under similar social and ecological conditions. Our experiments recreated conditions in which the predator model was more (e.g., habitat with low visual obstruction) or less (e.g., habitat with more visual obstruction) exposed, controlling for several confounding factors (e.g., flock size, neighbor distance, bird identity, body condition, and food deprivation).

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Recent studies have characterized some of the visual properties of our model species. European starlings have 28.5% higher visual acuity than house sparrows based on the density of retinal ganglion cells and eye size (Dolan T and Fernández-Juricic E, unpublished data). Both species have a relatively ample degree of eye movement. The blind area of European starlings, which ranges between 32° and 74° (Martin 1986), is larger than that of house sparrows, which ranges between 18° and 47° (Fernández-Juricic et al. 2008), depending on whether eyes are converged or diverged, respectively. Variations in peak sensitivity of visual pigments could influence predator detection through chromatic contrast; however, 3 of the main visual pigments (SW2, RH2, and LWS) described in both species are very similar (Hart and Hunt 2007).

Both species also differ in other traits: European starlings are larger (82.3 g), tend to forage in open areas, and generally probe the ground for invertebrates (Cabe 1993, Whitehead et al. 1995), whereas house sparrows are smaller (27.7g), prefer to forage close to cover, and usually feed on seeds (Lima 1987, Anderson 2006, Lowther and Cink 2006). European starlings travel in highly cohesive flocks during the nonbreeding season (Ballerini et al. 2008), which are larger and change in shape depending on predation risk (Carere et al. 2009). However, flock sizes of house sparrows during the winter tend to be smaller (Anderson 2006). Prey handling time is likely different between species because handling a seed requires less time than handling an insect (Popp 1988). Group size affects the foraging behavior of both species, but in slightly different ways. House sparrow foraging rate (taking into account handling time) increases up to groups of 3 individuals and then decreases as a result of higher handling times associated probably with more social vigilance to avoid aggressive conspecifics (Johnson et al. 2001). European starling foraging efficiency (prey captured per number of search probe) increases up to groups of 4 individuals, and then it levels off in larger groups probably due to time release from predator vigilance and local enhancement to find prey distributed in clusters (Smith 2002).

We acknowledge that between-species differences in anti-predator strategies could be caused by various traits (e.g., ecological, phylogenetic, etc.); yet we investigated changes in specific factors (distance to the predator, body posture, and head orientation) associated with visual acuity and visual fields that could limit predator detection (Fernández-Juricic et al. 2004). Thus, our predictions are based on how these factors affect detection and vigilance based on between-species differences in visual systems. Visual acuity could influence the size of predator detection windows (areas within which the chances of detecting a predator are higher; Blumstein et al. 2005), and thus, the distance at which predators can be visually resolved (e.g., higher acuity is associated with detection from farther away, Kiltie 2000). The size of the blind area in the visual field could affect the amount of visual coverage, and thus, the body posture (e.g., lower detection while head down) and head orientation while head-up (e.g., lower detection when the blind area faces the approaching object) at which predators can be detected (Lima and Bednekoff 1999; Guillemain et al. 2002; Kaby and Lind 2003; Devereux et al. 2006).

First, we predicted that the probabilities of detecting a predator would be limited more by the distance to the predator in the house sparrow than in the European starling because of the lower visual acuity of the former. Second, the probabilities of detecting a predator would be limited more by body posture and head orientation while head up in the European starling than in the house sparrow, as the former has a wider blind area and thus lower visual coverage. Third, because house sparrows have a narrower blind area, we expected them to allocate less vigilance effort than European starlings.

MATERIALS AND METHODS

General procedures

Experiments were carried out at the California State University Long Beach campus from March 2006 to July 2006 on a grassy area enclosed with a black fence. The fence had a gap through which a predator model was exposed to the birds (hereafter, predator exposure gap, Figure 1a). This gap had a black fabric background that was in front of a large tree such that it remained shaded throughout the day to minimize the confounding effects of light contrast.

We conducted 2 seminatural experiments in which birds in enclosures were presented a predator model flying by at the same speed but with different degrees of exposure. The predator exposure gap had a fixed length in the first experiment (shorter exposure time), resembling a scenario in which prey encounter a predator in a habitat with high visual obstruction. The predator exposure gap (PEG) was variable in the second experiment (longer exposure time): as distance between the birds and the PEG increased, so did the gap length, resembling a scenario in which prey encounters a predator in a habitat with less visual obstruction. We did not use an approaching predator situation to avoid looming and predator targeting effects.

One hundred eighty-two individuals (house sparrows: 58 females and 43 males; European starlings: 49 females and 32 males) were captured in different locations in Los Angeles and Orange Counties. We color banded, sexed and kept birds in indoor 0.80 m × 0.55 m × 0.60 m cages (3–6 house sparrows per cage, 2–4 European starlings per cage) on a 12:12 h light:dark photoperiod. Water and food (Royal Feeds Leach Seed and Milling Co. finch seed mix for house sparrows, Chicken Soup for the Cat Lover's Soul brand cat food and mealworms dusted in Zoo Med's Reptivite vitamins for European starlings) were available ad libitum except during experimental trials and food-deprivation periods. Food deprivation varied between species (house sparrows, 1.5–6 h; European starlings, 12–19 h, determined in a preliminary study) to equalize forage initiation times during trials. In preliminary trials, European starlings did not initiate foraging under shorter food-deprivation scenarios, which may be due to differences in body size and energy requirements (Lasewski and Dawson 1967). Animals did not exhibit breeding-associated behaviors while in the cages during the experiments.

