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Differences in foraging ecology determine variation in visual fields in ibises and spoonbills (Threskiornithidae)

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Variations in visual field topography among birds have been interpreted as adaptations to the specific perceptual challenges posed by the species' foraging ecology. To test this hypothesis we determined visual field topography in four bird species which have different foraging ecologies but are from the same family: Puna Ibis *Plegadis ridgwayi* (probes for prey in the soft substrates of marsh habitats), Northern Bald Ibis *Geronticus eremita* (surface pecks for prey in dry terrestrial habitats), African Spoonbill *Platalea alba* and Eurasian Spoonbill *Platalea leucorodia* (bill-sweeps for prey in shallow turbid waters). All four species employ tactile cues provided by bill-tip organs for prey detection. We predicted that the visual fields of these species would show general features similar to those found in other birds whose foraging is guided by tactile cues from the bill (i.e. bill falling outside the frontal binocular field and comprehensive visual coverage of the celestial hemisphere). However, the visual fields of all four species showed general features characteristic of birds that take food directly in the bill under visual guidance (i.e. a narrow and vertically long binocular field in which the projection of the bill tip is approximately central and with a blind area above and behind the head). Visual fields of the two spoonbills were very similar but differed from those of the ibises, which also differed between themselves. In the spoonbills, there was a blind area below the bill produced by the enlarged spatulate bill tip. We discuss how these differences in visual fields are related to the perceptual challenges of these birds' different foraging ecologies, including the detection, identification and ingestion of prey. In particular we suggest that all species need to see binocularly around the bill and between the opened mandibles for the identification of caught prey items and its transport to the back of the mouth. Our findings support the hypothesis that sensory challenges associated with differences in foraging ecology, rather than shared ancestry or the control of locomotion, are the main determinants of variation in visual field topography in birds.

Keywords: bill-tip organ, binocular vision, foraging ecology, prey capture, prey identification, tactile sensitivity, vision, visual field.

Relationships between the sensory challenges posed by particular environments and the information that organisms extract from them have long been recognized and described in general terms (Walls 1942, Lythgoe 1979, Archer *et al.* 1999). More recently, specific examples of how sensory capacities are linked to the challenges posed by particular foraging ecologies have been described. In birds these include the trade-off between visual and tactile information in the foraging of shorebirds and ducks (Charadriidae, Scolpacidae, Anatidae) (Martin & Piersma 2009), the link between vision and the foraging behaviour of

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Great Cormorants *Phalacrocorax carbo* (Martin *et al.* 2008), and the more general ways in which vision and foraging strategies render certain species more prone to collisions with man-made objects (Martin 2011). A general hypothesis which has emerged from such investigations is that the variability among birds in their binocular visual fields is best interpreted as adaptations to the specific perceptual challenges posed by each species' foraging ecology, rather than the more general perceptual challenges posed by locomotion, or are a consequence of shared ancestry (Martin 2007, 2009). This general hypothesis is based upon analysis of a broad comparative database (a sample of 36 bird species, from 21 families and 14 orders, where visual field topography was measured with the same method), in which phylogeny and foraging ecology are likely to be confounded (Martin 2007).

Marked differences in visual field topography have, however, been described within closely related taxa. Among three species of congeneric ducks (Mallards *Anas platyrhynchos*, Northern Shovellers *Anas clypeata* and Eurasian Wigeons *Anas penelope*), marked differences in visual fields have been described and explained by reference to differences in the extent to which vision or tactile cues are used to guide foraging (Guillemain *et al.* 2002, Martin 2007). Similar differences in visual fields have also been found between more distantly related species of ducks (Blue Ducks *Hymenolaimus malacorhynchos*, Pink-eared Ducks *Malacorhynchus membranaceus*), which also differ in their use of visual and tactile cues when foraging (Martin *et al.* 2007a). This suggests that within an avian family, close relationships can exist between sensory capacities and the perceptual challenges posed by foraging in different environments. This in turn suggests that sensory capacities can be fine-tuned to the particular perceptual challenges that are faced by species as they differentiate from recent ancestors. We investigated these ideas through the determination of visual field topography in a sample of species from another group of closely related birds within the family Threskiornithidae, ibises and spoonbills, which differ markedly in their foraging ecology.

