



**HAL**  
open science

## Visual abilities in two raptors with different ecology

Simon Potier, Francesco Bonadonna, Almut Kelber, Graham R Martin,  
Pierre-François Isard, Thomas Dulaurent, Olivier Duriez

► **To cite this version:**

Simon Potier, Francesco Bonadonna, Almut Kelber, Graham R Martin, Pierre-François Isard, et al..  
Visual abilities in two raptors with different ecology. *Journal of Experimental Biology*, 2016, 219 (17),  
pp.2639-2649. 10.1242/jeb.142083 . hal-02394164

**HAL Id: hal-02394164**

**<https://hal.umontpellier.fr/hal-02394164>**

Submitted on 4 Dec 2019

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

## RESEARCH ARTICLE

# Visual abilities in two raptors with different ecology

Simon Potier<sup>1,\*</sup>, Francesco Bonadonna<sup>1</sup>, Almut Kelber<sup>2</sup>, Graham R. Martin<sup>3</sup>, Pierre-François Isard<sup>4</sup>, Thomas Dulaurent<sup>4</sup> and Olivier Duriez<sup>1</sup>

## ABSTRACT

Differences in visual capabilities are known to reflect differences in foraging behaviour even among closely related species. Among birds, the foraging of diurnal raptors is assumed to be guided mainly by vision but their foraging tactics include both scavenging upon immobile prey and the aerial pursuit of highly mobile prey. We studied how visual capabilities differ between two diurnal raptor species of similar size: Harris's hawks, *Parabuteo unicinctus*, which take mobile prey, and black kites, *Milvus migrans*, which are primarily carrion eaters. We measured visual acuity, foveal characteristics and visual fields in both species. Visual acuity was determined using a behavioural training technique; foveal characteristics were determined using ultra-high resolution spectral-domain optical coherence tomography (OCT); and visual field parameters were determined using an ophthalmoscopic reflex technique. We found that these two raptors differ in their visual capacities. Harris's hawks have a visual acuity slightly higher than that of black kites. Among the five Harris's hawks tested, individuals with higher estimated visual acuity made more horizontal head movements before making a decision. This may reflect an increase in the use of monocular vision. Harris's hawks have two foveas (one central and one temporal), while black kites have only one central fovea and a temporal area. Black kites have a wider visual field than Harris's hawks. This may facilitate the detection of conspecifics when they are scavenging. These differences in the visual capabilities of these two raptors may reflect differences in the perceptual demands of their foraging behaviours.

**KEY WORDS:** Harris's hawk, Black kite, Raptor vision, Visual acuity, Visual field, Fovea

## INTRODUCTION

The ability of animals to detect food items and predators depends upon their sensory capabilities. As bird eyes are in general relatively large with respect to body size, it is assumed that vision is an important sensory modality (Schwab et al., 2012). Birds, however, are also known to differ highly in their visual capabilities (Hart, 2001; Kiltie, 2000; Martin, 2007) and these differences must result in differences in the ability of species to retrieve information from their environments.

Among birds, a wide range of foraging behaviours have been recorded (Remsen and Robinson, 1990) and these can be correlated with the different sensory challenges posed by the exploitation of different food sources in different environments (Robinson and Holmes, 1982). Visual capabilities may reflect different behavioural tactics such as scanning (Fernández-Juricic, 2012), prey detection or capture (Martin, 2009; O'Rourke et al., 2010a).

Birds of prey (hereafter called raptors) have always been considered to be highly dependent on their vision (Jones et al., 2007). Nevertheless, raptors differ greatly in their foraging ecology and consequently may also differ in their visual abilities. While some species search for food when flying at high altitude, others search from a perch or by walking on the ground (Del Hoyo and Elliot, 1994), and we suggest that raptor species with different foraging ecology might differ in their visual fields, eye and head movements (O'Rourke et al., 2010a,b) and perhaps in their visual acuity. Significant differences in the vision of closely related birds that differ in their foraging behaviour have been described in other species (Guillemain et al., 2002; Martin and Piersma, 2009; Martin and Portugal, 2011).