Antipredator responses with a fixed PEG

Each species was tested separately and aviary cage mates were not tested together. For each species, we used 2 individuals (1 focal, 1 conspecific) in 2 enclosures during each trial to reduce stress associated with solitary foraging. The bottomless enclosures (0.5 m × 0.5 m × 0.4 m) were constructed with 19-gauge galvanized hardware cloth with a front panel of Plexiglas, and were placed in direct line of sight of the PEG (Figure 1a); grass in the area was maintained at 2 cm. The focal individual was placed in the enclosure closest to the PEG, without separation between the focal and conspecific enclosures.

The PEG (p) was kept constant at 5 m across trials. The distance (d in Figure 1) from the front of the focal's enclosure to the center of the PEG was manipulated in 1-m intervals, with d varying from 1 to 40 m. A single trial was conducted at each distance. We used the same predator model, a mounted red-shouldered hawk *Buteo lineatus*, across trials. This may cause some pseudoreplication effects as we only had a single stimulus; however, to reduce these effects, we presented the model to different focal individuals. The predator model glided down a transparent monofilament line with a pulley

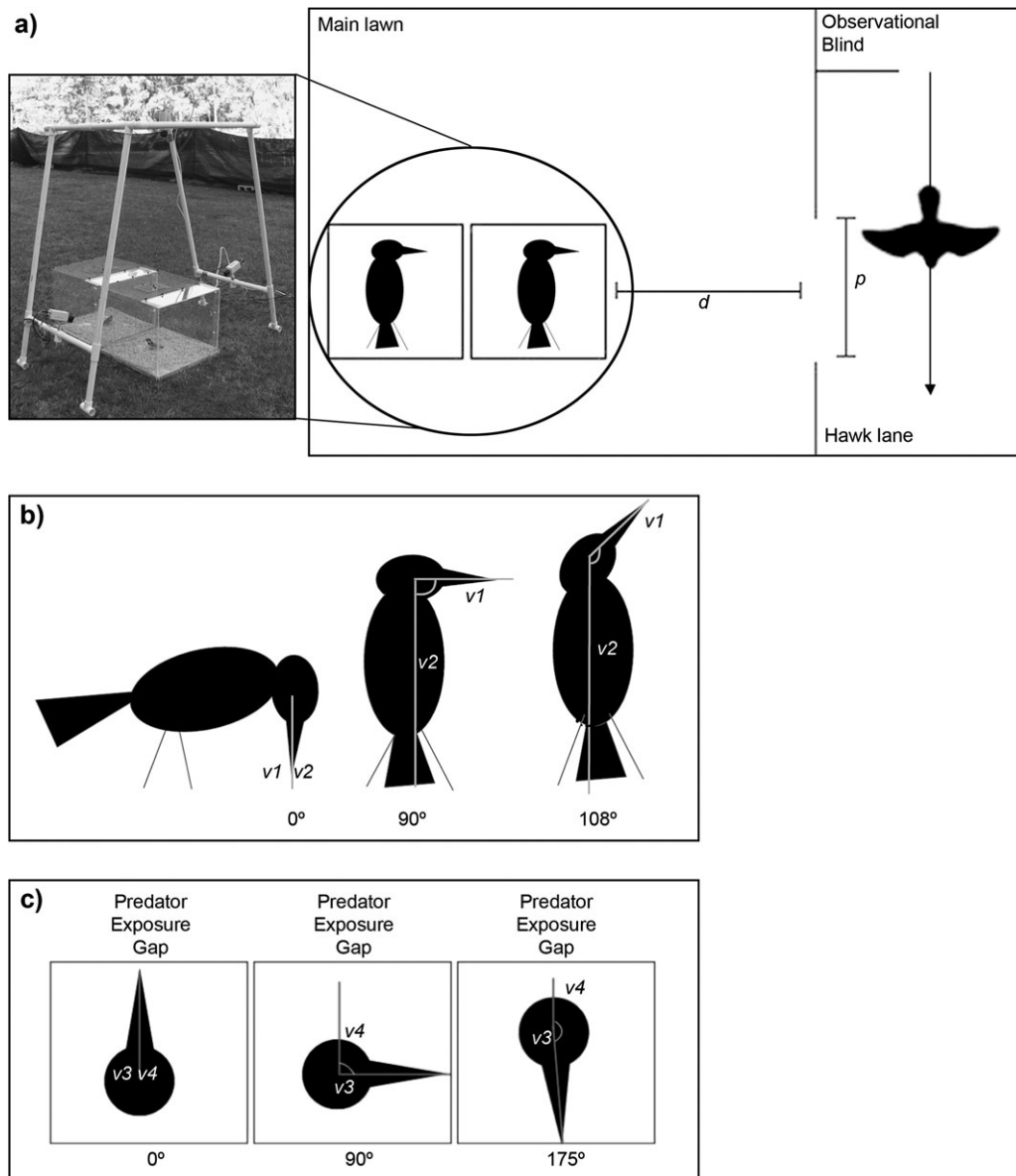


Figure 1

(a) Schematic representation of the experimental setup (not to scale) with 3 zones: experimental area (main lawn), hawk lane, and observational blind. The distance to the PEG, d , varied from 1 to 40 m. The length of the PEG, p , remained constant at 5 m in the experiment with fixed p , and varied between 0.35 and 14 m in the experiment with variable p . The picture displays the stand with the 3 cameras used to record the focal bird and conspecific behaviors. (b) Body posture angles were measured using the eye as the vertex of the angle. The 2 vectors, $v1$ and $v2$, extended through the tip of the bill and perpendicularly to the ground. (c) Head-orientation angles were measured using the center of the head as the vertex of the angle. The 2 vectors, $v3$ and $v4$, extended through the tip of the bill to the predator model.

system attached to its back. The height and tension of the line were standardized across trials, yielding a glide speed of 2.9 ± 0.17 m/s. We minimized noise from the pulley, but we also played white noise to mask other sounds (following Devereux et al. 2006).