The ibises and spoonbills are considered to be very closely related, much more so than the striking differences between their bills might suggest (Matheu & del Hoyo 1992). Cases of natural hybridization producing viable offspring between ibises and spoonbills have been reported (Matheu & del Hoyo 1992), indicating that these species may have differentiated only relatively recently, and recent phylogenomic evidence also suggests a close relationship (S. Olsen pers. comm.). However, marked differences are found within the Threskiornithidae in foraging strategies and their distinctive bill morphologies have been readily associated with differences in foraging ecology. Ibises have long, robust, decurved bills and spoonbills have long, robust straight bills with a characteristic spatulate end (Cramp & Simmons 1977, Matheu & del Hoyo 1992, Swennen & Yu 2004, 2005, 2008). Associated with these different bill morphologies are variations in numbers and densities of tactile receptors in their bill-tip organs. These bill-tip organs are clusters of mechanoreceptors embedded in pits contained within the bone of the distal portions of the mandibles, especially around the bill tip. It is argued that these receptors are employed for unsighted prey detection (Cunningham *et al.* 2010a, 2010b) including the use of remote touch in which prey is detected without the bill making direct contact with the item (Piersma *et al.* 1998). In other bird species that also have high concentrations of mechanoreceptors located at their bill tips, such as some long-billed waders (Eurasian Woodcocks *Scolopax rusticola*) and some dabbling ducks (Mallards, Northern Shovellers) (Martin 1994, Martin *et al.* 2007a), their visual fields provide comprehensive visual coverage of the celestial hemisphere and the bill tip lies at the very periphery or outside the visual field (Martin 2007). Parrots (Psittacidae) also have touch-sensitive bill-tip organs that are used in the manipulation of objects held within their highly curved bill tips, which in parrots lie at the very periphery of the visual field (Demery *et al.* 2011). These characteristics have been interpreted as the result of a lack of requirement to see the bill tip to guide foraging, as this can be achieved through tactile cues alone. This has favoured the selection of eye position high in the skull providing near or complete comprehensive vision of the celestial hemisphere (Martin 2007). In contrast, birds that require visual guidance of their bills during foraging for such tasks as selective grazing (e.g. some ducks), lunging at evasive prey (e.g. Ardeidae), capture of prey in the feet (e.g. Accipitridae) or pecking (e.g. Columbidae) have more frontally placed eyes. This results in a binocular field encompassing the projection of the bill tip and a blind area above and behind the head. The presence of a blind area behind the head has consequences for vigilance behaviour when foraging. Thus it has been shown that Eurasian Wigeons, which have a blind sector behind the head, spend more time being vigilant and not feeding compared with Northern Shovellers, which do not have a blind sector behind the head (Guillemain *et al.* 2002, Martin 2007).

If visual field topography in birds is determined primarily by common ancestry, we predicted that all Threskiornithidae would have similar visual field topography. In addition, because of the high concentration of bill-tip tactile receptors in these birds and their ability to forage using tactile cues alone, we predicted that their visual fields would be similar to those found in other bird species that employ tactile cues from a bill-tip organ to guide foraging, i.e. they would gain comprehensive visual coverage of the celestial hemisphere and the bill projection would be placed outside or at the very periphery of the binocular field. However, if differences in foraging behaviour are the main evolutionary drivers of visual field topography we predicted that visual field topography among the Threskiornithidae may differ and that differences would be correlated with differences in foraging ecology. Differences in foraging ecology and bill morphology are summarized in Table 1 for the four species studied. Among the Threskiornithidae we chose species whose foraging ecology includes surface pecking in dry terrestrial habitats (Northern Bald Ibis *Geronticus eremita*), probing in soft substrates of marsh habitats (Puna Ibis *Plegadis ridgwayi*), and bill-sweeping in shallow turbid waters (African Spoonbill *Platalea alba*, Eurasian Spoonbill *Platalea leucorodia*).

METHODS

The procedure used measured visual field characteristics in alert birds and has been detailed extensively in numerous publications (see Martin 2007, Martin & Shaw 2010 for a list). The procedure is non-invasive and has been performed on more than 40 different species. The procedure involves the restraint of birds for between 30 and 45 min, and was reviewed in 2007 by a UK Home Office Inspector. It was not considered to fall within the regulations that govern licensed procedures with animals that apply in the UK. However, the ethical guidelines with respect to handling and restraining birds required for licensed procedures in the UK (UK Animals (Scientific Procedures) Act 1986) were followed.

