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Short communication

Visual fields and foraging ecology of Blacksmith Lapwings *Vanellus armatus*

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The visual fields of Blacksmith Lapwings *Vanellus armatus* show the characteristics of visual guided foragers that use precision pecking for prey capture – a binocular field of narrow width and limited vertical extent, with the projection of the bill close to its centre and a large blind area above and behind the head. The topography of the total field, particularly the binocular field, is similar to that of European Golden Plovers *Pluvialis apricaria*. We suggest that the 'foot-trembling' behaviour associated with foraging in Plovers is not under visual guidance but forces the escape of hidden prey, which is detected when the prey item moves into the binocular field to enable its capture in the bill. Foot-trembling thus functions to extend the effective foraging area of a bird beyond the limits of its visual field.

Keywords: binocular field, Charadriidae, foot-trembling behaviour, plover, sensory ecology, vision.

Visual fields define the three-dimensional space around the head from which information can be extracted at any instant (Martin 2007). In birds, two key functions of visual fields are recognized: the detection of predators and conspecifics at distance (Fernández-Juricic *et al.* 2004, 2011) and the accurate control of bill (or feet) for the conduct of tasks at close range, primarily foraging, chick provisioning and nest-building (Martin 2014). Predator detection relies primarily upon information from the lateral or posterior fields, whereas accurate bill control depends upon information from the binocular field (Martin 2014, 2017b). These tasks make antagonistic informational demands upon vision, leading to a trade-off between these functions of visual fields (Martin 2017b).

Binocularity in birds provides information on the direction of travel towards, and time-to-contact with, an object by the bill or talons, dependent upon detection of the symmetrical optic flow-fields produced during the movement of the head towards the target (Martin 2017b). Extensive studies across a wide range of bird taxa show that interspecific variation in visual field topography is associated primarily with foraging ecology (Martin 2017a), dependent upon whether birds rely on visual or non-visual (tactile and filter) cues when foraging (Martin 2014). However, significant differences in visual fields have been described between closely related species within the same family that depend upon differences in their feeding ecology, e.g. Threskiornithidae species (Martin & Portugal 2011), and even those placed until recently within the same genus, e.g. Northern Shovelers *Spatula clypeata* and Eurasian Wigeons *Mareca penelope* (Guillemain *et al.* 2002), indicating that vision is finely tuned to the perceptual challenges of different foraging tasks.

The visual field characteristics of a single species in the Charadriidae (plovers) have been described, European Golden Plovers *Pluvialis apricaria*, and have been shown to exhibit the four general characteristics of a primarily visually guided forager (Martin & Piersma 2009): (1) the binocular field is relatively narrow and vertically long; (2) the bill tip projects centrally or just below the centre of the binocular field; (3) maximum binocular width occurs at or above the bill tip projection; and (4) the presence of a blind area to the rear of the head (Martin 2007, 2014). Here we describe the visual fields in another species of plover from a different genus, the Blacksmith Lapwing *Vanellus armatus*, a species associated with a variety of moist, open habitats in sub-Equatorial Africa (Piersma & Wiersma 1996). Like European Golden Plovers, these birds have short bills that are used to take invertebrate prey from hard or soft surfaces or just below the surface of mud or water, using a pecking action. The shared foraging behaviour of Blacksmith Lapwings and European Golden Plovers makes it likely that their visual field topography will be similar.

In addition to this pecking foraging behaviour, both species exhibit an unusual 'foot-trembling' behaviour during foraging (Simmons 1961, Johnsgard 1981), whereby the bird stands with one leg extended forward and the foot rapidly shaken on the surface of the substrate ('foot-tapping') or above it ('leg-shaking'; Heather *et al.* 1996). The exact function of this behaviour is unknown (Simmons 1961, Johnsgard 1981), but it is assumed to aid the location of invertebrates hidden in the substrate (Simmons 1961, Heather *et al.* 1996). We have used video evidence of 'foot-trembling' by Blacksmith Lapwings and combined it with visual field data

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to assess whether birds can see their trembling foot, or whether the foot might be used to move or flush prey into view to enable prey capture, hence extending the effective foraging area of a bird.

METHODS

The visual fields were measured in three individual Blacksmith Lapwings. All birds were adults (one male, one female, one unknown) and held in the zoological collection at Birdworld, Farnham, UK. Birds were examined close to their holding aviaries and were immediately returned to them after completion of the measurements.

