



Visual Fields Configuration and Eye Movements of a Passeriform Bird with a Varying Foraging Behaviour

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Abstract: Visual field is the main sensory modality for birds to gather information on food and threats; however, this has been largely unexplored for the passeriform birds having a varying foraging behaviour. Visual field and eye movements of the red-billed starling *Spodiopsar sericeus*, a passeriform bird with multiple foraging behaviours in different habitats, were determined using ophthalmoscope reflection technology. We found that projection of the bill was below the centre of the binocular field and part of the retinal visual field was impeded by the bill when eyes converged. The vertical extent of the binocular field above the bill was significantly longer than that below the bill. The amplitude of eye movement, mainly occurring in the regions of ventral-nasal and dorsal-temporal, had a very significant effect on the visual field. The widest extent of binocular field was at the elevation below bill when eyes converged forward, but was at the elevation above bill when eyes diverged backward. Our findings suggested that visual field configuration and eye movement in the red-billed starling may be the integrated adaptability to visual demand dependant on their varying foraging behaviour at different habitats.

Key words: visual ecology, visual field, eye movement, foraging behaviour, *Spodiopsar sericeus*

Introduction

A functional visual system is fundamental to the survival of most animal species (STEVENS 2013, MARTIN 2017). Visual field and eye movement, important components of the system, is the main sensory modality for birds to gather information on food and threat (MEYER 1977, FERNÁNDEZ-JURICIC et al. 2004, MARTIN 2007, 2017), and foraging behaviours and anti-predation capacity of most birds are constrained by the extent of visual field and eye movement (MARTIN 1999, 2007, 2014, LAND

2015). Assessing the visual field configuration and eye movement of birds is important for understanding the physiological mechanism of behavioural ecology.

Previous studies in different taxonomic groups indicate that the visual field configuration of birds is closely related to specific feeding techniques and /or foraging strategies, which form different types of visual field. The sit-and-wait foragers tend to have long and broader binocular field, relatively wide monocular field, wide blind area and a low amplitude of eye movement, such as diurnal rap-

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tors (REYMOND 1985, FROST et al. 1990, INZUNZA et al. 1991, MARTIN & KATZIR 1999, O'ROURKE et al. 2010, PORTUGAL et al. 2017), herons (MARTIN & KATZIR 1994, MARTIN et al. 2008) and flycatchers (COIMBRA et al. 2006, GALL & FERNÁNDEZ-JURICIC 2010). The visual field configuration of active-pursuit birds which hunt prey in flight is similar to that of the diurnal raptors than that of flycatchers (TYRRELL & FERNÁNDEZ-JURICIC 2017). For the ground and tree foragers which detect and grab prey items at close distances, their bills project toward the relatively wide binocular field with a large degree of eye movement (MARTIN 1986, MARTIN & KATZIR 1995, FERNÁNDEZ-JURICIC et al. 2008, DOLAN & FERNÁNDEZ-JURICIC 2010). The different visual demands of the specific feeding behaviours among closely related species lead to a subtle adaptability of their visual field (TROSCIANKO et al. 2012, MARTIN 2014). Until now however, the visual field of 13 passerine species have been studied (MARTIN 2017), accounting for only a small part of passerine bird species.

Several recent studies within the same taxonomic groups have shown that there are obvious inter-species differences in visual field and eye movements (MARTIN 2009, MOORE et al. 2015, POTIER et al. 2016). The birds that live in the same environment using different feeding strategies to obtain food also have different visual field characteristics (MOORE et al. 2013). These comparative studies suggest that the interspecies differences in visual field configuration are ecological adaptations for the visual demand of different feeding behaviours. Passerine birds use a variety of feeding tactics to obtain food items in different environments (ROBINSON & HOLMES 1982, REMSEN & ROBINSON 1990, RICKLEFS 2012), which is expected to enhance visual performance to meet the demand of the different foraging strategies in various habitats (BOUGHMAN 2002). Therefore, visual field configuration and eye movement for the passeriform birds with varying foraging strategies should probably be more complex. However, the features of visual field in these passeriform birds have been largely unexplored.