Three cameras recorded the behavior of the focal bird: 1 top-view and 2 lateral-view video cameras (PelikanCam digital color CCD) affixed to a stand that held the cameras at the same position and angle across trials (Figure 1a). The conspecific was also visible in the lateral-view cameras. In the few instances the conspecific detected the predator before the focal, we repeated the trials with new individuals. In none of the trials included in the analysis, individuals used vocal cues (e.g., alarm calls) when detecting the predator. A fourth camera

recorded the predator model through the PEG. All cameras were connected to a digital color quad splitter (Clover QC900) that enabled us to record them simultaneously on a Time Lapse VCR.

During trials, house sparrows were provided with a Royal Feeds Leach Seed and Milling Co. finch seed mix hidden in corn cob substrate (Green Pet Natural Corn Cobs) on top of a piece of wood. European starlings were tested directly on grass where mealworms were hidden in 2-cm holes on the ground (following Fernández-Juricic et al. 2005). The soft nature of the soil allowed starlings to probe into the ground for mealworms (or other invertebrates). Each trial began with the first foraging peck of the focal bird. After 3 min (European starlings) or 5 min (house sparrows) of foraging

behavior, we released the predator. This difference was established during preliminary trials and was necessary to ensure the birds were actively foraging and scanning during the predator exposure event.

To control for potential confounding effects, we recorded environmental variables (light intensity, wind speed, and ambient temperature), focal and conspecific body condition (body mass/wing cord), and food-deprivation time in each trial. Food deprivation was the same for each focal and conspecific in the same trial. Eighty trials were conducted (40 for house sparrows, 40 for European starlings). We used a different focal individual for each trial to avoid habituation-sensitization effects, and distance treatments were applied in a random order. Focals were used only once; however, conspecifics were used up to 4 times (no more than once per experimental day) due to constraints in the availability of animals.

Bird behavior was analyzed frame-by-frame (30 frames/s) using Adobe Premiere Pro 1.5 (Adobe Systems, Inc. 2004). Predator detection was categorized from the focal bird's reaction as either "detection" or "no detection." Detection was coded as the focal bird freezing, crouching, moving away by flying or running, assuming an upright posture (head elevated, neck extended, and feathers flat against the body), or changing its scanning pattern (longer pause between food searching bouts, between lateral head turns, or sudden lateral head turns relative to the focal's previous pattern). Following previous studies (e.g., Lima and Bednekoff 1999; Kaby and Lind 2003; Whittingham et al. 2004), we assumed that any of the aforementioned responses while the predator was in the gap was a proxy of predator detection. Nondetection was defined as the focal bird maintaining the same scanning and foraging pattern while the predator crossed the gap. We also recorded and analyzed response times, but we got similar results that are available from the authors on request.

We established the response frame in which the focal exhibited the first of any of the aforementioned detection behaviors. However, we used the frame prior to the response frame to measure body posture and head orientation with ImageJ (<http://rsb.info.nih.gov/ij/>), following the assumption that predator detection occurred immediately before the individual exhibited alarm behaviors (Harkin et al. 2000; Fernández-Juricic and Schroeder 2003). We measured body posture as the angle from the tip of the bill to the ground (Figure 1b). The vertex of the angle was placed on the center of the eye, and 2 vectors defined the angle: one vector, $v1$ extended through the tip of the bill, and the other vector, $v2$, formed a line perpendicular to the enclosure's floor (Figure 1b). Body postures varied from 0° to 108° , where 0° was the tip of the bill toward the ground (head-down posture), 90° was the bill parallel to the ground (head-up posture), and 108° was the bill elevated toward the sky (Figure 1b).

We also measured head orientation as the angle from the tip of the bill to the predator model. The vertex of the angle was placed on the center of the focal's crown, and 2 vectors defined the angle: one vector, $v3$, extended through the tip of the bill and the other vector, $v4$, formed a line parallel to the left side of the enclosure, which corresponded to the center of the PEG (Figure 1c). At the time of response, however, the predator model was not always in the center of the gap; consequently, we calculated head orientation using a correction factor (Appendix A). Corrected head-orientation angles ranged from 0° to 175° , where 0° was the bill pointed directly toward the predator model, 90° was the bill parallel to the predator model, and 175° was the bill pointed away from the predator (Figure 1c). For birds that did not detect the

predator model, we measured body posture and head orientation when the predator model was visible.

Antipredator responses with a variable PEG

In the fixed PEG experiment, the size of the gap (p) on the focal bird's visual field decreased as the distance (d) between the focal bird and the PEG increased (e.g., the fixed PEG may have been perceived smaller by the bird with increasing distance). In the second experiment, we manipulated p so that the image size of the PEG remained relatively constant to the bird with variations in d . The length of the PEG was calculated based on d using the formula:

$$p = d(\tan\theta) \quad (1)$$

keeping θ constant at 19.29° . θ was determined based on the limits of the experimental area. The largest PEG available was 14 m, and the farthest distance tested was 40 m.

This experiment was conducted following exactly the same experimental design and analytical procedures as the fixed PEG experiment (see above). The only difference is that the total number of frames the predator model was visible varied across trials (from 4 to 145 frames), because p varied (from 0.35 to 14 m). For birds that did detect the predator, we used the first frame prior to the detection as a proxy (see above). For birds that did not detect the predator model, we sampled body posture and head orientation in the frame where the predator model was visible in the gap.

