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Looking above the prairie: localized and upward acute vision in a native grassland bird

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Visual systems of open habitat vertebrates are predicted to have a band of acute vision across the retina (visual streak) and wide visual coverage to gather information along the horizon. We tested whether the eastern meadowlark (*Sturnella magna*) had this visual configuration given that it inhabits open grasslands. Contrary to our expectations, the meadowlark retina has a localized spot of acute vision (fovea) and relatively narrow visual coverage. The fovea projects above rather than towards the horizon with the head at rest, and individuals modify their body posture in tall grass to maintain a similar foveal projection. Meadowlarks have relatively large binocular fields and can see their bill tips, which may help with their probe-foraging technique. Overall, meadowlark vision does not fit the profile of vertebrates living in open habitats. The binocular field may control foraging while the fovea may be used for detecting and tracking aerial stimuli (predators, conspecifics).

The physical structure of a habitat can be considered the visual background upon which animals direct their visual attention. Visual systems are generally configured with acute sensory areas that gather information from parts of visual space that are relevant to an organism¹. These areas of acute vision are called retinal specializations (e.g., foveae), which generally have high density of photoreceptors (i.e., cells involved in phototransduction) and/or retinal ganglion cells (i.e., cells transferring information from the retina to the brain)².

Interestingly, there is evidence that the type of retinal specialization of some vertebrates may be tuned to specific visual backgrounds^{1,3}. Hughes³ proposed that organisms in open habitats (e.g., grasslands, prairies, oceans) should have a horizontal band of acute vision across the whole retina (visual streak) aligned with the horizon (i.e., terrain hypothesis). This visual streak would provide a band of high visual resolution across the extensive flat terrain around the organism where important objects and events are most likely to occur³ and also aid in spatial orientation by using the horizon as a reference point⁴. The terrain hypothesis has been well supported by the predominance of visual streaks reported in open habitat species^{1,5}. For example, within the Family Macropodidae, the open plains red kangaroo (*Macropus rufus*) possesses a visual streak whereas the arboreal Doria's tree kangaroo (*Dendrolagus dorianus*) possesses an *area centralis*⁶. Visual streaks are also found across a wide range of taxa, including selachian sharks whose visual environment is dominated by the sand-water interface and air-water interface⁷, anatid ducks that sit on the water⁸, shorebirds⁹ and seabirds¹⁰ that spend a great deal of time on open shorelines or over the water, and even in the spotted hyena (*Crocuta crocuta*)¹¹ that primarily lives and hunts in grasslands. Despite major ecological differences, all these species live in open habitats with an unobstructed view of the horizon.

Visual streaks in open habitat species are often associated with wide fields of view (i.e., wide lateral fields, narrow binocular and blind areas) to maximize the coverage of high resolution around the head³. For example, the mallard (*Anas platyrhynchos*) has a visual field with complete coverage around the head with narrow blind and binocular areas¹², and a visual streak⁸ that allows it to see almost the entire horizon with high visual resolution.

In this study, we use a combination of physiological, ophthalmological, and behavioral approaches to characterize the visual configuration of the eastern meadowlark (*Sturnella magna*). Under the terrain hypothesis, we predict that the eastern meadowlark will have wide fields of view and a horizontal visual streak to maximize visual coverage along the horizon. To our knowledge, this is the first study characterizing the visual fields and retinal configuration of an open habitat specialist belonging to Passeriformes, which is an Order that includes nearly 60% of all extant bird species¹³. More specifically, the meadowlark forages and nests on the ground in native North American grasslands. Meadowlarks are highly territorial during the breeding season, checking visually for the



approach of potential territory intruders and aerial predators¹⁴. We determined the type and position of the retinal specialization, measured the visual field configuration, estimated spatial visual resolution (i.e., visual acuity) and the distances meadowlarks could detect visual stimuli, and established whether visual obstruction by the habitat (i.e., vegetation height) could influence the orientation of the retinal specialization.