The red-billed starling *Spodiopsar sericeus* (Gmelin, 1789) (Sturnidae) is a passeriform species having a varying foraging behaviour to feed prey items, and mainly foraging on the ground (WILMAN et al. 2014) where they extract invertebrates employing the foraging techniques similar to that of the European starling *Sturnus vulgaris* (see MARTIN 1986). This means that visual field configuration and eye movement of the red-billed starling may be similar to that of European starling. However, the red-billed starling is a typical fruit-eating bird (WILMAN et

al. 2014). It is considered that fruit-eating starlings could not see the space between the opening mandibles when prying the ground surface, because the anterior part of the skull in these starlings is wider than that of omnivore starlings (BEECHER 1978). In addition, the red-billed starlings forage at multiple strata, including ground, understory, midhigh and canopy (WILMAN et al. 2014). The predation risk for the birds foraging in the canopy stratum is different to that of the birds foraging in the lower stratification and on the ground (SUHONEN 1993a, 1993b, BLUMSTEIN et al. 2004, ANDERSSON et al. 2009), which indicates that different visual detectability is needed. In the current study, we characterized and detailed the visual field configuration and eye movement of the red-billed starling to explore the relationship of visual features and multiple foraging behaviours.

Materials and Methods

Subjects captured and feed

Totally, seven adult red-billed starlings (4 males and 3 females, Appendix 1) were captured at the central-south areas of Yunnan Province (23° 43.21' N, 102° 29.13' E), southwest China. All starlings were housed on campus with one or two birds per cage (60 cm × 40 cm × 40 cm). Birds kept under natural light /dark cycle and temperature. Food (chicken food and *Tenebrio molitor* mix) and water were provided every day *ad libitum*. One week later, the visual field of the starlings was measured. All visual field measurements were conducted at Chuxiong Normal University.

Measurements of visual field

The retinal visual fields and eye movement of red-billed starlings were determined by the ophthalmoscopic reflex technique with a visual field apparatus, which is a non-invasive operation and has been used in a wide range of birds (MARTIN 2007, 2017). The detailed description of the apparatus and measurement procedures was described in MARTIN (1984, 1986). Briefly, each bird was secured in a foam cradle using Velcro straps and the head was positioned at the central of the apparatus with the legs taped lightly together and held behind the body (Appendix 2). The line between the two eyes of the starling aligned with the pivot points of the visual field apparatus. The bill was firmly attached to a metal sheet with Micropore Tape™, and the bill position was fixed at an angle (10°), between the bill and the horizontal plane while the bird was perching. We also used a string to calibrate and determine the alignment between the central line of bill to tail and

the median sagittal plane of the visual field apparatus. This arrangement permitted the visual field to be determined at all elevations except where the retinal margin was obscured by the bird's own body and the apparatus. The apparatus' coordinate system followed conventional latitude and longitude with the equator aligned perpendicularly in the birds' median sagittal plane, and this co-ordinate system is also used for presentation of visual field data. Prior to measurement, the stationary individual was quietly adapted for at least 10 min in the darkroom. The functional visual field of the starling was measured in a polar coordinate system, in which the 0° elevation lay directly above the head of each bird, 90° in front, 180° below the bird and 270° behind the bird (Fig. 1). The 90°–270° plane was parallel to the ground and defined as the horizontal plane. The measured values of visual field were corrected according to a hypothetical viewpoint placed at infinity. This correction is based upon the distance used in the measurements taken with the visual field apparatus and the horizontal separation of the eyes (MARTIN 1984).

Each bird was kept alert (no anaesthetic was used). The projection of the retinal margins of each eye was measured using an ophthalmoscope mounted on the perimeter arm with an accuracy of $\pm 0.4^\circ$ at each elevation, which was varied in 10° increments in the median sagittal plane. The margins of the pecten were also recorded. It is highlighted that birds' eyes could not remain in a resting position without anaesthesia for a long time (MARTIN 1986). In each case, to ensure the two eyes of the measured bird was at relative rest, we placed symmetrically two flashing lights (i.e., candle sealed lantern with holes facing the bird eyes), at 1.5 m in front of both sides of the measured bird. The angle from the middle point between the two eyes of the measured bird to the two lights was about 110° , which was similar to the divergence of the optic axes in European Starling (MARTIN 1986). In addition, the measurement process was completed during short duration (about 6 minutes). We thus assumed the measurement in this state was in a resting state. To determine the maximum and minimum visual fields, eye movements were then elicited using a small light source and sharp sounds (whistle sound, tapping or finger snapping). The position of the retinal field margins produced by the movement of eyes towards the limit front and rear of head at each elevation was recorded. The measurement was quickly repeated 3 times on every elevation, both left and right eye simultaneously. From this process, the resting position, converging position and diverging position of two eyes were determined. If the body

or head position of the individual was altered during the measurement process, we put it back into the cage and measured another bird. In order to ensure the independence of the data, the individuals who failed to measure were placed in different cages to the successful individuals, and the measurements were made the next day. Each individual was measured and recorded only once.