The ophthalmoscopic reflex technique was used to measure the visual field characteristics of individuals, which involves restraining an alert bird to immobilize its body while keeping its head fixed by holding its bill in a specially designed holder (Martin *et al.* 2007). This technique has been consistently applied across more than 60 bird species (Martin 2017a) and provides a reliable method for interspecific comparisons of visual field topography across birds with different foraging ecologies and phylogenies (Martin 2007). The procedure is non-invasive, and birds are restrained for a short period of time, and thus the UK Animals (Scientific Procedures) Act 1986 is not applicable (Martin & Portugal 2011). The procedure has been described elsewhere (Martin *et al.* 2007, Martin & Piersma 2009, Martin & Portugal 2011, Martin & Wanless 2015). There were no spontaneous eye movements observed in this species, nor could eye movements be induced using previously described methods (Martin & Katzir 1994).

We also conducted a search of the Internet for videos of Blacksmith Lapwings from a variety of ornithological and social media sources to find sequences showing birds exhibiting 'foot-trembling' behaviour. One video showed this foraging technique (https://www.youtube.com/watch?v=bzvn0n_nk4s&app=desktop; accessed 26 June 18, uploaded by Shellie Brown), and we used this to assess this behaviour in relation to visual field topography.

RESULTS

The mean angular separation of the retinal field margins as a function of elevation in the median sagittal plane of the head is shown in Figure 1, which is based upon the data obtained from the three birds (Tables S1–S3). Topographical maps illustrate the visual fields in different planes (Fig. 2). The binocular field of Blacksmith Lapwings is vertically long and relatively narrow (Fig. 2a), with a maximum width of approximately 19° (Fig. 2b) and vertical extent of 76° (Fig. 2c). The projection of the bill is just below the centre of the binocular field (Fig. 2a,c). The extent of the monocular fields for both eyes averages 166° in the horizontal plane (Fig. 2b). The lateral placement of the eyes in the skull, combined with the wide monocular fields and small binocular overlap, results in this species having a cyclopean field of 313° in the horizontal plane (Fig. 2b). The blind area extends from the front of the head (around 62° in the median sagittal plane) to continue behind the head (Fig. 1) and below the body (Fig. 2a). The blind area has maximum width of 53° at −40° elevation behind the head (Fig. 1), which narrows to 47° at the horizontal (−90° elevation).

Figure 3 shows a vertical section through the projection of the binocular field when the bird adopts its typical upright stance during foraging and when it is crouched forward prior to pecking. This illustrates that when the bird is upright (Fig. 3a), it is unable to see the surface directly below, as the head needs to be pitched forward by at least 30° (Fig. 3b) for the bird to see the surface close to its feet.

DISCUSSION

General characteristics of the visual fields

Blacksmith Lapwings exhibit the general visual field characteristics of visually guided foraging birds (Martin 2007). Their visual field shows a narrow and vertically elongated frontal binocular field, with the projection of the bill tip within the field, slightly below the centre (Fig. 2), which has a similar arrangement to a wide range of bird species which are reliant upon visual cues for precise bill (or feet) control to capture prey (Martin 2014). This shared frontal binocular field topography (with the bill placed at or below the centre) occurs across species that vary in their foraging behaviour and evolutionary background (Martin 2014): those that peck at food items, e.g. Eurasian Wigeons (Guillemain *et al.* 2002); those that lunge for or pursue evasive prey (e.g. fish) for capture in the bill, e.g. Common Guillemots *Uria aalge* (Martin & Wanless 2015) and Great Cormorants *Phalacrocorax carbo* (Martin *et al.* 2008); those that require precision-grasping for the manipulation of food in the bill, e.g. Bucerotidae species (Martin & Coetzee 2004); and those that capture prey in their talons, e.g. Accipitridae species (O'Rourke *et al.* 2010, Martin *et al.* 2012, Potier *et al.* 2018).

Observations of foraging Blacksmith Lapwings show that they run for short distances on the ground, or wade in shallow water and then make quick, downward pecking movements to capture prey, including insects, worms, crustaceans and small molluscs (Johnsgard 1981). This foraging ecology requires accurate bill control for the capture of mobile prey, as is evident in the key features of their binocular field: maximum binocular field width of 19° and vertical extent of 76°, with the bill tip projecting just below the centre of the binocular area (Fig. 2).