Results

Instead of a visual streak, we found that the density of ganglion cells increased in a concentric manner from the periphery towards the center of the retina (Fig. 1a). We identified the spot with the highest cell density ($32,863 \pm 2,125$ cells/mm²) as a fovea (Fig. 1b). Interestingly, the meadowlark fovea was located in a ventro-temporal position (coordinates -0.16 ± 0.02 on the nasal-temporal axis and -0.05 ± 0.01 on the dorso-ventral axis; Fig. 1). The 95% confidence intervals for the temporal (-0.173 to -0.127) and ventral (-0.069 to -0.027) positions of the fovea did not overlap with zero, suggesting that the fovea is indeed temporally and ventrally shifted. This ventro-temporal position results in the fovea projecting slightly forward and upward into the visual field, providing acute vision approximately $32.5 \pm 1.2^\circ$ forward (Fig. 2b) and $4.3 \pm 0.9^\circ$ above the horizon (Fig. 1c), assuming regions across the retina of equal size subtend equal angles of visual space¹⁵. Our estimate of the fovea projection was corroborated by our measurement of the optic axes, which projected $33.5 \pm 1.0^\circ$ forward and $4.5 \pm 0.3^\circ$ above the horizontal.

The average binocular field width along the horizontal plane with the eyes at rest was $24.0 \pm 0.4^\circ$ (Fig. 2b), however the tip of the beak blocked the view of the retinal margins at elevations 80° – 100° (Fig. 2d, e). Assuming the retinal margin follows a circular path^{16,17}, the extrapolated binocular field on the horizontal plane was actually wider, $32.3 \pm 1.9^\circ$ (Fig. 2b). The implication is that meadowlarks may be able to see their bill tips with the eyes at rest and converged

(Fig. 2a–b, d–e). The blind area width along the horizontal plane with the eyes at rest was $32.7 \pm 1.7^\circ$ (Fig. 2b). The averaged binocular field and blind area across all measured elevations was $20.5 \pm 3.0^\circ$ and $11.4 \pm 2.8^\circ$, respectively (Fig. 2). With the eyes at rest and diverged, the blind area blocked vision above the meadowlark's head (Fig. 2e–f). The pecten, a vascular structure in the eye of birds that is devoid of photoreceptors, created a blind spot in the visual field that had a vertical length of 60° , with an average width of $14.0 \pm 0.7^\circ$ (Fig. 2e).

We found that meadowlarks moved their eyes an average of $13.0 \pm 1.1^\circ$ (single eye movement amplitude) across all elevations, with the maximum amplitude of $20.0 \pm 1.2^\circ$ occurring 30° below horizontal. Convergent eye movements increased the width of the extrapolated binocular field and blind area to $45.0 \pm 3.4^\circ$ and $51.4 \pm 2.2^\circ$, respectively (Fig. 2a). When the eyes were diverged, the binocular field and blind area were $12.0 \pm 1.3^\circ$ and $18.3 \pm 1.1^\circ$, respectively (Fig. 2c).

Our estimate of maximum spatial resolving power was 10.3 ± 0.3 cycles/degree based on eye axial length (10.2 ± 0.1 mm) and peak density of retinal ganglion cells ($32,863 \pm 2,125$ cells/mm²). At 10.3 cycles/degree, a meadowlark would be able to resolve an object with the wingspan of a red-tailed hawk (*Buteo jamaicensis*), Cooper's hawk (*Accipiter cooperii*), and sharp-shinned hawk (*Accipiter striatus*) at maximum distances (and heights due to the upward fovea projection) of 729 m (55 m), 449 m (34 m), and 292 m (22 m), respectively (Fig. 1c). Thus, meadowlarks would have 41, 18, and 11 s after detection to respond to approaching hawks based on their attack speeds¹⁸.

When meadowlarks held the regular head-up body posture, we did not find significant differences in the proportion of time spent in horizontal or elevated head positions between short and tall grass areas (Table 1). However, the proportions of time in horizontal and elevated head positions for the stretched head-up body posture (necks and legs extended) were significantly higher in tall than in short grass areas (Table 1). The combined head movement rate for horizontal and elevated head positions was 48.6 ± 6.0 events/min,