We did not modify the height of the PEG; however, the height of the predator model within the focal's visual field could have varied with increasing distances to the gap. We assessed whether the height of the predator model may have been perceived differently between species due to their size differences. We calculated the vertical angle λ of the predator model to the focal's eye height with the following formula:

$$\lambda = \frac{t - e}{d}, \quad (2)$$

where t is the height of the predator model, e is the height of the focal bird's eye, and d is the distance to the PEG. Because the predator model varied in height during the course of a trial, we used the mean heights (112.34 ± 2.56 cm).

Vigilance behavior

We recorded scanning behavior of the focal birds from the experiment in which the PEG was fixed using JWatcher 1.0 (Blumstein et al. 2006). While on the ground, house sparrows and European starlings alternated bouts of food-seeking behavior with their heads down and bouts of scanning behavior with their heads up. After the first peck, we recorded the number of head-up scanning bouts and their duration for 3 min, which included bouts with and without food-handling events, because head-up food handling is also involved in vigilance behavior (Cowlshaw et al. 2004). For house sparrows, the mean number of head-up and pecking events was 26.40 ± 2.95 and 54.20 ± 5.35 , respectively, over the 3-min period. For European starlings, the mean number of head-up and pecking events was 11.47 ± 1.36 and 22.25 ± 16.05 , respectively, over the 3-min period. We calculated the following dependent variables: head-up scan bout duration (s), head-up scan rate (events per min), and the proportion of time head-up scanning. At the time of recording, the observer had been trained in recording the behaviors of both species, with a difference of less than 5% in the rate of occurrence of different behaviors recorded on the same tapes.

Statistical analysis

Some variables were log transformed prior to the analysis to homogenize their variability. Throughout, we report means \pm standard error.

We assessed between-species variations in the height of the predator model in the focal's visual field using a general linear model with the vertical angle between the focal and the predator model (λ) as the dependent factor; species and distance to the PEG were included as independent factors. We ran a single analysis because the average height of the predator model and distance to the PEG were the same in both experiments.

We first established between-species differences in the probability of predator detection across all conditions by using generalized linear models with a binomial distribution for the dependent factor (detection, no detection) and a logit link function, and species included as the independent factor. Mean probabilities of predator detection were estimated with Statistica 8.0 routines (StatSoft 2007). We then assessed the probabilities of predator detection separately to test the specific predictions made for each species in relation to the factors of interest (distance to the PEG, body posture, and head orientation). The independent factors (distance to the PEG, body posture, and head orientation) were not correlated among each other (r ranged from -0.67 to 0.98 , $P > 0.640$) across species and experiments, with the exception of body posture and distance to the PEG in the fixed PEG experiment with house sparrows ($r = 0.33$, $P = 0.039$).

For each species, we followed a 3-tiered approach to establish the effects of the factors of interest but controlling for potential confounding factors. First, we determined the degree of covariation among potential confounding factors (temperature, light intensity, wind speed, food-deprivation time, focal body condition, and conspecific body condition) with Pearson product moment correlations. We also determined the relationship between focal body condition and focal sex with a 1-way analysis of variance (ANOVA). We did not include variables that were highly correlated. Second, we ran a Principal Component Analysis (PCA) to summarize the confounding factors selected in the first step into fewer variables. We selected factors with eigenvalues > 1 , and rotated axis with a varimax normalized transformation. Third, we ran final models, assessing the effects of distance to the PEG, body posture, and head orientation, but controlling for confounding factors by including the factors generated by the PCA. We used generalized linear models with a binomial distribution for the dependent factor (detection, no detection) and a logit link function. Given our sample sizes, this 3-tiered approach allowed us to increase the power of the tests by minimizing the number of confounding factors included in the generalized linear models. We also tested for interaction effects but none were significant.

The different vigilant behaviors (head-up scan bout duration, head-up scan rate, proportion of time spent head-up) were analyzed with general linear models using species as an independent factor. Of the potential confounding factors (temperature, log-light intensity, and wind), we only found a significant correlation between temperature and (log) light intensity ($r = 0.71$, $P = 0.001$), so we decided to remove light intensity rather than temperature to maintain consistency between analyses.

RESULTS

The vertical angle of the predator model (log transformed) in the focal's field of view decreased as distance to the PEG increased ($F_{1,156} = 789.13$, $P = 0.001$). However, there was no difference between species in this angle (European starling,

$1.91 \pm 0.04^\circ$; house sparrow, $1.92 \pm 0.04^\circ$; $F_{1,156} = 0.02$, $P = 0.880$), nor was there a significant interaction effect between species and distance ($F_{1,156} = 0.001$, $P = 0.982$).

Antipredator responses with a fixed PEG

The probability of predator detection differed significantly between species (Wald₁ = 6.81, $P = 0.009$), with European starlings (0.88 ± 0.36) exhibiting a higher probability of predator detection than house sparrows (0.63 ± 0.62) across all conditions.

House sparrows

Considering the house sparrow data set, 6 confounding factors were correlated: temperature and (log) light intensity ($r = 0.63$, $P = 0.001$), temperature and wind speed ($r = -0.35$, $P = 0.029$), and focal body condition and conspecific body condition ($r = 0.70$, $P < 0.001$). We did not find significant relationships among the other potentially confounding factors (r ranged from -0.28 to 0.14 , $P > 0.079$; ANOVA, focal sex and focal body condition $F_{1,38} = 0.05$, $P = 0.830$). We did not include in the analysis conspecific body condition, (log) light intensity, and wind speed. Light intensity and wind speed were removed rather than temperature to keep the number of confounding factors as low as possible. We included in the PCA: temperature, food-deprivation time, focal body condition, and focal sex. Two factors were generated: PC1 (positively associated with temperature, factor loading = 0.701; negatively associated with food deprivation, factor loading = -0.794 ; eigenvalue = 1.30; variance explained = 32.58%), and PC2 (negatively associated with focal sex, factor loading = -0.940 ; eigenvalue = 1.01; variance explained = 25.23%).