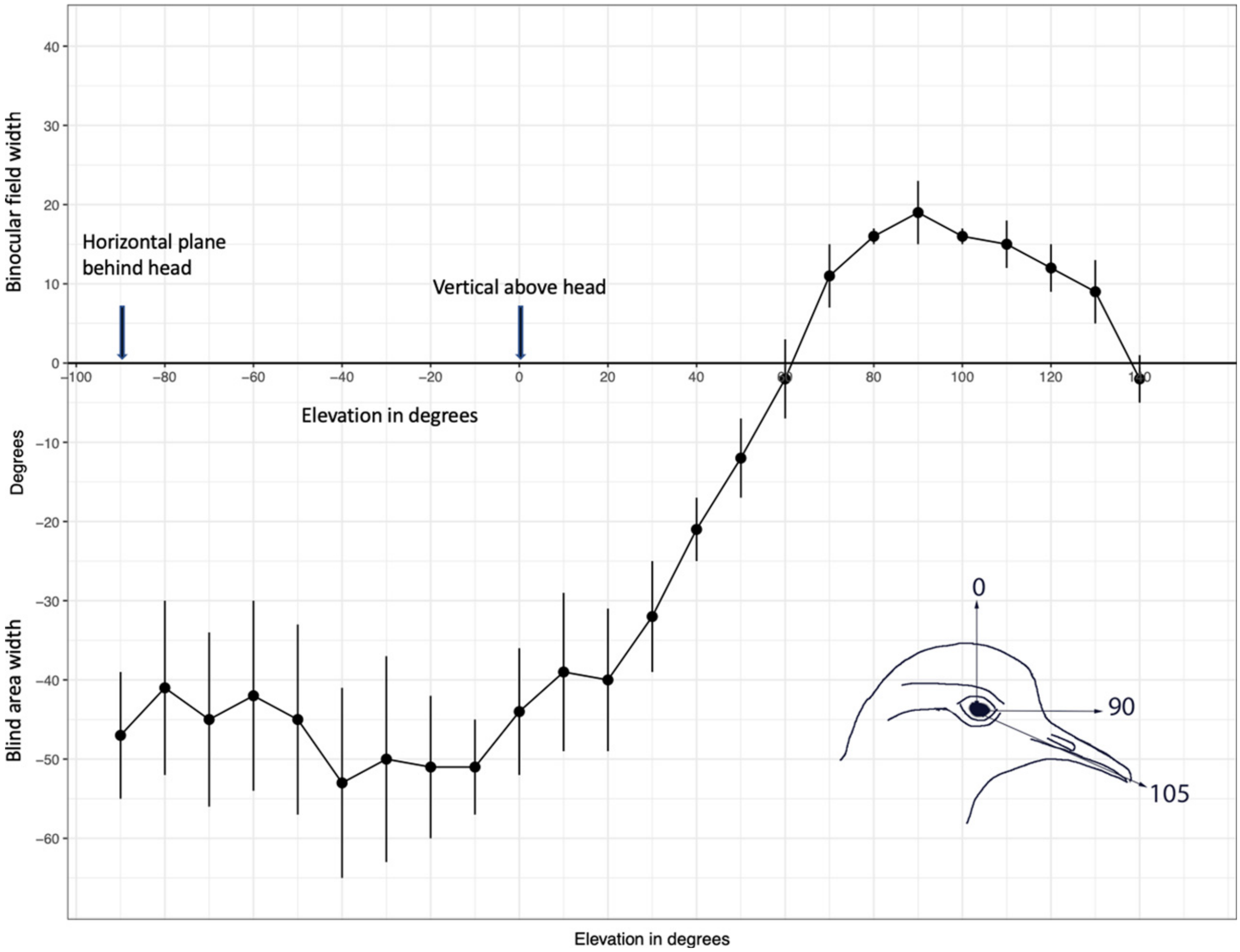

Figure 1. The mean ± se angular separation (n = 3) of the retinal field margins as a function of elevation in the median sagittal plane in Blacksmith Lapwings. Positive values indicate overlap of the field margins (binocular vision) and negative values indicate the width of the blind area. The coordinate system is such that the horizontal plane is defined by the elevations −90° (behind the head) and 90° (in front of the head), and 0° is directly above the head. The drawing shows the bird's head in profile with key coordinates indicated, with the projection of the eye–bill tip axis (105° for all individuals); this head position is approximately that spontaneously adopted by a bird held in the hand.