All birds studied were held in zoological collections. Birds were adults and had been held in captivity for a number of years. Birds were studied close to their holding aviaries to which they were immediately returned after measurement. Sexes were unknown. Visual fields were measured in two individuals of each species. Photographs showing a side view of the head and bill of each species are presented in Figure 1. Visual field measurements were undertaken at the following collections: Northern Bald Ibis and African Spoonbill, Birdworld, Farnham, Surrey, UK; Puna Ibis, Twycross Zoo, Twycross, Leicestershire, UK; Eurasian Spoonbill, The Wildfowl and Wetlands Trust, Slimbridge, Gloucestershire, UK.

Calibrated photographs of the head of each bird when held in the hands and in the apparatus were taken. These were used to determine eye positions within the skull, the horizontal separation between the nodal points of the two eyes, the distance between eye and bill tip, bill length, and the angle between the horizontal and the eye–bill-tip direction when the bird was held in the hand and in the apparatus. The birds were also photographed when foraging and walking within their holding aviaries and photographs were used to determine the approximate height of the eyes from the ground and the angle of the bill with respect to the horizontal when the birds were standing in a relaxed posture.

Visual field parameters were determined using an ophthalmoscopic reflex technique. This has been used in a range of birds with different phylogeny, ecology and feeding techniques and readily permits interspecific comparisons (Martin 2007). For a detailed description of the apparatus and methods, see Martin *et al.* (2007a) and Martin and Shaw (2010). Each bird was hand-held with the breast resting on a foam rubber cradle and the body supported by an assistant (experienced in handling larger, long-legged birds), who was seated behind the apparatus. The bird's legs were taped lightly together, cushioned by foam rubber and were allowed to fall naturally below the body. The head was held in position at the centre of a visual perimeter (a device which permits the eyes to be examined from known positions around the head) by specially manufactured steel and aluminium bill holders. Different bill holders were used for each of the species to take account of differences in the size and shape of the bills. In the spoonbills the bill

Table 1. Summary data on bill morphology, eye position and foraging ecology in the four species of birds from the family Threskiornithidae in which visual fields were determined. Data on eye position and bill length are from this study; data on bill-tip organs are from Cunningham *et al.* (2010a); and data on foraging ecology are from Cramp and Simmons (1977), Matheu and del Hoyo (1992), and Cramp and Simmons (1977).

	Bill morphology			Eye position		Foraging ecology		
Species	Shape	Length (mm)	Bill-tip organ, number of sensory pits	Eye–bill-tip distance (mm)	Eye–ground distance (mm)	Behaviour	Habitat	Diet
Puna Ibis	Long decurved	134	2300	125	271	Probes soft substrates	Swampy areas, rushy pastureland, mudflats, ponds, streams	Arthropods and other invertebrates
Northern Bald Ibis	Long decurved	131	420	140	380	Pecks at ground and at individual prey items on surface, or probes into fissures	Dry terrestrial	Invertebrates (grasshoppers, locust, crickets, beetles), reptiles, frogs, fish, small mammals, nestling birds, some plant material
African Spoonbill	Long, straight, flattened spatulate end	165	20 000	176	328	Sweeping bill from side-to-side in water column, dabbling in mud and shallow water	Aquatic, lakes, marshes, inland large shallow water bodies, salt pans, creeks	Small fish, aquatic invertebrates
Eurasian Spoonbill	Long, straight, flattened spatulate end	220	20 000	240	447	Sweeping bill from side-to-side in water column, dabbling in mud and shallow water	Aquatic, shallow extensive wetlands, marshes, sheltered marine habitats, deltas, estuaries, coastal lagoons	Small fish, aquatic invertebrates, molluscs, crustaceans, amphibians, some plant material