Twenty-five of 40 house sparrows detected the predator model. The house sparrow probability of predator detection was significantly affected by distance to the PEG and by head orientation; however, body posture, PC1, and PC2 were not significant (Table 1, Figure 2). House sparrows had lower chances of detecting the predator as distance to the PEG increased (Figure 2a): from approximately 80% at 0 m to 35% at 40 m from the PEG. Head-orientation values from 110° to 120° had a probability of detection above 80% (Figure 3).

European starlings

Considering the European starling data set, we found significant relationships between the following potential confounding factors: temperature and (log) light intensity ($r = 0.82$, $P = 0.001$), food-deprivation time and (log) light intensity ($r = 0.35$, $P = 0.023$), focal body condition and (log) light intensity ($r = -0.32$, $P = 0.045$), wind speed and conspecific body condition ($r = 0.32$, $P = 0.045$), and focal body condition and focal sex ($F_{1,38} = 4.36$, $P = 0.044$). Light intensity, wind speed, and focal sex were not considered in further analyses due the degree of correlation. We removed light intensity and wind speed rather than temperature to keep the number of confounding factors as low as possible. All other confounding factors were not significantly associated among each other (r ranged from -0.31 to 0.29 , $P > 0.067$). We included in the PCA: temperature, food-deprivation time, focal body condition, and conspecific body condition. The PCA generated only 1 factor: PC1 (negatively associated with focal body condition, factor loading = -0.728 ; eigenvalue = 1.68; variance explained = 41.94%).

Thirty-five of 40 European starlings detected the predator model. The European starling probability of predator detection was significantly affected by body posture, but not by distance to the PEG, head orientation, and PC1 (Table 1, Figure 2). Individuals had lower chances of detecting the predator model as they went from head up (almost 100%) to head down (ca. 35%) postures (Figure 2b).

Table 1

Effects of distance to the predator exposure gap, body posture, and head orientation, controlling for various confounding factors (see text), on the probability of predator detection of house sparrows and European starlings under 2 experimental conditions: fixed and variable predator exposure gaps

	Wald	df	<i>P</i>
Antipredator responses with a fixed predator exposure gap			
House sparrow			
Intercept	0.03	1	0.871
Distance	4.56	1	0.033
Body posture	0.27	1	0.601
Head orientation	4.32	1	0.038
PC1	0.09	1	0.754
PC2	0.01	1	0.993
European starling			
Intercept	0.64	1	0.421
Distance	0.01	1	0.930
Body posture	3.95	1	0.047
Head orientation	1.44	1	0.231
PC1	0.06	1	0.802
Antipredator responses with a variable predator exposure gap			
House sparrow			
Intercept	3.07	1	0.079
Distance	5.58	1	0.018
Body posture	5.66	1	0.017
Head orientation	0.86	1	0.354
PC1	0.83	1	0.364
PC2	0.14	1	0.712
European starling			
Intercept	1.01	1	0.314
Distance	0.32	1	0.569
Body posture	0.13	1	0.718
Head orientation	0.06	1	0.814
PC1	1.15	1	0.284
PC2	0.57	1	0.450

Results from generalized linear models with a binomially distributed dependent factor (detection, no detection). Significant values are bolded.

Antipredator responses with a variable predator exposure gap

The probability of predator detection with a variable PEG was higher in the European starling (0.95 ± 0.22) than the house sparrow (0.78 ± 0.48 ; Wald₁ = 5.39, $P = 0.020$) across all conditions.

House sparrows

Considering the house sparrow data set, 6 confounding factors were significantly correlated: temperature and light intensity ($r = 0.47$, $P = 0.002$), temperature and wind speed ($r = -0.33$, $P = 0.039$), and conspecific body condition and food-deprivation time ($r = -0.41$, $P = 0.010$). Light intensity, wind speed, and conspecific body condition were not included in the analyses. We removed light intensity rather than temperature to maintain consistency across analyses. All other correlations were not significant (r ranged from -0.19 to 0.22 , $P > 0.178$; ANOVA, focal sex and focal body condition $F_{1,38} = 0.11$, $P = 0.747$). We included in the PCA: temperature, food-deprivation time, focal body condition, and focal sex. Two factors were generated: PC1 (positively associated with focal sex, factor loading = 0.680; eigenvalue = 1.24; variance explained = 30.92%), and PC2 (positively associated with focal body condition, factor loading = 0.873; eigenvalue = 1.06; variance explained = 26.44%).

Twenty-five of 40 house sparrows detected the predator model. The house sparrow probability of predator detection