The binocular field characteristics of Blacksmith Lapwings (Fig. 2) are very similar to those of European Golden Plovers, which have a maximum binocular field width of 15°, and vertical extent of 75° with the bill projecting into the field below its centre (sample size of four) (Martin & Piersma 2009). This similarity in binocular field topography is not surprising, as European Golden Plovers also capture aquatic and terrestrial invertebrates by precision pecking (Vaughan 1980), being primarily reliant upon visual cues (Barnard & Thompson 1985, Piersma & Wiersma 1996). Despite the small areas of the binocular fields in these plover species, this configuration would still enable accurate bill control for prey capture (Martin 2017b).

Both European Golden Plovers and Blacksmith Lapwings (Martin & Piersma 2009) lacked spontaneous eye movements, which leads to their maximum degree of binocular overlap being fixed within individuals, as also found in other visually guided foraging species, e.g. Common Guillemots and Atlantic Puffins *Fratercula arctica* (Martin & Wanless 2015). The lack of spontaneous eye movements in these plover species may be associated with their large eye size relative to their skull and specific skull anatomy, e.g. the supraorbital aliform bone observed in European Golden Plovers (Martin & Piersma 2009), as these factors would restrict eye movements within the orbit. Visual field examinations of other plover species would be required to determine whether the lack of spontaneous eye movements is a consistent feature across the family Charadriidae. Some variation in the binocular field widths at the different elevations is evident among individual Blacksmith Lapwings (Tables