Visual acuity is a measure of the maximum resolving capacity of a visual system for stimuli of high contrast, and is relatively easy to compare across species. Diurnal raptors have been shown to have the highest visual acuity among animals (Land and Nilsson, 2012). They have high photoreceptor and ganglion cell densities in the fovea and this provides high visual resolution (Jones et al., 2007; Raymond, 1985, 1987). However, acuity has been measured in only a relatively small number of raptor species and the generality of high acuity among raptors is assumed rather than established by behavioural measures (Fischer, 1968; Fox et al., 1976; Hirsch, 1982; McIsaac, 2001; Potier et al., 2016; Raymond, 1985, 1987) (see Table 1 for details). All these behavioural experiments on visual acuity have been done on only a few individuals per species (one individual for most studies, sometimes two or three), although it is known that individuals can differ in their visual acuity, as found in American kestrels (visual acuity estimated by electroretinogram; Gaffney and Hodos, 2003). Furthermore, it has been shown that raptors differ in their head movements, which could reflect different foraging tactics (O'Rourke et al., 2010b). Because inter-individual problem-solving abilities have been found in a raptorial species, the chimango caracara, *Phalcoboenus chimango* (formerly named as *Milvago chimango*; Biondi et al., 2010), it is possible that individuals may also differ in their behaviour when presented with a visually challenging task; for instance, the number of head movements may differ before making a visual discrimination or there may be differences in the time delay before showing a response towards a stimulus. These behavioural differences may also reflect inter-individual differences in visual capacity, particularly of visual acuity.

The retinas of raptors show a deep and convexiculate central fovea (looking sideways) in which there are higher densities of ganglion cells and photoreceptors compared with the peripheral

<sup>1</sup>Department of Evolutionary Ecology and Department of Biodiversity and Conservation - CEFE UMR 5175, CNRS-Université de Montpellier-Université Paul-Valéry Montpellier-EPHE, 1919 route de Mende, 34293 Montpellier, Cedex 5, France. <sup>2</sup>Department of Biology, Lund University, Sölvegatan 35, Lund S-22362, Sweden. <sup>3</sup>School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK. <sup>4</sup>Centre Hospitalier Vétérinaire, Unité d'Ophtalmologie, 275 route Impériale, Saint-Martin Bellevue 74370, France.

\*Author for correspondence (simon.POTIER@cefe.cnrs.fr)

 S.P., 0000-0003-3156-7846

**Table 1. Review of visual acuity of diurnal raptor species**

Order: Family	Common name	Species	N	Corneal diameter (mm)	Visual acuity (cycles deg <sup>-1</sup> )	Method for estimating acuity	Reference	
Accipitriformes: Cathartidae	Turkey vulture	<i>Cathartes aura</i>	3	9.0	15.4	Retinal cell densities	Lisney et al., 2013	
	Black vulture	<i>Coragyps atratus</i>	3	9.7	15.8	Retinal cell densities	Lisney et al., 2013	
Accipitriformes: Accipitridae	Red-tailed hawk	<i>Buteo jamaicensis</i>	1	14.7*	16.8	Behavioural experiment	Mclsaac, 2001	
	Black kite	<i>Milvus migrans</i>	2	10.7	25.9–32.9	Behavioural experiment	Present study	
	Harris's hawk	<i>Parabuteo unicinctus</i>	5	10.3	27.4–43.7	Behavioural experiment	Present study	
	White-backed vulture	<i>Gyps africanus</i>	10	12.5	57.5	Corneal measurements	Spiegel et al., 2013	
	Lappet-faced vulture	<i>Torgos tracheliotus</i>	6	17.0	88.9	Corneal measurements	Spiegel et al., 2013	
	Griffon vulture	<i>Gyps fulvus</i>	1	11.9*	104	Behavioural experiment	Fischer, 1968	
	Egyptian vulture	<i>Neophron percnopterus</i>	2	9.9*	108–135	Behavioural experiment	Fischer, 1968	
	African serpent eagle	<i>Dryotriorchis spectabilis</i>	1	NA	120	Optical measurements	Shlaer, 1972	
	Indian vulture	<i>Gyps indicus</i>	1	NA	135	Behavioural experiment	Fischer, 1968	
	Wedge-tailed eagle	<i>Aquila audax</i>	1	15.0*	132–142	Behavioural experiment	Reymond, 1985	
	Falconiformes: Falconidae	Chimango caracara	<i>Phalcoboenus chimango</i>	3	8.4	15.1–39.8	Behavioural experiment	Potier et al., 2016
American kestrel		<i>Falco sparverius</i>	3	7.3*	15.9–40.5	Behavioural experiment	Mclsaac, 2001	
			1	7.3*	40	Behavioural experiment	Hirsch, 1982	
				1	7.3*	160	Behavioural experiment	Fox et al., 1976
				9	7.3*	39.7–71.4	Electroretinogram	Gaffney and Hodos, 2003
		Brown falcon	<i>Falco berigora</i>	1	10.8*	73	Behavioural experiment	Reymond, 1987

N refers to the number of individuals.