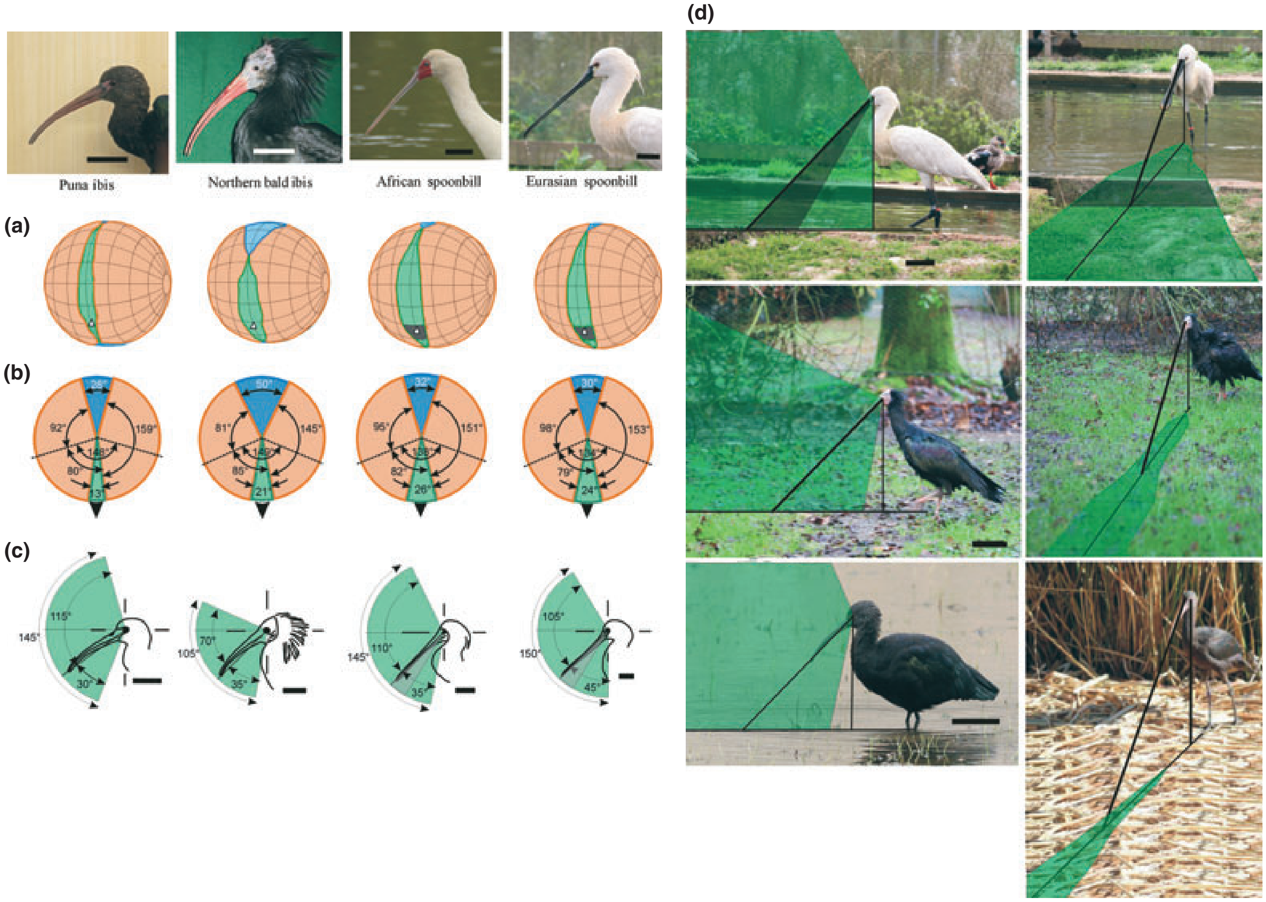

Figure 1. Visual fields in Puna Ibises, Northern Bald Ibises, African Spoonbills and Eurasian Spoonbills. The figure is a matrix that allows interspecific comparison of the same information across rows, while columns show information for each species. Each species is depicted by a photograph showing a lateral view of the head in its characteristic resting position. (a) Perspective views of orthographic projections of the boundaries of the retinal fields of the two eyes and the line of the eye–bill-tip projection (indicated by a white triangle). The diagrams use conventional latitude and longitude coordinate systems with the equator aligned vertically in the median sagittal plane of the bird (grid at 20° intervals). It should be imagined that the bird's head is positioned at the centre of a transparent sphere with the bill tips and field boundaries projected onto the surface of the sphere, with the heads in the orientations shown in (c). (b) Horizontal sections through the visual fields in a horizontal plane defined by the horizontal line shown in (c); dashed lines indicate the directions of the optic axes. (c) Vertical sections through the binocular fields in the median sagittal plane of the head defined by the vertically oriented equators of the diagrams in (a). The line drawings of the heads of the birds show them in the approximate orientations typically adopted by the species when foraging and at rest, as determined from photographs of birds held in the hand and in their aviaries (see discussion in Methods section). Green areas, binocular sectors; pink areas, monocular sectors; blue areas, blind sectors; downward pointing black arrowheads in (b), direction of the bill; white triangle in (a), direction of bill projection. Scale bars: 50 mm. (d) Diagrams of the projections into a foraging environment of the binocular fields of Eurasian Spoonbills (top), Northern Bald Ibises (middle) and Puna Ibises (bottom). The left column presents a side view showing the projections (green shading) of vertical sections through the binocular fields based upon the diagrams of Figure 1(a). The right column presents a perspective view of the projections of the binocular field onto the ground below and in front of a foraging bird. Solid lines show the projection of the eye–bill-tip direction and of the direction vertically below the eye. In the Eurasian Spoonbills the projection of the blind area caused by the intrusion of the bill into the binocular field is indicated by grey shading. Scale bars in the left column: 100 mm.

was held closed; in the ibises the bill was held slightly open. The surfaces of the holders were coated in cured silicone sealant to provide a non-slip cushioned surface. The bill was held in place by Micropore tape. The perimeter's coordinate system followed conventional latitude and longitude with the equator aligned vertically in the median sagittal plane of the head (a vertical plane which divides the head symmetrically into its left and right halves) and this coordinate system is used for the presentation of visual field data (Fig. 1). When the measurements were made, the tips of the mandibles projected at approximately 40° below the horizontal. The eyes were examined using an ophthalmoscope mounted against the perimeter arm and its position read to ± 0.5°. Alignment of the birds' heads