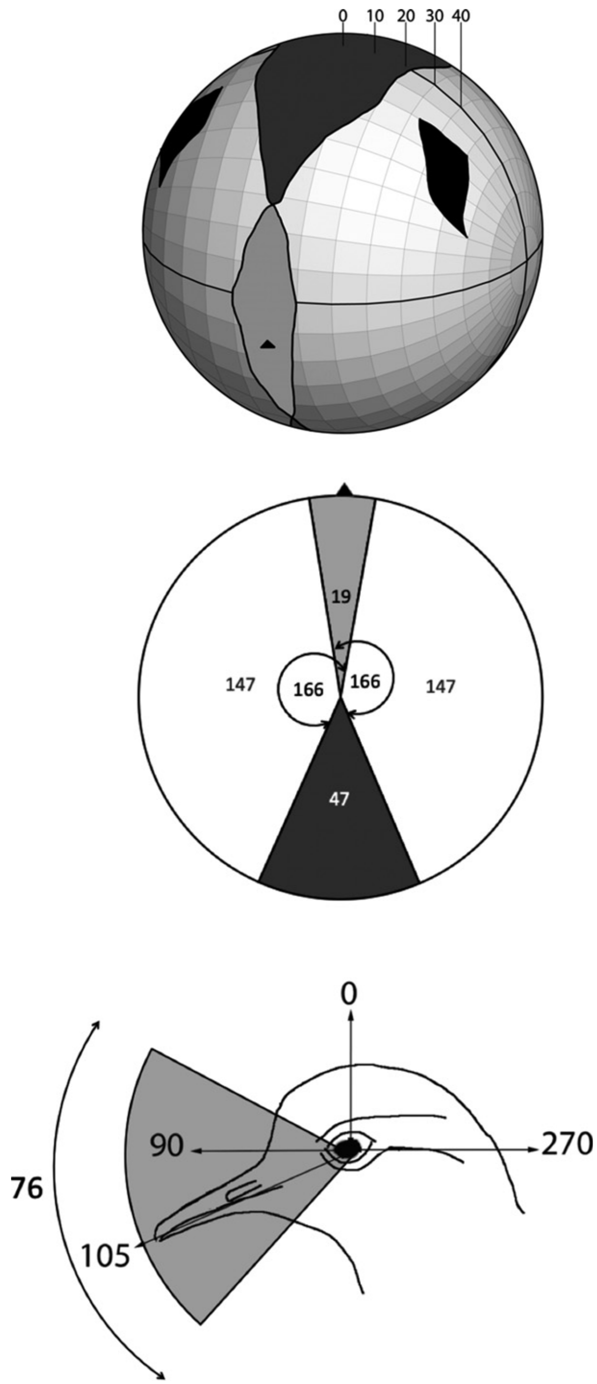

Figure 2. Visual field diagrams of Blacksmith Lapwings in three views based upon mean measurement values ($n = 3$). (a) A perspective view of an orthographic projection of the retinal field boundaries of the two eyes. The projection of the bill tip is indicated by a black triangle, and the projection of the pectens is drawn in black. The diagram uses a conventional longitude and latitude coordinate system with the equator aligned vertically in the median sagittal plane of the bird (grid at 10° intervals) and values in the sagittal plane correspond to those shown in Fig. 1. The bird's head can be visualized to be positioned at the centre of a transparent sphere with the bill tip and field boundaries projected onto the surface of the sphere, with the head in the orientation shown in the drawing on Fig. 1. (b) Horizontal section through the visual fields in the horizontal plane, defined by elevations 90° and −90° in Fig. 1. The curved arrows show the extent of the monocular fields of the right and left eyes (the combined mean values for both eyes are presented). The direction of the bill is indicated by a black triangle. (c) Vertical section through the binocular field in the median sagittal plane. This is defined by the vertically orientated equator of diagram (a). For Fig. 2(a), (b) and (c), the light grey areas represent the binocular field and dark grey areas represent blind areas. Measurements are in degrees.

S1–S3), similar to other studies in which individual differences have been recorded within species (Martin & Katzir 1994, Martin *et al.* 2012), which may be expected due to individual variation and the limitations of the measurement method when examining live birds.

As Blacksmith Lapwings are ground-dwelling birds found in open habitats, they are vulnerable to both aerial and terrestrial predators (Walters 1990, Parr 1993), and individuals have been observed to exhibit vigilance behaviour for significant periods of time (Walters 1990). This species has extensive blind areas above and behind the head (Figs 1 and 2a), which would restrict a bird's ability to detect predators, thus highlighting the evolutionary trade-offs between the tasks of predator detection and foraging in the function of avian visual fields (Martin 2017b). Although Golden Plovers also have extensive blind areas (Martin & Piersma 2009), some variation in the shape of the blind areas is evident between Blacksmith Lapwings (Figs 1 and 2a,b) and Golden Plovers. Investigation of the differences in the vigilance behaviours of these two species may shed light on the evolutionary significance of this variation in blind areas.

Visual fields and foot-trembling

Video analyses of foraging posture and behaviour indicated that the head and body were usually held upright during 'foot-trembling'. The bird cannot see the surface below it when standing upright (Fig 3a) and the head must be pitched forward and downward for the bird to see what lies beneath the head (Fig. 3b). During 'foot-trembling', the foot appears to be outside the bird's field of view in the blind area beneath the head, and thus a bird cannot see prey to target its disturbance with the foot. It seems likely that 'foot-trembling' functions to disturb prey hidden in the substrate and trigger an escape response, so it is revealed either directly or indirectly (by causing a surface movement). If prey moves forward into the field of view, the bird may utilize its binocular field to