Data analysis

The width of the binocular and lateral field and the extent of the blind areas behind the head in the horizontal plane were calculated. The width of binocular field and blind area was the difference between the projection sites on the perimeter arm of the retinal jagged of two eyes on the same elevation as the eyes at resting, diverging and converging position. The width of the unilateral area for each eye in the horizontal plane was calculated using the following formula $[(360 - (\text{mean blind area} + \text{mean binocular field}))/2]$ (FERNÁNDEZ-JURICIC et al. 2008). The monocular visual field, the scope that can be covered by one eye, was calculated according the formula $[\text{monocular visual field} = \text{mean lateral field} + \text{mean binocular field}]$. The cyclopean visual field was the sum of visible range $[\text{cyclopean visual field} = 360^\circ - \text{blind area}]$. The vertical extent of binocular field and the length of pecten per eye were estimated from the readings number of consecutive 10° elevations. The maximum amplitude of eye movement at each elevation for each eye was half the difference of the value in the retinal visual fields between the converging and the diverging position.

To examine if eye movement and sex affected the extent of visual field (including binocular overlap and blind area) with the elevation changes, generalized linear mixed model with Gaussian distribution was used. The same method was used to examine if sex affected the width of pecten changed with the elevation changes between left and right eye. Bird ID was as the random factor and all other independent variables were fixed variables. To compare the vertical extent of binocular field above and below the bill at different eye status (resting, converging and diverging), paired Wilcoxon signed-rank test (two-tailed) was used. Statistical analysis was done in R language (R Core Team 2016). All results are reported as means \pm SE.

Results

When the eyes were at resting position, the vertical extent of the binocular field in the red-billed starlings was $136.97 \pm 2.16^\circ$ in median sagittal plane

(Fig. 1). The vertical extent of the binocular field was significantly longer ($p = 0.016$) above the bill ($74.61 \pm 1.46^\circ$) than that below the bill ($62.36 \pm 2.24^\circ$, Fig. 1). The length of pecten in the red-billed starling was about 70° per eye from the elevation of 10° to 80° (Fig. 1), with an average width of $4.39 \pm 0.38^\circ$ for all elevations. The widest of pecten was about $7.14 \pm 0.40^\circ$ at the elevation of 30° . The width of pecten significantly changed with elevation but without difference in both eyes regardless of the sex (Table 1). In horizontal plane, the width of the binocular field of the red-billed starling was $33.79 \pm 0.56^\circ$, and the blind area, the monocular field and the lateral field was $50.43 \pm 1.04^\circ$, $171.68 \pm 0.72^\circ$, $137.89 \pm 0.43^\circ$ respectively (Fig. 2a). The cyclopean visual field was $309.57 \pm 1.04^\circ$.

When the eyes are converging forward, the vertical extent of binocular field of the red-billed starling was the longest ($154.76 \pm 1.71^\circ$, Fig. 3) in median sagittal plane. The vertical extent of binocular field was significantly longer ($p = 0.035$) above the bill ($81.06 \pm 1.17^\circ$) than that below the bill ($73.70 \pm 0.95^\circ$). In horizontal plane, the width of binocular field was $40.88 \pm 0.90^\circ$, the blind area, the monocular field and the lateral field was $57.03 \pm 0.19^\circ$, $171.93 \pm 0.45^\circ$, $131.05 \pm 0.47^\circ$ respectively (Fig. 2b). The cyclopean visual field was $302.97 \pm 0.19^\circ$.

As the eyes were diverging backward, the vertical extent of binocular field in median sagittal plane was the shortest ($74.72 \pm 1.43^\circ$, Fig. 3), less than $\frac{1}{2}$ that of their converging position. The vertical extent of binocular field was significantly longer ($p = 0.015$) above the bill ($59.98 \pm 1.61^\circ$) than that below the bill ($14.74 \pm 0.51^\circ$). In the horizontal plane, the width of binocular field, blind area, monocular field, and lateral field was $6.82 \pm 0.53^\circ$, $44.93 \pm 0.64^\circ$, $160.94 \pm 0.49^\circ$, $154.13 \pm 0.36^\circ$ respectively (Fig. 2c). The cyclopean visual field was $315.07 \pm 0.68^\circ$.