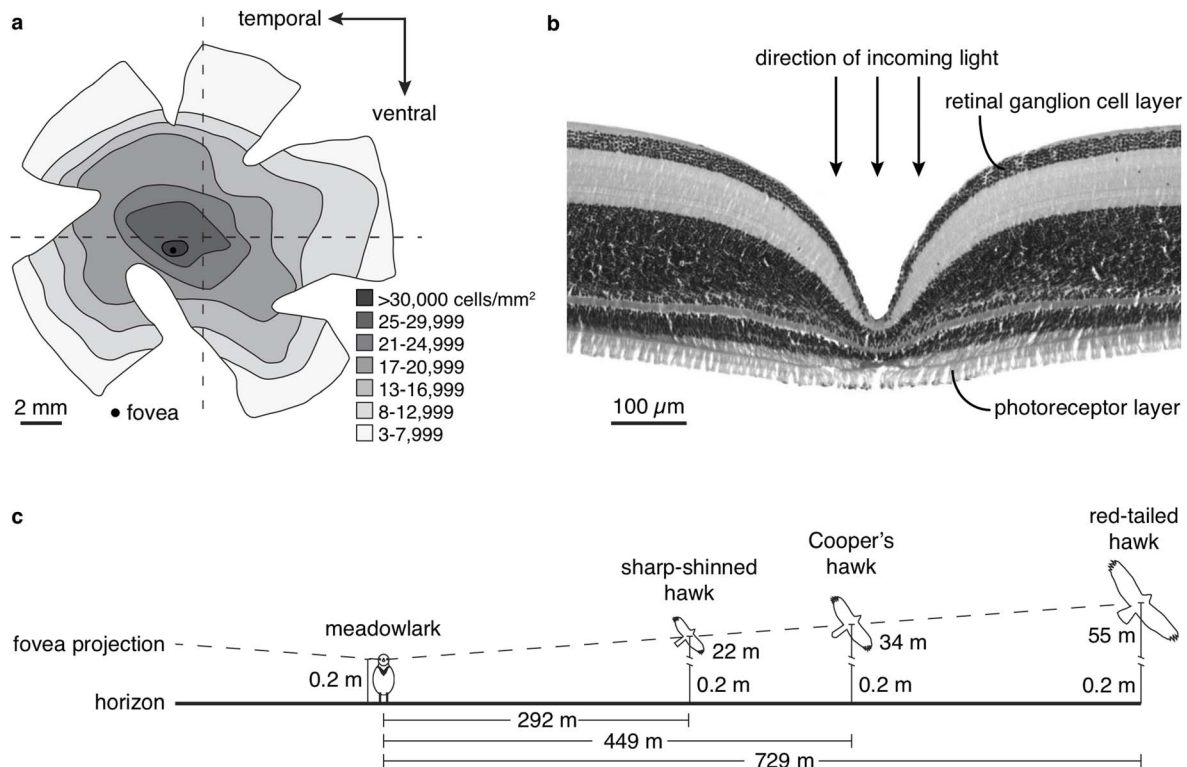


Figure 1 | (a) Meadowlark retinal ganglion cell topographic map. (b) Cross section through the foveal pit. (c) Schematic representation of the projection of the fovea (dotted lines) while the meadowlark is on the ground, facing the viewer, with its head parallel to the ground.

