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Anomalous binocular vision in African Harrier-Hawks

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An animal's visual field is the three-dimensional space around its head from which it can extract visual information at any instant[1]. Bird visual fields vary markedly between species, and this variation is likely to be driven primarily by foraging ecology[1–3]. The binocular visual field is the region in which the visual fields of the two eyes overlap; thus, objects in the binocular field are imaged by both eyes simultaneously. The binocular field plays a pivotal role in the detection of symmetrical optic flow-fields, providing almost instantaneous information on the direction of travel and the time to contact a target towards which the head or feet is travelling; thus, information from the binocular field is crucial in guiding key foraging behaviours[2,3]. Here, we demonstrate an unusual visual field and binocular extent above the head in African Harrier-Hawks, also known as Gymnogenes (*Polyboroides typus*) compared to 18 other members of the Accipitridae[4,5]. We argue that the observed visual field can be attributed to the unusual and specific foraging behaviour of African Harrier-Hawks.

Diurnal raptors, within which the Accipitridae sit, typically have broad binocular fields coupled with a substantial blind region in the anterior-dorsal region that extends above the head[3–5]. The presence of this large blind region is correlated with the presence of large supraorbital ridges ('eyebrow bone'), which function to prevent imaging of the sun on the retina to maintain high spatial resolution[4]. Such high spatial resolution, combined with the visual field topography of these birds, appear to have evolved to meet the primary perceptual challenges of their foraging behaviour. High resolution facilitates the detection of moving or static prey remote from a bird, allowing them to forage efficiently for prey items over large areas[2]. The binocular field configuration mediates precise control of flight direction and the timing of talon deployment during prey capture, which may occur at high velocity[3]. African Harrier-Hawks, however, employ a different and specialised method of foraging which presents them with different perceptual challenges. Their foraging primarily involves using wing-assisted climbing within and around trees to locate cavities or the nests of weaver birds (Ploceidae), and the extraction of bird eggs and nestlings, invertebrates, and reptiles using either their beak or feet[6]. Thus, prey are not located at a distance and precise timing of prey capture is not necessary (Figure 1; Video S1). Of particular importance when extracting prey from restricted spaces with the feet are the African Harrier-Hawk's unique double-jointed legs[7,8], which assist them with grabbing prey items from within enclosed spaces even when adopting extreme postures, for example, hanging upside down. Moreover, previously it has been demonstrated that the eye size of African Harrier-Hawks is one of the smallest compared to the other members of the Accipitridae family[9]. We predicted that this different and unusual foraging technique, with its different perceptual challenges, would result in African Harrier-Hawks having visual fields that differ from close relatives within the Accipitridae family.

We used the ophthalmoscopic reflex technique[1–5] (Supplemental information; Data S1A) to determine the binocular visual fields of African Harrier-Hawks and compared this with similar data available for other species from the Accipitridae family (Gypaetinae, Circaetinae, Aegypiinae, Aquilinae, Accipitrinae, Buteoninae) (Supplemental Figure S1). This comparative analysis used a combination of new data collected for this study from birds held by The Hawk Conservancy Trust (Andover, UK) and previously published data (Data S1A).

We found that most aspects of the general visual field topography of the African Harrier-Hawks are typical of the Accipitridae, with a maximum binocular width of 27°, which is comparable to other members of the family (Figure 1; Data S1B); maximum binocularity width for active hunting members of the Accipitridae range from 24° in Short-toed Snake Eagles (*Circaetus gallicus*) to 56° in Black-chested Buzzard Eagles (*Geranoaetus melanoleucus*; Figure 1; Data S1B). In contrast, however, to all other Accipitridae measured, African Harrier-Hawks have no blind anterior-dorsal area due to the supraorbital process not being well developed and have binocular coverage directly above their head (Figure 1). Indeed, the vertical extent for the binocular field from the bill tip to above the head is 20 to 100% higher in the African Harrier-Hawks than in any other member of the Accipitridae (Wilcoxon signed rank test, $V = 0$, $p < 0.001$).

African Harrier-Hawks are distinct among Accipitridae with respect to the degree of binocularity present in the upper portion of their visual field. We suggest that this distinctive binocular field topography is related to the African Harrier-Hawks' foraging strategies and prey location behaviours and are associated with their double-jointed ankle/intertarsal joints[7,8]. For example, binocularity above the head means that African Harrier-Hawks can retain their feet within the binocular field when hanging upside down or when angling their head to locate prey in small crevices (Figure 1), thus ensuring accurate placement of the bill or feet into an aperture, while keeping the head still and prey in view. The lack of development of the supraorbital bones, slim head, and the persistence of binocularity above the head in African Harrier-Hawks share similarities with the New World vultures (Cathartidae)[10]. We conclude that African Harrier-Hawks exhibit a distinct relationship between their specialized foraging strategy and the degree of binocularity that they exhibit above their head. This makes them unique among the active hunting Accipitridae and presents a further example of fine-tuning between sensory ecology and foraging strategies in birds[1].