The eye movement amplitude was $11.09 \pm 0.74^\circ$ for each eye across elevations, mainly in the nasal ventral area (90° to 180°) and dorsal temporal area (270° to 360°) (Fig. 4). The largest amplitude of eye movement ($\sim 22^\circ$) was at the elevation from 120° to 130° in the nasal ventral area. Eye movements had a very significant effect on the binocular field and blind area at different elevations, but there was no significant difference in visual field between the females and the males (Table 1). When the eyes converged forward, the widest extent of binocular field in red-billed starling was at the elevations below the bill but was at the elevations above the bill when the eyes diverged backward (Fig. 3).

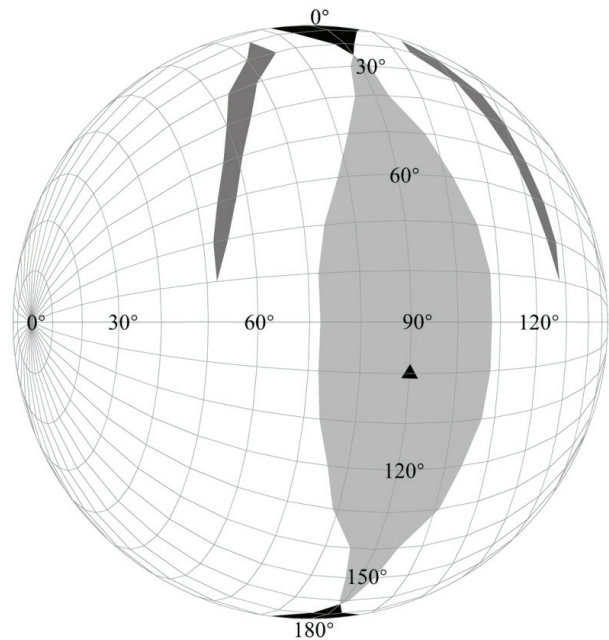


Fig. 1. Perspective view of an orthographic projection of the mean width of the starling's frontal visual field when the eyes are at rest ($N = 7$). The head is at the centre of the sphere with the tip of the bill projected towards the point shown (black triangle, 100°) and the fields projected onto the surface of the sphere (grid at 10° intervals in both latitude and longitude). The grey area shows projection of retinal binocular fields, black areas are the blind areas and the dark grey areas are the pecten.

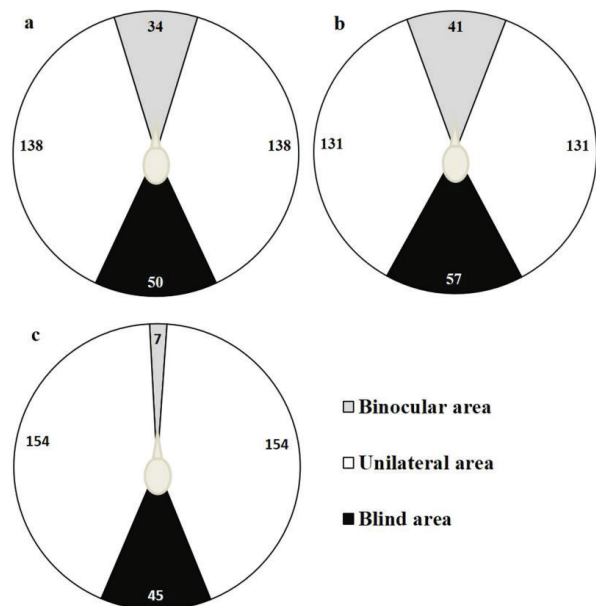


Fig. 2. Horizontal sections through the average retinal visual field in the horizontal plane (90° – 270°) of red-billed starlings when the eyes are at rest (a), converged (b) and diverged (c) ($N = 7$). The size of each segment is indicated in degrees.