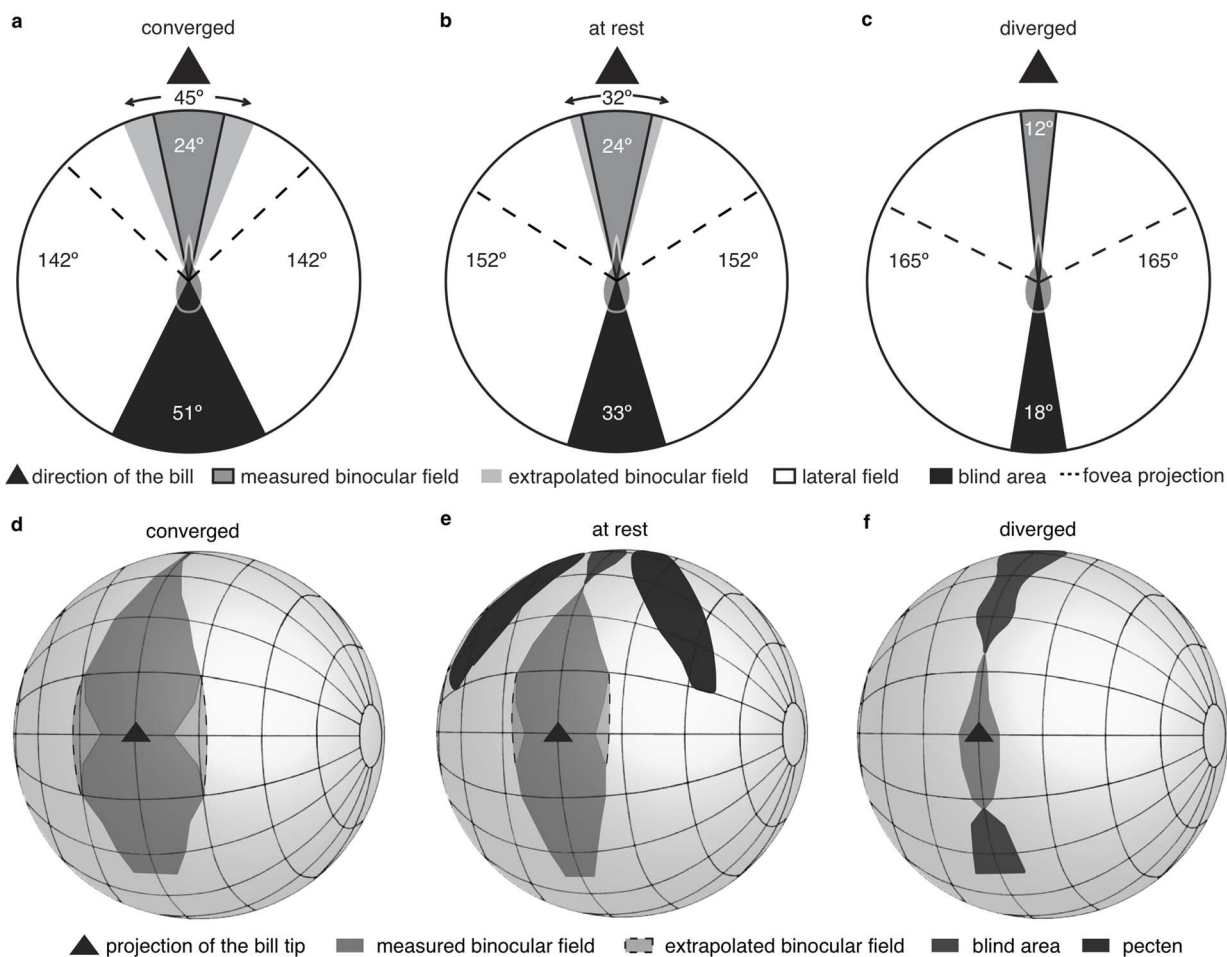


Figure 2 | Meadowlark visual fields. (a–c) Top views through the horizontal plane (90°–270°) when the eyes were (a) converged, (b) at rest, and (c) diverged. (d–f) Projection of the retinal margin boundaries of the two eyes when the eyes were (d) converged, (e) at rest, and (f) diverged. A latitude and longitude coordinate system was used with the equator aligned vertically in the median sagittal plane (head is envisioned at the center of the globe).

but did not differ significantly between short (40.7 ± 6.7 events/min) and tall (56.5 ± 9.3 events/min) grass areas ($F_{1,10} = 1.88$, $p = 0.200$).

Discussion

The configuration of the eastern meadowlark visual system does not follow that of other vertebrates inhabiting open areas. Instead of a visual streak with a band of high cell density across the retina, the meadowlark has its center of acute vision concentrated in a single fovea, which reduces the *proportion* of the visual field with high visual resolution. However, strictly foveate species have been found to have higher visual resolution *within* the retinal specialization compared to species with strictly visual streaks^{19–21}. The implication is that the detection of conspecifics and predators from far distances in meadowlarks would be enhanced in the fovea relative to other retinal portions. This supports the idea that bird species in open habitats may be more limited by visual resolution than by visual coverage as aerial predators tend to attack from far away and from specific directions (e.g., above the head)²².