in the perimeter was such that the ophthalmoscope viewing aperture was, in effect, moved over the surface of a sphere (radius 320 mm) centred on the mid-point of the line joining the centres of the pupils. This point was defined as the cyclopean projection centre (a single reference point for describing the total visual field about the head which results from the combination of the visual fields of each eye), and the position of the visual fields are described by reference to it. The measured values of visual field features were corrected to those that would be determined at a hypothetical infinite viewing distance. This correction is based upon the estimated horizontal separation of the eyes' nodal points (Martin 1984).

In all species, eye movements were present and, as in other birds, were non-conjugate (Martin 2007). Due to time constraints on holding the birds in the apparatus, we were only able to quantify eye movement amplitude at a small number of elevations around the horizontal plane where binocular field width was close to the maximum and eye movements typically have their largest amplitude (Martin 2007). We observed spontaneous eye movements away from their forward positions, which defined the maximum degree of binocular overlap that we report here. Amplitudes of eye movements were determined by making a rapid series of observations of the position of the retinal margin as the eye spontaneously moved from the forward resting position. In this way the maximum and minimum position at which the retinal margin could be seen for a given elevation in the frontal hemisphere was determined and the difference between them defined the maximum amplitude of eye movement at that elevation.

In each individual the measured visual field parameters were very similar (± 2°) for repeated measurements at a number of selected elevations, and differences between individuals for the same species at the same elevation did not differ by more than 5° and typically differed by < 2°. Therefore we present mean visual field data for each species.

In all birds the direction of the optic axis of each eye was determined by recording the positions at which the first and second Purkinje images (reflections from the cornea and from the anterior surface of the lens) of a discrete source of light, held close to the line of sight on the perimeter arm, were most closely aligned.

From these combined data, a mean topographical map of the visual field and its principal features was constructed for each species. These features are: monocular fields, the visual field of a single eye; binocular field, the area where monocular fields overlap; and cyclopean field, the total visual field produced by the combination of both monocular fields. As in other studies of this kind (Martin *et al.* 2007a, Martin & Shaw 2010) the aim was to measure limits of the visual field at 10° intervals of elevation in an arc from the horizontal directly behind the head, to above the head and then down to 60° below the horizontal in front of the head. However, this was not possible in all birds at all elevations below the horizontal since the bill holder intruded into the view of the eyes at certain elevations. Therefore at these elevations below the bill, binocular field widths were estimated as the mean value of the binocular field widths immediately above and below these elevations.