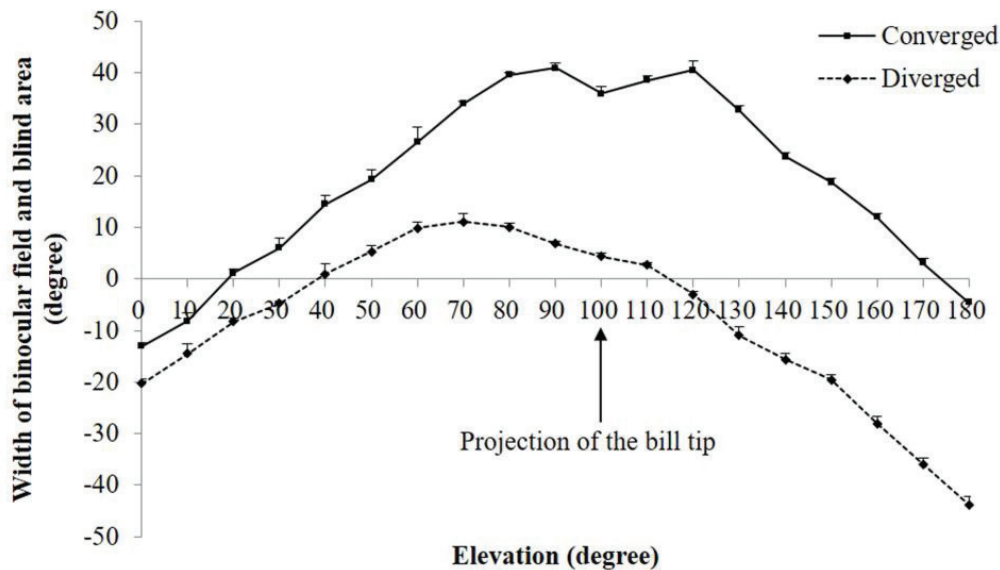


Fig. 3. Mean width of the binocular and blind area (\pm SE) of red-billed starlings ($N = 7$) as a function of elevation in the median sagittal plane when the eyes are maximally converged and diverged. The elevations shown, beginning directly above the head (0°) and moving to front the head (90°) and directly below the head (180°). Negative values (below the x-axis) indicate blind areas, while positive values (above the x-axis) indicate areas of binocular field.

Table 1. Effect of sex, status, elevation on the width of visual field (including the binocular field and blind area) and pecten in *Spodiopsar sericeus*. Results from generalised linear mixed models with the fixed factors (sexes, elevation and status), one random factor (bird_ID) and the interaction. Bold highlights statistically significant.

Variables	df	LRchisq	P
Binocular field			
Sex	1	0.074	0.786
Status	2	1298.336	<0.001
Elevation	15	1703.371	<0.001
Sex : Status	2	2.949	0.229
Sex : Elevation	15	13.026	0.600
Status : Elevation	20	202.453	<0.001
Sex Status : Elevation	19	6.059	0.997
Blind area			
Sex	1	0.002	0.963
Status	2	127.265	<0.001
Elevation	20	4470.926	<0.001
Sex: Status	2	1.731	0.420
Sex: Elevation	20	14.564	0.420
Status: Elevation	29	1311.829	<0.001
Sex: Status: Elevation	26	6.165	1.000
Pecten			
Sex	1	0.014	0.904
Elevation	7	66.802	<0.001
Eyes	1	0.052	0.819
Sex: Elevation	7	3.951	0.785
Sex: Eyes	1	0.277	0.598
Elevation: Eyes	7	1.724	0.973
Sex: Elevation: Eyes	7	7.249	0.403

Discussion

This study showed that the red-billed starling has broad binocular field in the forehead and the bill is at the lower centre of the long and narrow binocular field, which is a unique feature to the species that use vision to precisely control bill feeding (MARTIN 2017). The visual of red-billed starling were apt to the tree birds using active foraging strategy, the eye movement was similar to birds which forage on the ground in open habitat. These results indicated that the visual features of red-billed starlings may be related to their varying foraging behaviour in different habitats.