Thus, visual specializations that enhance directional predator detection, like the meadowlark fovea, would lengthen predator exposure times (i.e., time between detection and response by the prey). An alternative interpretation to meadowlarks having a fovea could be due to phylogenetic relatedness²³, as most studied passerines seem to be foveate (e.g., Chievitz⁹, Slonaker²⁴, Wood²⁵). However, this interpretation requires studies assessing the evolution of the type of retinal specialization in relation to different habitat types in birds while controlling for phylogenetic effects.

Interestingly, the meadowlark fovea does not project to the horizon but about 4° above the horizon. Some fish have ventro-temporally shifted retinal specializations, presumably for attacking prey from below [e.g., Temple et al.²⁶], and some afoveate, arboreal mammals have relatively low resolution ventral specializations, presumably for foraging and climbing^{27,28}. We speculate that the meadowlark's ventral fovea may be a different sensory adaptation to life on the ground for continuously tracking flying conspecifics and aerial predators, particularly with the blind area blocking the top of the

Table 1 | Proportion of time (mean \pm SE) meadowlarks spent in different body postures in short and tall grass

body posture	head position	short grass (proportion of time)	tall grass (proportion of time)	$F_{1,10}$	P
normal head-up	horizontal	0.271 ± 0.065	0.248 ± 0.062	0.06	0.806
	elevated	0.045 ± 0.022	0.002 ± 0.002	3.75	0.082
stretched head-up	horizontal	0.016 ± 0.014	0.194 ± 0.050	11.90	0.006
	elevated	0	0.091 ± 0.040	5.15	0.047

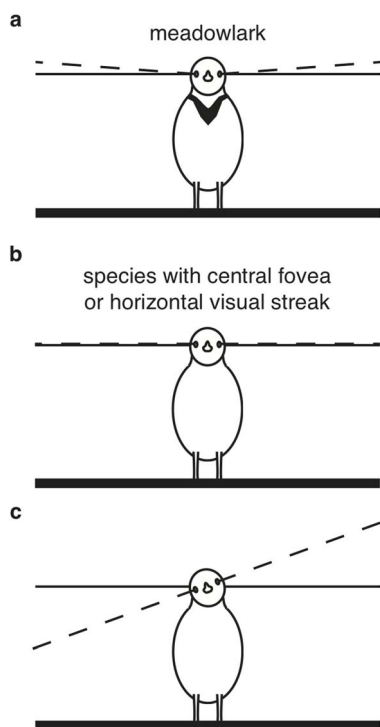


Figure 3 | (a) When the eastern meadowlark head is held in a normal, horizontal position, the foveae from both the left and right eye project above the horizon. (b) When a species with a centrally placed retinal specialization holds the same head posture, the retinal specialization of both eyes project to the horizon. (c) If a species with a centrally placed retinal specialization were to tilt its head to view the sky, only one retinal specialization images the sky while the other projects to the ground. The unique ventral position of the eastern meadowlark fovea allows it to view the sky with the retinal specialization of both eyes simultaneously in a normal, head-up posture.

head. In the resting head position, meadowlarks could resolve approaching raptors early (Fig. 1c) because the projections of both foveae are directed towards the sky simultaneously. Other open bird species with a horizontal visual streak would need to tilt their heads sideways to orient their retinal specialization to the sky with only one eye at a time (Fig. 3). Furthermore, meadowlarks appear to maintain the upward orientation of the fovea in relation to the horizon even in microhabitats with high visual obstruction (e.g., tall grass) by adjusting their body posture (Table 1).

An obvious disadvantage to a fovea is that it views a small area of space, rather than the extensive region viewed by a visual streak. A foveate species could use head or eye movements to increase the amount of the environment covered by the fovea, whereas a species with a visual streak would be less reliant on head and eye movements to sample their visual environment at the highest visual resolution attainable within their visual system³. Although data for head movement rates in visual streak species are limited to the Canada goose (*Branta canadensis*), meadowlarks appear to have a higher overall head movement rate (48.6 ± 6.0 events/min) than Canada geese (19.9 ± 1.9 events/min)²⁹. The combination of head movements and amplitude of eye movements in meadowlarks may allow them to use their fovea to scan the open habitat around their heads with high acuity.