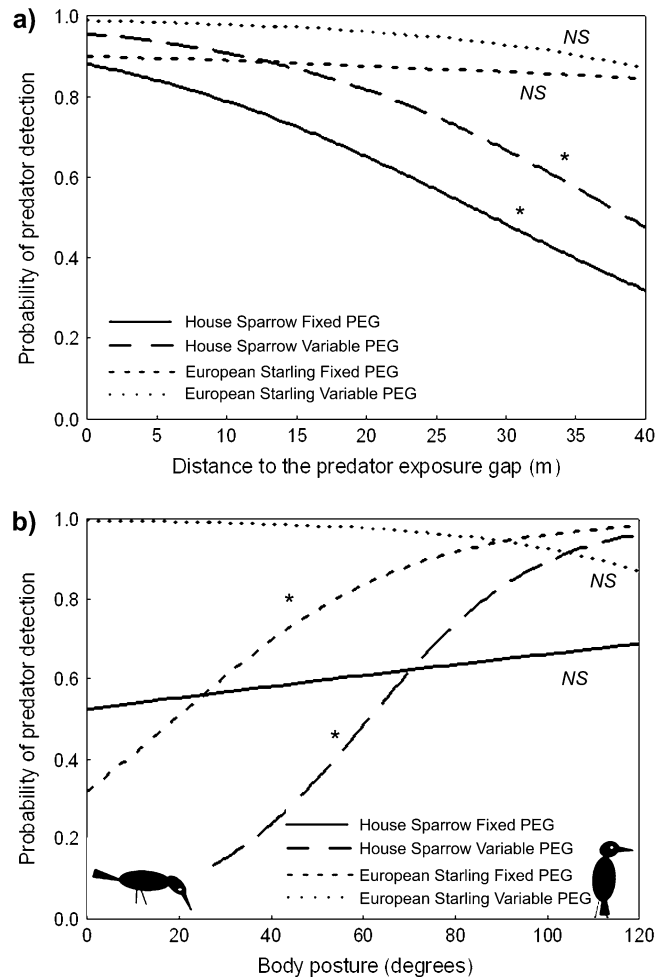


Figure 2

Probabilities of house sparrows and European starlings detecting the predator model in relation to (a) distance to the PEG and (b) body posture. Body posture varied from 0° (head down) and 107° (head up). Two conditions were studied: fixed and variable lengths of the PEG. House sparrow fixed PEG $y = e^{(2.01045 - 0.06919x)} / (1 + e^{(2.01045 - 0.06919x)})$; house sparrow variable PEG $y = e^{(3.09464 - 0.07981x)} / (1 + e^{(3.09464 - 0.07981x)})$; European starling fixed PEG $y = e^{(2.21901 - 0.01292x)} / (1 + \exp^{(2.21901 - 0.01292x)})$; European starling variable PEG $y = e^{(4.52977 - 0.06541x)} / (1 + e^{(4.52977 - 0.06541x)})$. *, significant effect; NS, nonsignificant effect.

was influenced by distance to the PEG and body posture; however, head orientation, PC1, and PC2 did not exert significant effects (Table 1, Figure 2). Individuals had lower chances of detecting a predator as the distance to the PEG increased (Figure 2a): from approximately 97% at 0 m to 50% at 40 m from the PEG. House sparrows decreased the chances of detecting a predator as they went from head-up (about 97%) to head-down (2%) postures (Figure 2b)

European starlings

Considering the European starling data set, we found significant correlations between the following factors: temperature and light intensity ($r = 0.39$, $P = 0.013$), focal body condition and conspecific body condition ($r = 0.67$, $P = 0.001$). Light intensity and conspecific body condition were removed from further analyses. We removed light intensity rather than temperature to maintain consistency across analyses. We did not find significant correlations among the other factors (r ranged from -0.19 to 0.15 , $P > 0.143$; ANOVA, focal body

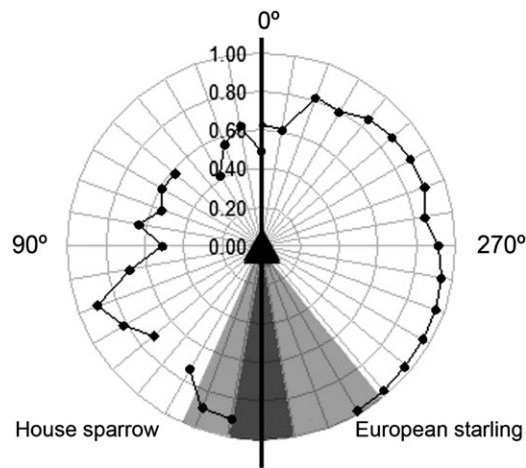


Figure 3
Schematic representation of the probability of predator detection in relation to head orientation of house sparrows (left side) and European starlings (right side) tested with a fixed PEG. Concentric circles represent the probability of predator detection; the farther from the center, the higher the probability. The arrow in the center of the diagram indicates the direction of the bill. We also show the width of the minimum blind area (dark shading) and the maximum blind area (light shading) based on Fernández-Juricic et al. (2008). For representation purposes only, head-orientation values are shown in 10° categories, and probabilities within each category were averaged (n varied from 1 to 6 per category).

condition with focal sex, $F_{1,38} = 1.14$, $P = 0.292$). We included in the PCA the following variables: temperature, wind speed, food-deprivation time, focal body condition, and focal sex. Two factors were generated: PC1 (positively associated with focal sex, factor loading = 0.751; eigenvalue = 1.38; variance explained = 27.60%), and PC2 (negatively associated with temperature, factor loading = -0.867; eigenvalue = 1.31; variance explained = 26.23%).

Thirty-eight of 40 European starlings detected the predator model. In the final model, the probability of predator detection was not influenced by distance to the PEG, body posture, head orientation, PC1, and PC2 (Table 1, Figure 2).

Vigilance behavior

Head-up scan bout duration was significantly different between house sparrows and European starlings ($F_{1,75} = 7.75$, $P = 0.007$), after controlling for the significant effects of temperature (coefficient = 0.02, $F_{1,75} = 5.12$, $P = 0.020$). House sparrow scan bouts (0.16 ± 0.06 min) were shorter than those of the European starling (0.37 ± 0.06 min). Distance to the PEG ($F_{1,75} = 0.65$, $P = 0.421$) and wind speed ($F_{1,75} = 0.24$, $P = 0.627$) did not significantly affect head-up scan bout duration.