In common with most other birds when held at various body angles, head position in all four species was relatively stable. This eye–bill-tip angle was approximately 40° below the horizontal in the Puna Ibises and 50° in the other species (verified from photographs of the birds held prior to or after removing them from the bill holders). Photographs of the birds when at rest in the holding facilities also confirmed these approximate bill angles in unrestrained but alert birds. Photographs of birds taken at rest in their aviaries showed similar bill angles to the horizontal and these are depicted in the photographs of birds in Figure 1. Data on the direction of the optic axes were combined with scaled photographs of a dorsal view of the head to make an estimate of eye axial length in each bird. This estimate was based upon the assumption that the fundus (the back of the eye) is semicircular and that the eyes meet in the median sagittal plane of the skull. These estimates were used to determine the horizontal separation between the nodal points in the two eyes.

RESULTS

Photographs of the lateral views of the heads of the four species, with the heads held at a typical resting angle, are presented in Figure 1. The visual fields shown in Figure 1 depict the situation when the eyes have rotated forwards in a typical resting position for the eyes. Maps of the visual fields in the frontal sector are shown in Figure 1(a). Vertical sections through the binocular field in the median sagittal plane of the head are shown in Figure 1(c). In these figures, the birds' heads are depicted at eye–bill-tip angles similar to those typically adopted by the birds at rest. Sections through the visual fields are shown in Figure 1(b). These sections are at an approximately horizontal plane when the head is held in the positions shown in Figure 1(c).

General topography of visual fields

Figure 1 indicates that the general topography of the binocular visual fields of these four species is similar. They show the general characteristics of birds that employ visual cues for the guidance of bill position during foraging. Thus all four species have a relatively narrow but vertically long binocular field with the projection of the bill falling within the binocular field in its lower sector. Maximum binocular field width occurs approximately horizontally. In all species there is a blind area above and behind the head, i.e. the birds do not gain comprehensive visual coverage of the celestial hemisphere.

Interspecific differences in visual fields

Although the visual fields of all four species show the same general characteristics, there are important differences between them. Comparison of the three diagrams of the visual fields for each of the species (Fig. 1) indicates that visual field parameters are nearly identical for the two spoonbill species but that there are clear differences between the spoonbills and the two species of ibises, and that the ibises also show clear interspecific differences. The similarities between the spoonbills and the differences between the ibises extend to all parameters of the visual fields, including the maximum width and vertical extent of the binocular sector, the extent of the blind sector above and behind the head, and the degree to which the birds can see below them when standing. In both spoonbills there is a sector below the bill in which binocularity is abolished due to the intrusion of the spatulate bill tip into the field, but there is no blind sector below the bill in either of the ibises. These blind areas immediately below the bill and how they project onto the ground below the birds are depicted in Figures 1(a,c) and 2. The blind area behind the head is relatively larger, 50° wide at the horizontal, in the Northern Bald Ibis compared with the other three species, in which it is approximately 30° wide. This larger blind area may be associated with the crest of feather at the back of the skull, a feature of the head plumage of Northern Bald Ibis (Fig. 1a).

Eye movement amplitude

In all birds, casual observations through the ophthalmoscope showed spontaneous and non-conjugate eye movements to be present and of sufficient amplitude to abolish binocularity in the region about the horizontal. As in other birds (Martin 2007), eye movements were complex rotations of the eyes such that lateral displacement of the field margins varied in their amplitude as a function of elevation. Maximum amplitude occurred in the frontal region and no movements of the retinal field margins occurred above and behind the head. Maximum eye movement amplitude was 14°, which is sufficient to abolition binocularity in the frontal field in all of the species.