One potential drawback of a ventral retinal specialization is that the sun is imaged on the ventral region of the retina. This can degrade the retinal image³⁰ or generate glare effects³¹. The pecten has been proposed to protect the eye from direct light³², as it projects into the celestial hemisphere above the fovea (Fig. 2e). Meadowlarks may

orient the pecten or the blind area above and behind the head towards the sun to reduce glare, and thus protect the foveal high visual resolution when scanning for predators.

Meadowlarks' binocular fields and blind areas are wider than other species inhabiting open areas^{10,29,33}, but are also narrower than some other passerines^{34,35}. It is possible that meadowlarks have a narrower blind area behind the head, and thus a narrower binocular field, than other passerines to increase visual coverage of their expansive open habitat. At the same time, meadowlarks' blind area is not as narrow as open habitat non-passerines because the meadowlark must maintain sufficient binocular overlap to see the region around their bill, thereby increasing the size of the blind area behind the head. Meadowlarks' ability to see their bills could enhance their open-billed probe-foraging technique (i.e., the closed beak is inserted into the ground and the mandibles are spread apart to expose food items^{36,14}), because the bill could be inspected with the binocular field when the eyes converge. Actually, the largest degree of eye movement occurred within the region between opened mandibles. Common starlings (*Sturnus vulgaris*) have also been proposed to use their binocular field while open-billed probing³⁷. Both starlings and meadowlarks have relatively long bills compared to other passerines, which probably allows them to more easily see the area around their bill tip³⁴, and both have maximum binocular fields greater than 40° within the region of the opened mandibles (Fig. 2d)³⁷.

Overall, the meadowlark visual system does not fit the profile of vertebrates living in open habitats, suggesting that the visual specializations of ground dwelling and open habitat species may be more diverse than those proposed by the terrain hypothesis (see also Fernández-Juricic et al.²⁹). A localized center of acute vision projecting upwards could be more advantageous for early detection and tracking of aerial predators and conspecifics than a horizontal visual streak.

Methods

Birds. Four eastern meadowlarks were captured in collaboration with the United States Department of Agriculture-Animal Plant and Health Inspection Service from a population near Indianapolis, Indiana. The Purdue Institutional Animal Care and Use Committee (1201000567) approved all procedures.

Tissue sampling. We euthanized four individuals with CO₂, removed the eyes by cutting the conjunctiva and pulling the optic nerve with forceps. We then measured the eye axial length using digital calipers (0.01 mm accuracy). We hemisected six eyes at the ora serrata, removed the vitreous humor, and fixed the retinæ with 4% paraformaldehyde while still in the eyecup. We successfully extracted, wholemounted, and stained with cresyl violet all six retinæ following the techniques presented in detail in Ullmann et al.³⁸. In all six retinæ, we measured the location of the retinal specialization in relation to the center of the retina using a Cartesian coordinate system following Moore et al.¹⁹.

Microphotographs of the retinal ganglion cell layer were taken on four retinæ using an Olympus BX51 microscope at 1000× total magnification and an Olympus S97809 camera. We captured images at ~410 sites across a single retina using Stereo Investigator (MBF Bioscience, Williston, Vermont) and counted the ganglion cells within a 50 μm × 50 μm counting frame at each site to estimate cell density (number of cells/mm²). The area sampling fraction (i.e., proportion of each grid that was occupied by the counting frame) was 0.00598 ± 0.00045 . The ganglion cell layer can also include other cell types (e.g. amacrine, glial cells, etc.) that were identified and excluded based on their soma size, shape, Nissl accumulation in the cytoplasm, and staining of the nucleus^{39–42}. To visualize the distribution of ganglion cells, we constructed topographic maps using isodensity lines along the boundaries of seven categories of cell density ranges (Fig. 1a).

To confirm the type of retinal specialization, we performed a histological cross section on one eye. After hemisecting the eye at the ora serrata and removing the vitreous humor, we placed the eyecup into Bouin's fixative for 24 hours and washed the eyecup in 0.01 M phosphate buffered saline pH 7.4 (PBS) following fixation. We then located the presumed retinal specialization under a light microscope and cut out a 2 mm thick strip of the eyecup, which was placed in 70% ethanol for 1 week to pull out excess Bouin's fixative while maintaining fixation. We embedded the tissue in paraffin wax, and serial sectioned it along the anterior-posterior axis with a Thermo Scientific Shandon Finesse ME microtome (Waltham, Massachusetts). Sections were stained with haematoxylin/eosin in a Thermo Scientific Shandon Varistain 24-3.