Head-up scan rate (log transformed) differed between species ($F_{1,75} = 23.40$, $P = 0.001$): House sparrows (log transformed, 1.89 ± 0.13 events per min) raised their heads more often than European starlings (log transformed, 1.03 ± 0.13 events per min). Distance to the PEG ($F_{1,75} = 0.53$, $P = 0.467$), temperature ($F_{1,75} = 3.31$, $P = 0.073$), and wind speed ($F_{1,75} = 0.64$, $P = 0.425$) did not significantly affect head-up scan rate.

The total proportion of time house sparrows (0.66 ± 0.03) and European starlings (0.69 ± 0.04) allocated to head-up scanning did not differ significantly between species ($F_{1,75} = 0.81$, $P = 0.370$). None of the other factors influenced proportion of time scanning: distance to the PEG ($F_{1,75} = 3.79$,

$P = 0.055$), temperature ($F_{1,75} = 0.93$, $P = 0.338$), and wind speed ($F_{1,75} = 0.55$, $P = 0.461$).

DISCUSSION

We found that the factor associated with the degree of visual acuity (distance to the PEG) influenced significantly the species with the relatively lower acuity (house sparrow), but not the species with the relatively higher acuity (European starling), supporting our predictions. However, the factors associated with the configuration of the visual fields (body posture and head orientation) influenced both species despite our directional prediction based on the between-species difference in the size of the blind area. Furthermore, vigilance strategies varied between species: European starlings had longer scan bout durations, whereas house sparrows had higher scanning rates. We acknowledge this is a between-species comparison (rather than a comparative study), so the differences found could be explained by a wide range of factors besides those associated with visual traits. We first discuss the potential role of visual properties following our predictions, and then we consider alternative explanations.

House sparrows were less likely to detect a predator under the fixed and variable PEGs as distance to the predator increased, with a drop of 50% in detection probabilities across 40 m given a difference of about 30% in visual acuity in relation to European starlings. Visual acuity may constrain house sparrow detection abilities by decreasing the resolution of objects presented farther away (Smith and Laitvaite 1999). However, there are alternative explanations. First, house sparrows' eyes were closer to the ground than European starlings' due to body size differences, which may have changed the angle of elevation between the focal birds and the predator model, but no difference between species was found. Second, house sparrows may have reduced visual attention to the PEG at increasing distances. For instance, Blue Jays *Cyanocitta cristata* have lower visual detection ability when their attention is focused on solving a complex foraging task (Dukas and Kamil 2000). However, food attention costs may not have varied substantially as seeds were readily available for house sparrows across distances. Third, motion detection abilities may have differed between species, which could be tested in the future by comparing the density of double cones, likely associated with motion detection (Hart and Hunt 2007), in the retinas.

The probability of predator detection by European starlings with a fixed PEG decreased by 65% as individuals' body posture varied from head-up to head-down positions, probably as a result of the blind area limiting visual coverage above and at the rear of the head. This finding challenges the classic assumption of mutual exclusivity between vigilance and foraging (Lima and Bednekoff 1999; Guillemain et al. 2001; Cresswell et al. 2003; Bednekoff and Lima 2005; Fernández-Juricic et al. 2005; Quirici et al. 2008). The implication is that in species with intermediate-sized blind areas, body posture is nonlinearly related to the costs of vigilance (e.g., 98%, 75%, and 35% probability of predator detection in vigilance, food searching, and pecking postures, respectively). Body posture also influenced house sparrow probability of predator detection under the variable PEG. However, distance to the PEG was significantly correlated with house sparrow body posture (see Materials and Methods), which may have confounded this effect.

One of the reasons why the factors associated with the configuration of the visual field affected both species, despite the relative size differences in their blind areas, may be because they cannot abolish completely this blind spot even when their eyes are diverged (e.g., minimum blind area size), eventually constraining visual coverage. Body posture and head orientation were limiting mostly when both species were under the

fixed rather than the variable PEG. This scenario resembles habitats with greater visual obstruction (e.g., tall grass) that can conceal predator attacks, thereby increasing perceived predation risk (Whittingham et al. 2004). Empirical observations support this argument in both species, which increase vigilance with visual obstruction as a compensatory mechanism (Lazarus and Symonds 1992; Harkin et al. 2000; Fernández-Juricic et al. 2005), and European starlings also prefer to forage away from cover on short grass swards, where visual obstruction is minimized (Whitehead et al. 1995; Devereux et al. 2004). Thus, the presence of blind areas could make prey more vulnerable to predator attacks specially in habitats in which predators are less exposed or perform ambush attacks.

Previous studies found that head orientation influences the latency to detect a predator, with quicker detection times when prey were facing with their lateral visual fields instead of their blind areas (Kaby and Lind 2003; Devereux et al. 2006). Our results suggest that specific areas “within” the lateral visual field may be associated with enhanced detection. For example, house sparrow probability of predator detection under the fixed PEG was higher in the angular range corresponding to an area of high density of retinal ganglion cells (Dolan T and Fernández-Juricic E, unpublished data) and thus higher acuity. The image of the predator crossing this high-resolution area (Reymond 1987) may have been necessary to resolve it due to the short exposure time in the fixed gap.

The between-species differences in the size of the blind area could have affected vigilance strategies. European starlings had longer scan bout durations than house sparrows probably to compensate for a relatively wider blind area. Longer scan bouts may facilitate monitoring a larger spatial extent around the head. In contrast, it may take house sparrows less time to get a snapshot of the surroundings with their wider visual field coverage. House sparrows had high scanning rates probably to ensure a certain level of predator detection with short interscans intervals (Glück 1987; Cresswell et al. 2003), maybe because low acuity may require more frequent information updates. Alternatively, scan bout duration may be shorter and scan rate higher in house sparrows than in European starlings because handling a seed requires less time than handling an insect (Popp 1988). This difference in food-handling time can affect vigilance costs and thus vigilance strategies (e.g., Cowlshaw et al. 2004).