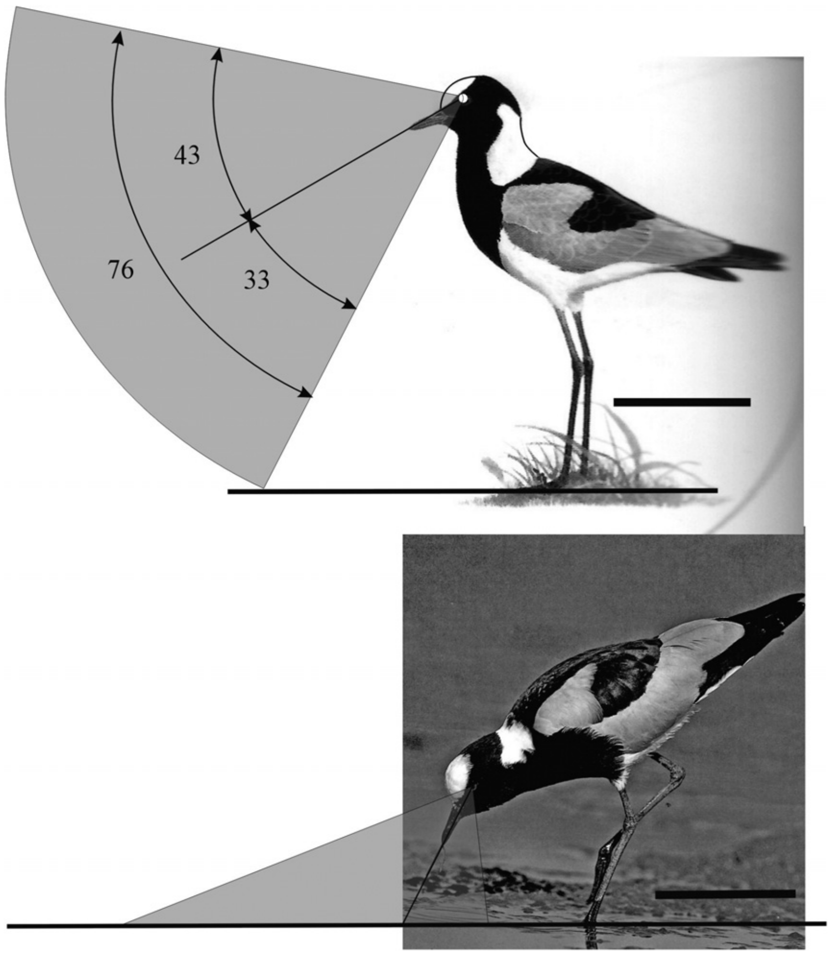

Figure 3. Diagrams of side views of Blacksmith Lapwings with the projection of a vertical section through the binocular field. The binocular field (represented in light grey) is projected on to the ground in front of the bird when standing upright (a) and when crouched forward prior to pecking (b), with measurements in degrees. The birds are redrawn from scans of the images found in Sinclair *et al.* (1997; p. 171) for (a), and Piersma and Wiersma (1996; p. 399) for (b). Scale bars: 100 mm.

locate it accurately for capture in the bill. This type of foraging technique relies upon detecting the prey once it has escaped from its hiding place and is similar to the strategy used by Great Cormorants in their 'flush-foraging' of hidden fish (Martin *et al.* 2008). We suggest that 'foot-trembling' is not visually guided but is an effective way of increasing the foraging area of the bird beyond the limits of its immediate visual field. As this 'foot-trembling' technique has been observed in several Charadriidae species found in the Northern and Southern hemispheres (Simmons 1961, Vaughan 1980, Armitage 2008), it is likely that examination of their binocular field characteristics may show similarities to Blacksmith Lapwings.

Overall, this study of Blacksmith Lapwings illustrates that they are visually guided foragers reliant upon information from the binocular field for accurate bill placement and timing (Martin 2017b) to capture invertebrate prey. The same conclusion applies in European Golden Plovers (Martin & Piersma 2009) and may hold true for other Charadriidae species. The 'foot-trembling' behaviour found in several Charadriidae species (Simmons 1961, Vaughan 1980, Armitage 2008) appears to be a specialized foraging technique whereby the bird's foot movement causes prey to make an escape movement, which may bring it into the bird's field of view. Visual field studies of other Charadriidae species, combined with observations of the 'foot-trembling' technique, would help support this suggestion.

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REFERENCES

Armitage, I. 2008. Foot-trembling and beak probing by the Shore Plover (*Thinornis novaeseelandiae*) on sandy beaches. *Notornis* **55**: 38–39.

Barnard, C.J. & Thompson, D.B.A. 1985. *Gulls and Plovers. The Ecology and Behaviour of Mixed-species Feeding Groups*. New York, NY: Columbia University Press.

Fernández-Juricic, E., Erichsen, J.T. & Kacelnik, A. 2004. Visual perception and social foraging in birds. *Trends Ecol. Evol.* **19**: 25–31.

Fernández-Juricic, E., Gall, M.D., Dolan, T., O'Rourke, C., Thomas, S. & Lynch, J.R. 2011. Visual systems and vigilance behaviour of two ground-foraging avian prey species: White-crowned sparrows and California Towhees. *Anim. Behav.* **81**: 705–713.

Guillemain, M., Martin, G. & Fritz, H. 2002. Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). *Funct. Ecol.* **16**: 522–529.