DISCUSSION

We hypothesized that if visual field topography in birds is driven primarily by common ancestry, then the visual fields of our sample of closely related species from the Threskiornithidae should be highly similar. Clearly, this was not the case. Although the two species of spoonbills show highly similar visual field characteristics, these differed markedly from those of the two ibis species, which also differed from each other. This variation in visual field characteristics among a closely related group of species is similar to that found among duck species (Martin 2007). Ducks are also regarded as a closely related family in which foraging behaviours are guided primarily by either tactile or visual cues. Marked differences are found in their visual fields and these have been associated with the use of either tactile or visually guided foraging (Guillemain *et al.* 2002, Martin *et al.* 2007a). We argue that this finding of variation in visual field characteristics within two distinct taxa (Anatidae, Threskiornithidae) supports the general hypothesis that the variability among birds in their visual fields is best interpreted as adaptations to the specific perceptual challenges posed by a species' foraging ecology, rather than the more general perceptual challenges posed by locomotion, or are a consequence of shared ancestry (Martin 2007, 2009).

We also proposed that because Threskiornithidae are species capable of foraging guided by non-visual cues derived from a bill-tip mechanoreceptor organ (Cunningham *et al.* 2010a) (Table 1), their visual fields should resemble those of other bird species, such as some ducks and some long-billed shorebirds, known to employ tactile cues in their foraging (Martin 2007). However, none of the visual fields depicted in Figure 1 shows the characteristic of comprehensive visual coverage of the celestial hemisphere previously found in other bird species that are exclusively tactile-guided foragers. That the visual fields of spoonbills and Puna Ibises do not resemble those of other tactile-guided foragers is surprising, as spoonbills have the ability to forage on invisible prey in turbid water and mud (Swennen & Yu 2005), and Puna Ibises can detect buried prey, apparently guided solely by tactile cues.

Visual fields and foraging in ibises

Puna Ibises probe for food items hidden in soft substrates, typically in aquatic habitats. In comparison, Northern Bald Ibises take items from the surface of the ground and amongst vegetation in dry terrestrial habitats. Moreover, Northern Bald Ibises rarely probe, but if they do so, it is into fissures and rock crevices, not a soft substrate. Also Northern Bald Ibises have relatively few tactile receptors in their bills (Table 1). Thus, when foraging, the bill of a Northern Bald Ibis is probably guided primarily by visual cues. This can be correlated with their broader binocular field (maximum width 21°) which results in them having a more extensive blind area above and behind the head (55°) compared with Puna Ibises (28°) (Fig. 1). These broader binocular fields of Northern Bald Ibises are similar in width to those found in birds that employ visually guided pecking or lunging at food items that are taken directly in the bill under visual control. This includes species such as herons (Ardeidae), pigeons (Columbidae), hornbills (Bucorvidae), eagles (Accipitridae) and plovers (Charadriidae) (Martin 2007). Because of their technique of probing in soft substrates, Puna Ibises are probably less reliant upon visual cues and can clearly forage in their absence. This can be correlated with their very narrow binocular fields (maximum width 13°), in which the bill falls close to its periphery, and their more comprehensive visual coverage of the celestial hemisphere (blind area maximum width in Puna Ibises is approximately half that of Northern Bald Ibises).

These two examples illustrate the trade-off already described in ducks (Martin *et al.* 2007a) and shorebirds (Martin & Piersma 2009), between the requirement for a broader frontal binocular field for the visual control of accurate bill placement and the ability to gain comprehensive visual coverage for the detection of predators and conspecifics. The degree of coverage of the celestial hemisphere has been shown to have a strong influence on the amount of vigilance behaviour that duck species exhibit, which in turn has impacts on their daily energy budgets and the availability of suitable habitat in which to forage (Guillemain *et al.* 2002). We predict that there are similar trade-offs between vigilance and foraging behaviour in these two ibis species.

Visual fields and foraging in spoonbills

The visual topography of the spoonbills is particularly interesting. It is clear that these birds can see their own bill tips, despite their ability to rely exclusively upon tactile cues when foraging. However, the wide breadth and spatulate shape of their bill tip results in a large portion of the potential binocular field beneath the bill being obscured. This blind region is not found in the ibises. These blind areas are seen clearly in Figure 1. However, this figure also shows that with the bill held at its typical posture during foraging, the spoonbills gain extensive vision beneath the bill very close to their feet.