SUPPLEMENTAL INFORMATION

Supplemental information includes one figure, supplemental experimental procedures, author contributions, supplemental references, data file and a video and can be found with this article online at: https://doi.org/10.1016/j.cub.2023.09.016. All data are available in the supplemental information. Short videos can be found as supplemental information; full videos

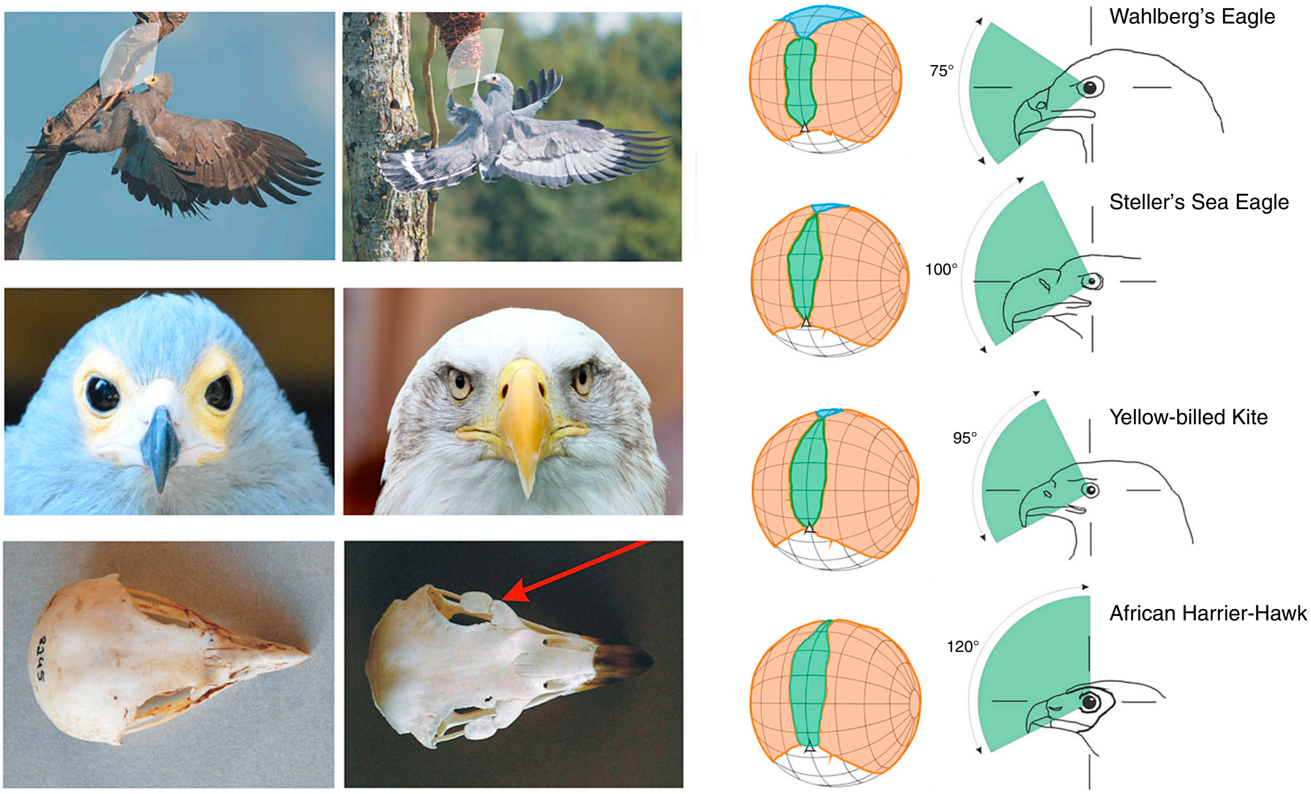

Figure 1. Visual fields in the Accipitridae.
Left panel (photographs): Top left: African Harrier-Hawk hanging upside down from a tree cavity and a weaver nest (photo credit: Marietjie Froneman). The white shaded area denotes projection into the foraging environment of the binocular field. Middle left: Front view of an African Harrier-Hawk (left) showing the absence of supraorbital ridges versus a Bald Eagle (right) (photo credits: James Knight, Peter Kraayvanger). Bottom left: Dorsal view of the skull of an African Harrier-Hawk (left) versus a Bald Eagle (right) showing the lack of development of the supraorbital bones in the African Harrier-hawk, which are characteristic of all other Accipitridae (photos: Jan Jansen, Wouter van Gestel). The red arrow highlights the highly developed supraorbital bones. Middle panel: 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) in three examples of Accipitridae species versus the African Harrier-Hawk (bottom). The diagrams use the 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. Green areas, binocular sectors; orange areas, monocular sectors; blue areas, blind sectors. Right panel: Vertical sections through the binocular fields in the median sagittal plane of the head.

can be accessed at: https://www.dropbox.com/scl/fo/xy680x8936rjuzd2jm62n/h?rlkey=dbvw8ghglexx3jk6m7xzz50da&dl=0

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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