Heather, B.D., Robertson, H.A. & Onley, D.J. 1996. *The Field Guide to the Birds of New Zealand*. Aukland: Viking.

Johnsgard, P.A. 1981. *The Plovers, Sandpipers, and Snipes of the World*. Lincoln: University of Nebraska Press.

Martin, G.R. 2007. Visual fields and their functions in birds. *J. Ornithol.* **148**: 547–562.

Martin, G.R. 2014. The subtlety of simple eyes: the tuning of visual fields to perceptual challenges in birds. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **369**: 20130040.

Martin, G.R. 2017a. *The Sensory Ecology of Birds*. Oxford: Oxford University Press.

Martin, G.R. 2017b. What drives bird vision? Bill control and predator detection overshadow flight. *Front. Neurosci.* **11**: 1–16.

Martin, G.R. & Coetzee, H.C. 2004. Visual fields in hornbills: precision-grasping and sunshades. *Ibis* **146**: 18–26.

Martin, G.R. & Katzir, G. 1994. Visual fields and eye movements in herons (Ardeidae). *Brain. Behav. Evolut.* **44**: 74–85.

Martin, G.R. & Piersma, T. 2009. Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper. *Proc. R. Soc. Lond. B Biol. Sci.* **276**: 437–445.

Martin, G.R. & Portugal, S.J. 2011. Differences in foraging ecology determine variation in visual fields in ibises and spoonbills (*Threskiornithidae*). *Ibis* **153**: 662–671.

Martin, G.R. & Wanless, S. 2015. The visual fields of Common Guillemots *Uria aalge* and Atlantic Puffins *Fratercula arctica*: foraging, vigilance and collision vulnerability. *Ibis* **157**: 798–807.

Martin, G.R., Jarrett, N. & Williams, M. 2007. Visual fields in Blue Ducks *Hymenolaimus malacorhynchos* and Pink-eared Ducks *Malacorhynchus membranaceus*: visual and tactile foraging. *Ibis* **149**: 112–120.

Martin, G.R., White, C.R. & Butler, P.J. 2008. Vision and the foraging technique of Great Cormorants *Phalacrocorax carbo*: pursuit or close-quarter foraging? *Ibis* **150**: 485–494.

Martin, G.R., Portugal, S.J. & Murn, C.P. 2012. Visual fields, foraging and collision vulnerability in Gyps vultures. *Ibis* **154**: 626–631.

O'Rourke, C.T., Hall, M.I., Pitlik, T. & Fernández-Juricic, E. 2010. Hawk eyes I: diurnal raptors differ in visual fields and degree of eye movement. *PLoS ONE* **5**: e12802.

Parr, R. 1993. Nest predation and numbers of Golden Plovers *Pluvialis apricaria* and other moorland waders. *Bird Study* **40**: 223–231.

Piersma, T. & Wiersma, P. 1996. Family Charadriidae (Plovers). In del Hoyo, J., Elliott, A. & Sargatal, J. (eds) *Handbook of the Birds of the World*, *Vol. 3. Hoatzin to Auks*: 384–442. Barcelona: Lynx Edicions.

Potier, S., Duriez, O., Cunningham, G.B., Bonhomme, V., O'Rourke, C., Fernández-Juricic, E. & Bonadonna, F. 2018. Visual field shape and foraging ecology in diurnal raptors. *J. Exp. Biol.* **221**: 1–9.

Simmons, K.E.L. 1961. Foot movements in plovers and other birds. *Br Birds* **54**: 34–39.

Sinclair, I., Hockey, P. & Tarboton, W.R. 1997. *Sasol Birds of South Africa*, 2nd edn: Capetown: Struik Publishers.

Vaughan, R. 1980. *Plovers*. Lavenham: Terence Dalton Ltd.

Walters, J.R. 1990. Anti-predatory behaviour of Lapwings: field evidence of discriminative abilities. *Wilson Bull.* **102**: 49–70.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1–S3. Visual field measurements of three individual Blacksmith Lapwings. For each bird, the measurements for the maximum extent of the right and left eye retinal field margins at each 10 degree elevation between 270 and 150 degrees are presented. The difference between these two values is calculated in the final column, with positive values indicating binocular field width and negative values indicating blind area width. The measurements for the projection for the minimum and maximum extents of the right and left pectens are also presented when sufficient time enabled these measurements to be made.