Figure 1 depicts the birds' heads held at a typical resting and foraging posture with the bill projecting 50° below the horizontal in the spoonbills. A detailed study of foraging behaviour in Black-faced Spoonbills *Platalea minor* reported that the bill is typically held at an angle of 60° below the horizontal when the birds are foraging with their characteristic bill-sweeping action (Swennen & Yu 2005). Therefore we suggest that the data shown in Figure 1 depict the projections of visual fields into the environment when these birds are foraging. Clearly, some variation about these head positions is likely to occur when foraging. This will not alter the visual fields of the birds but will influence slightly their projections into the environment (Fig. 1d).

Visual coverage close to the feet is also seen in the ibises but because of the greater eye-to-ground distance in spoonbills (Table 1), the area of surface close to the birds that can be seen binocularly beneath the bill is considerably larger in the spoonbills than in the ibises (Fig. 1d).

Given the well known tactile-based bill-sweeping foraging technique of spoonbills (Swennen & Yu 2005, 2008) and their ability to forage successfully in highly turbid water, the ability to see the bill and beneath it would seem to be unimportant in prey detection and capture. Therefore, the function of this arrangement of the visual field in the spoonbills needs explanation beyond prey detection and capture. We suggest that the function of the extensive binocularity of spoonbills may lie in the identification of larger prey after its capture and possibly in the transport of prey from the bill tip into the oesophagus.

Visual fields, prey identification and prey ingestion

Spoonbills and ibises typically take discrete food items such as fish, crustaceans and molluscs (Table 1). Although the detection and securing of items in the bill tip may not require visual guidance, it cannot be guaranteed that caught items are suitable prey; this may require visual inspection of items held in the bill tip. Such items could be seen when they extend sideways beyond the margins of the bill tip and also when tossed in the air, a characteristic behaviour of spoonbills following the capture of larger prey items (Matheu & del Hoyo 1992). Such visual inspection of prey items has been suggested to occur in skimmers (Rhynchopidae) after unsighted capture guided by tactile cues (Martin *et al.* 2007b) and in cormorants where low visibility in turbid waters may prohibit identification of prey until after capture when the items have been brought to the surface (Martin *et al.* 2008).

In spoonbills, and possibly in ibises, the ingestion of caught items may also require visual guidance. Some long-billed shorebirds can detect buried prey in the absence of visual cues but cannot see their own bill and so could not visually identify prey if brought to the surface and held in the bill tip (Martin 1994). However, these birds have long tongues which extend close to the bill tip and these are used to ratchet items to the back of the mouth when the bill is closed or partially open (Burton 1984). However, ibises and spoonbills have very short tongues relative to bill length (Swennen & Yu 2004) and the transport of items from the bill tip into the oesophagus requires items to be tossed back inside the opened mouth (Matheu & del Hoyo 1992). This presumably requires accurate visual estimation of the position and speed of movement of a tossed item. Binocular viewing may be particularly suited to this task as it has been argued that binocular vision in birds functions primarily in the detection of optic flow fields produced by moving objects, rather than in relative depth perception based upon static stereoscopic cues (Martin 2009). Such flow fields can specify directly both the direction of travel and time to contact an object, and do not require high visual resolution. Thus actually seeing a tossed item may be necessary for catching the item further back in the mouth, especially in young birds and even in experienced birds when handling unusual prey items. Prey transport cannot always rely upon skilled practice, and tactile cues from the bill tip cannot be employed once the prey has been released from the grip of the bill tip. In spoonbills it is only the spatulate tip that intrudes into the binocular field; the more proximal region of the bill is relatively narrow and it is possible that the spoonbills and ibises can see binocularly between the opened mandibles in this region. This is the case in some other large-billed birds such as the hornbills (Martin & Coetzee 2004) and cormorants (Martin *et al.* 2008), which seize prey items in their bill tips before tossing them to the back of the mouth.

CONCLUSIONS

Among the Threskiornithidae the perceptual challenges presented by foraging in different ecological conditions determine variation in visual field topography. Among birds generally the sensory challenges associated with differences in foraging ecology rather than the control of locomotion are the main evolutionary drivers of variation in visual field topography. Sensory capacities, of which visual fields are a striking example, can be fine-tuned to the perceptual challenges that are faced by species as their foraging ecology differentiates from that of recent ancestors.

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