Visual field configuration

When the eyes are at rest, the vertical extent of binocular field ($\sim 134^\circ$) of red-billed starling in median sagittal plane is similar to that of the passeriform birds which feed on the ground ($\sim 102^\circ$ - 200° ; see MARTIN 1986, 2007, FERNÁNDEZ-JURICIC et al. 2008, 2011, GALL & FERNÁNDEZ-JURICIC 2010). At the horizontal plane (elevation 90° , 10° above the bill), the width of binocular field in red-billed starling is similar to that of corvid (FERNÁNDEZ-JURICIC et al. 2010) and flycatcher species (GALL & FERNÁNDEZ-JURICIC 2010), but narrower than that of the ground-foraging birds (FERNÁNDEZ-JURICIC et al. 2008, FERNÁNDEZ-JURICIC et al. 2011). This may be due to the difference of eye position in head and the extent of the eyes forward tilt. The starling's optic axis is closer to the front of the head (MARTIN

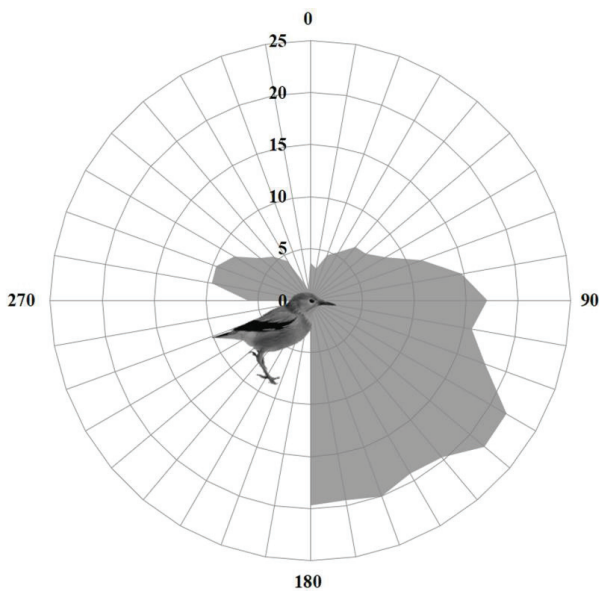


Fig. 4. The average amplitude of eye movements as a function of elevation in the median sagittal plane of the red-billed starling ($N = 7$). The size of each segment is indicated in degrees.

1986), while the ground-foraging birds are more lateral (FERNÁNDEZ-JURICIC et al. 2008, MOORE et al. 2013). This also led to the average blind area of the starlings in the horizontal plane wider than that of those ground-foraging birds. Compared with *S. vulgaris* (MARTIN 1986), monocular field (including binocular and lateral field) of red-billed starlings were wider in the horizontal plane and the planes above bill, when the eyes are at resting and converging position. The width of monocular field may be related to the tracking of prey and the detection of threat (TISDALE & FERNÁNDEZ-JURICIC 2009, GALL & FERNÁNDEZ-JURICIC 2010, MARTINHO et al. 2014, MARTIN 2017) and to ensure access to information on companion feeding and danger signals in the environment during foraging (FERNÁNDEZ-JURICIC et al. 2007, BLACKWELL et al. 2009). The red-billed starling mainly feed on fruit in the canopy stratum (WILMAN et al. 2014), where they are more likely to be exposed to their natural enemies than the birds in the lower stratification (ANDERSSON et al. 2009, MOORE et al. 2013).

When eyes of the red-billed starling converged, the prefrontal binocular field narrowed in the bill plane (Fig. 3), because that part of retina projection was blocked by the bill. Due to bill obstruction, the binocular field around bill is not measured accurately in *S. vulgaris* (MARTIN 1986), *Corvus brachyrhynchos* (FERNÁNDEZ-JURICIC et al. 2011) and *Sitta carolinensis* (MOORE et al. 2013). The broad bill affects the binocular range of finches

(FERNÁNDEZ-JURICIC et al. 2008). Those indicate that the red-billed starling could guide the bill to glean surface insects and peck fruits through the binocular field. The range of mouth opening in red-billed starlings ($43^\circ \sim 51^\circ$) is similar with that of the *S. vulgaris* (46° , MARTIN 1986). When the eyes converged forward, the vertical extent of the binocular field below bill was approximately 70° (Fig. 3). This meant that the maximum range of mouth opening in this starling was completely covered by the binocular field when the eyes converged. It is possible that the binocular field of the red-billed starling as the eyes move forward is used to examine the area between the upper and lower mandibles when the mouth opened. The binocular field of the red-billed starling was narrower below bill but wider above bill than that of European starling as eyes converged forward. This is possible due to the fact that anterior part of the skull in the red-billed starling is wider than that of the European starling (BEECHER 1978).