The take-home message of our study is that sensory constraints can affect predator detection through changes in the position of the prey’s eyes in a 3D space (e.g., body posture, head orientation) and the location of the predator (e.g., linear distance to the predator). There are several important theoretical and empirical implications. First, theoretical models need to relax assumptions on fixed predator detection distances, as species with small detection windows may not detect predators as soon as they break cover. Second, the relative role of the perceptual limit hypothesis (e.g., response times to predator attacks are limited by the time it takes individuals to detect a threat through personal observation or through flock-mate behavior, e.g., Quinn and Cresswell 2005) may differ between species due to different rates of information transfer over a given distance. Thus, sensory constraints may influence the optimal neighbor distance that facilitates detection under different ecological conditions. Third, it is worth testing at the comparative level whether species with relatively low visual acuity use other antipredator strategies (e.g., alarm calls, foraging closer to flock mates) to compensate for the potentially higher predation risk. Finally, we recommend recording body posture and head orientation as continuous variables in future antipredator studies, as they could give a better estimate of predator detection probabilities at the individual and group levels. For instance, even if prey scan independently,

predator detection probabilities can be calculated at any given point in time as the product of the individuals probabilities based on the spatial orientation of their heads and bodies. These sensory-based estimates could provide more realistic scenarios to study the transmission of different types of information in flocks.

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APPENDIX A

Estimation of head orientation under fixed and variable predator exposure gaps

A head-orientation measurement for each trial was taken from the same frame used to calculate body posture (see text). Each frame

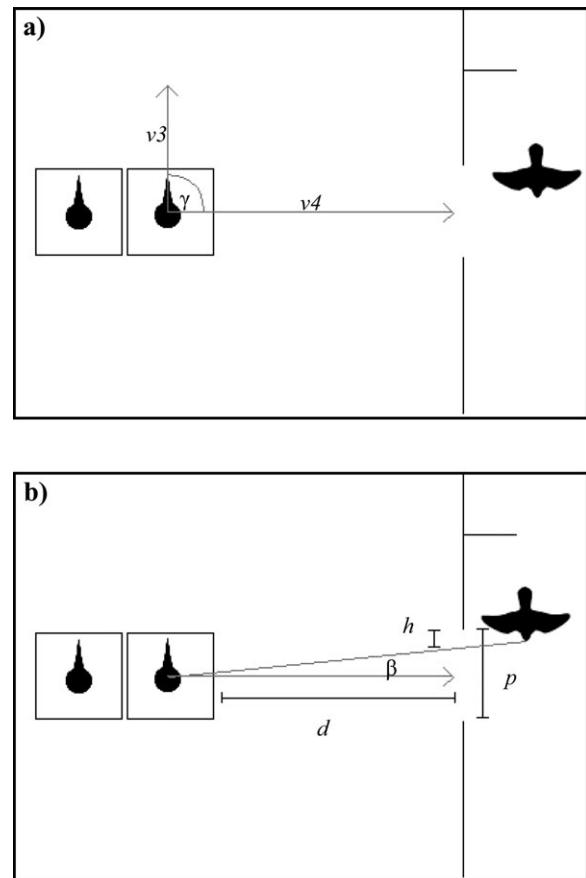


Figure 4

The head orientation of the focal bird was calculated by measuring the angle of the head in relation to the predator exposure gap and applying a correction factor to account for the position of the predator model in the PEG. (a) Initial head orientation, γ , was measured with the vertex of the angle on the center of the focal’s crown, 1 vector ($v3$) extending through the tip of the bill and another vector ($v4$) drawn parallel to the side of the enclosure, which corresponded to the center of the PEG, p . (b) A correction factor, β , was applied to the initial head-orientation measurement, γ , to calculate the approximate head orientation in relation to the predator model.

showed 2 side views of the focal, 1 overhead view of the focal, and a view of the predator model in the predator exposure gap. From this camera arrangement, we measured head orientation to the center of the predator exposure gap and then calculated a correction factor based on the distance the predator model had moved through the gap. A final head-orientation value was calculated by combining the initial head orientation to the PEG and the correction factor.

The initial head-orientation measurement was an angle γ between the tip of the focal bird's bill and the center of the predator exposure gap. The vertex of the angle was placed on the center of the focal's crown in line with the eyes, and 2 vectors defined the angle: 1 vector extended through the tip of the bill and the other vector formed a line parallel to the side of the enclosure, which corresponded to the center of the PEG (Figure 4a).

At the time of response, however, the predator model was not always at the center of the PEG. Therefore, we applied a correction factor, angle β , to the initial head orientation γ :

$$\omega = \gamma \pm \beta, \quad (\text{A1})$$

where ω is the corrected head-orientation value. If the focal bird's bill was facing right, β was added to γ ; if the bill was facing left, β was subtracted from γ .

β was calculated as

$$\beta = \frac{\arctan(p/2) - h}{d}, \quad (\text{A2})$$

where p was the width of the predator exposure gap (Figure 4b), h was the distance the predator model had traveled into the PEG (Figure 4b), and d was the treatment distance (Figure 4b).

We calculated h using the following equation:

$$h = (h'/p') * p. \quad (\text{A3})$$

The actual width of the PEG, p , was known. On the frame, we measured in pixels the distance the predator model had traveled through the PEG, h' and the size of the PEG, p' .

For the statistical analysis, we used the corrected head-orientation value, ω .

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