Visual fields. We measured the visual field configuration of three eastern meadowlarks with a visual field apparatus following Martin⁴³. Live individuals were restrained at the center of the apparatus with the bill held parallel to the ground. We



used an angular coordinate system where the head was positioned at the center of a globe with the axis passing through both eyes. In this system, 0° elevation is above the head, 90° is in front of the bird, and 270° is behind the bird's head. We measured the retinal visual field while the eyes were in a resting position using the ophthalmoscopic reflex technique⁴³ with a Keeler Professional ophthalmoscope. Measurements were taken in 10° increments from 140° (below the beak) to 270° (behind the head), where the body or the visual field apparatus would not obstruct the observer. We also measured the retinal visual fields and the degree of eye movement when the eyes were converged and diverged.

The optic axis (i.e., line passing through the center of the cornea and lens) is often closely aligned with the laterally projecting retinal specialization in birds (e.g., Nalbach et al.⁴⁴, Pettigrew⁴⁵). To measure the projection of the optic axis into visual space, we mounted a white LED onto the side of the ophthalmoscope and turned off the ophthalmoscope light source. The optic axis was judged to be point where the three discernable Purkinje images (i.e., reflections from the anterior and posterior surfaces of the cornea and of the lens) were superimposed following Martin⁴³.

Spatial resolving power. We estimated spatial resolving power (i.e., visual resolution) in cycles per degree following the sampling theorem^{46,47}. The posterior nodal distance (PND) was calculated as 0.6 multiplied by the axial length of the eye^{38,48}, and the retinal magnification factor (RMF) was calculated as⁴⁶ $RMF = 2\pi PND/360$. We then

calculated the theoretical maximum spatial resolving power as $SRP = \frac{RMF}{2} \sqrt{\frac{2D}{\sqrt{3}}}$

where D is the retinal ganglion cell density⁴⁷. Based on spatial resolving power, we calculated the distance (d) at which an object of known size (different predators) would occupy the same angle of retinal space as one cycle at the threshold of resolution (i.e., theoretical maximum distance objects could be resolved under optimal ambient light conditions) using $d = \frac{r}{\tan \frac{\alpha}{2}}$, where r is the radius of the object,

and α is the inverse of spatial resolving power.

Behavior. To determine overall head movement rate and differences in body posture and head position in long and short grass (grass height was higher or lower than the height of the bird in a normal, head-up body posture, respectively), we coded twelve 15–60 s videos (six in each microhabitat type) of foraging eastern meadowlarks from the Macaulay Library (<http://macaulaylibrary.org>) and the Internet Bird Collection (<http://ibc.lynxeds.com>). By extending the neck and legs, a meadowlark could increase its overall height to minimize visual obstruction by tall grass. It could also change the orientation of the retinal specialization by tilting the head upwards. Therefore, we recorded the proportion of time meadowlarks spent in four combinations of head and body postures with JWatcher⁴⁹: (1) normal head-up body posture with the bill held parallel to the ground $\pm 2^\circ$ (hereafter, horizontal head position), (2) normal head-up body posture with the bill elevated 2° – 10° (hereafter, elevated head position), (3) stretched head-up body posture with an horizontal head position, and (4) stretched head-up body posture with an elevated head position. In the stretched body posture, the bird extended its neck and legs to increase its overall height. Additionally, we coded the same twelve videos for overall head movement rate. In this case, we defined a head movement as any movement of the head to or within a horizontal or elevated head-up position. Throughout, we present means \pm standard error.

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Author contributions

L.P.T. and E.F.J. conceived the study. L.P.T. and C.L. captured the subjects. C.L. provided intellectual input. L.P.T. and B.A.M. performed the experiments. L.P.T. and E.F.J. wrote the manuscript. All authors reviewed the manuscript.

Additional information

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