When the eyes are at diverging position, the widest extent of forehead binocular field was above the bill. This is similar with that of the most of other passerine birds (MARTIN 1986, FERNÁNDEZ-JURICIC et al. 2010, GALL & FERNÁNDEZ-JURICIC 2010, FERNÁNDEZ-JURICIC et al. 2011, MOORE et al. 2013), except for the House Finch and the House Sparrow (FERNÁNDEZ-JURICIC et al. 2008), where the widest extent of forehead field is below the bill, which is related to the difference in foraging behaviour. The widest area in House Finches and House Sparrows can be used to effectively locate seeds and insects scattered on the ground (FERNÁNDEZ-JURICIC et al. 2008), while the widest extent of the binocular field above the bill could be used to exactly estimate the position of the prey and the time it touches the prey (COIMBRA et al. 2006, MARTIN 2007, TROSCIANKO et al. 2012, MARTIN 2014). In addition, the bird's binocular field improves its ability to obtain visual flow-field information and detect predators (MARTIN 2007, 2014, FERNÁNDEZ-JURICIC et al. 2008).

Eye movement

Similar with other passerine birds, the red-billed starling significantly changed the width and the vertical extent of binocular field through eye movement (Table 1). The average eye movements amplitude ($\sim 11.09^\circ$) at all altitudes for each eye in the red-billed starling is similar to that of ground foragers ($\sim 10\text{--}16^\circ$; see MARTIN 1986, FERNÁNDEZ-JURICIC et al. 2008, 2011), but less than that of tree foragers ($\sim 61\text{--}76^\circ$, MOOR et al. 2013), the corvids

(~ 22–38°, TROSCIANKO et al. 2012), and the avian emberizid foragers (~ 23–27°, MOORE et al. 2015). This may be related to the size of the pecten on the retina. The average pecten width of the red-billed starling for all elevations ($4.39 \pm 0.38^\circ$) is narrower than that of the tree foragers (~19.72–25.74°, MOORE et al. 2013) and the avian emberizid foragers (~14.55–26.96°, see MOORE et al. 2015). To increase their foraging efficiency, birds need to increase the visible range (MARTIN 2007, 2014, LAND 2015). So birds with larger pecten have higher eye movement amplitude. Eye movement allows the area with high retinal resolution to be centred in the monocular field (LAND 2015), which can be used to track and examine prey item and predator (MARTIN 2007, MOORE et al. 2015, TYRRELL et al. 2015). Non-conjugate movement of the birds' eyes allows each eye to perform a different task (LAND 2015, TYRRELL et al. 2015), and looking backwards can increase the coverage of the visual field (Fig. 2c), which improves their ability in vigilance and anti-predation (DAWKINS & WOODINGTON 2000, DAWKINS 2002, FERNÁNDEZ-JURICIC et al. 2008).

Our results indicate that the visual configuration and eye movement of the red-billed starling were the visual adaption to visual demand to foraging at different habitats. The broader monocular field and the forehead binocular field above the bill of the red-billed starling could be used to examine food and aerial threats when at rest and foraging in the canopy, and the eye movements of starlings in the ventral-nasal and dorsal-temporal could improve the detection ability for soil animals when foraging on the ground and the anti-predator ability when looking for food with head lowered at both ground and canopy. Comparing the difference of the trade-offs between foraging behaviour and vigilance behaviour in the red-billed starlings and other passerine birds in the same community and assessing the phylogenetic relationship of their visual system could be better to test the hypothesis that plasticity in foraging strategy together with vigilance against predators have shaped the visual field configuration of the red-billed starlings.

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Author Contributions: FK and ZW designed the research; FK, FL SG carried out the experiments. FK and FL analysed the data and wrote the manuscript with contribution from SG and ZW. All authors read and approved the final version of manuscript.

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Appendix 1. Morphology of seven red-billed starlings.

Characters	SS151	SS152	SS153*	SS161*	SS162*	SS163	SS164
Total length (mm)	188.0	215.8	208.9	216.9	216.9	203.1	169.6
Bill length (mm)	25.0	24.0	23.6	22.8	24.6	22.9	23.3
Tail length (mm)	60.0	70.0	66.2	67.0	74.9	70.8	70.5
Tarsus (mm)	23.1	23.2	23.1	23.0	23.1	23.2	23.3
Head-bill length (mm)	40.0	41.0	39.6	41.5	38.9	39.9	41.1
Body mass (g)	51.89	53.58	52.22	51.85	51.94	54.26	52.87

* Female

Appendix 2. Experimental apparatus used to measure visual fields of a male *Spodiopsar sericeus*.