\*Corneal diameter obtained from Ritland (1982).

retina (Inzunza et al., 1991; Jones et al., 2007; Reymond, 1985). However, it seems that the number of foveas differs among raptors, with only one central fovea in carrion eaters but a central and a temporal fovea (looking forward) in predators (Fite and Rosenfield-Wessels, 1975; Inzunza et al., 1991). These differences could be reflected in different behavioural visual acuity but also in different visual fields as each fovea seems to be linked to different axes in the visual field.

The visual field defines the amount of space around the head from which an individual can potentially gather visual information at any one instant (Martin and Katzir, 1999). The visual fields of diurnal raptors have received little attention (Martin and Katzir, 1999; Martin et al., 2012; O'Rourke et al., 2010a) and they can differ significantly between species (O'Rourke et al., 2010a). Binocularity, for instance, plays a key role in the foraging behaviour of raptors, especially in the control of bill position and/or the position of the feet at the moment of prey capture (Martin, 2009).

In this study, we aimed to understand whether two species of raptors (family Accipitridae), which differ in their foraging tactics, vary in their vision. We measured visual field characteristics, visual acuity by an operant conditioning technique and the physical characteristics of the fovea(s) in two species: Harris's hawks, *Parabuteo unicinctus* (Temminck 1824), and black kites, *Milvus migrans* (Boddaert 1873). The two species are of similar

size (Harris's hawk and black kite respective measurements: body mass: 550–1200 and 630–1080 g, wingspan: 92–121 and 120–153 cm, length: 45–59 and 44–66 cm; Del Hoyo and Elliot, 1994) but differ in their ecology. Harris's hawks forage exclusively using a sit-and-wait tactic, scanning their environment to detect and catch mainly ground-dwelling mammals and reptiles (Del Hoyo and Elliot, 1994). Black kites are opportunistic foragers that search mainly in flight for carrion but also catch small live prey such as rodents, reptiles or insects on the ground (Del Hoyo and Elliot, 1994). Black kites are also social birds, which commonly forage in groups in which they can acquire 'public information' on food presence (Sergio, 2003), and migrate and roost in large groups.

## MATERIALS AND METHODS

### Subjects

Dependent upon their availability, we used different numbers of Harris's hawk and black kites for each experiment. All these raptors were healthy hand-raised animals held in raptor facilities for public shows during the summer season. Six Harris's hawks and six black kites were used for the visual acuity experiment, seven Harris's hawks and three black kites for the foveal measurements and six Harris's hawks and three black kites for the visual field experiment.

All Harris's hawks were from the collection of birds held at the Falconry park Les Ailes de l'Urga (site 1) and black kites were from the collection held at Le Grand Parc du Puy du Fou (site 2), France (see Table 2 for details). The birds of each species were generally housed together in an aviary but, during the experiment, they were placed outside their aviaries and attached to a falconry perch adapted to each species.

### Ethics

The study was conducted under a formal agreement between the animal rearing facilities, Le Grand Parc du Puy du Fou and Les Ailes de l'Urga, CNRS, and Centre Hospitalier Vétérinaire of Saint Martin de Bellevue. In agreement with French law, birds were handled by their usual trainer, under the permit of Le Grand Parc du Puy du Fou (national certificate to maintain birds 'Certificat de capacite' delivered to the director of the falconry, Jean-louis Liegeois, on 7 April 1994) and of Les Ailes de l'Urga (national certificate to maintain birds 'Certificat de capacite' delivered to the director of the falconry, Patrice Potier, on 20 June 2006).

### Experiment 1: visual acuity

During the training and test phases, birds received their daily diet of small pieces of chicken meat as rewards only during the experiment. To control body condition and maintain a stable body mass, birds were weighed every day with a balance that had an accuracy of  $\pm 10$  g.

### Experimental aviaries

Two test aviaries were used for the determination of visual acuity in Harris's hawks and black kites, depending on the site. Aviaries were 8 m wide, 5 m high and either 12.5 m (site 1: Harris's hawks) or 10 m (site 2: black kites) long. A starting perch was placed at 10 m (site 1) and 8 m (site 2) distance from two wooden boxes (6 m from each other), each of which housed a monitor screen (Samsung S22C300H) that was used to present the visual stimuli (created in R.3.1.2, R Development Core Team 2014, and presented using Microsoft Office PowerPoint 2010; see Fig. 1). Monitor screen size was 510×398 mm, which corresponded to 2.92×2.28 deg visual angle when observed by the birds at 10 m distance. The boxes housing the monitors were 700 mm wide, 800 mm high and 1200 mm long, and were painted on the inside and outside in matt black to create a 'dark room'. The boxes shielded the monitor screen from direct sunlight. The illuminance (mean $\pm$ s.e.m.) of the screens in the two boxes while they were turned off was measured for each test phase and did not differ between the boxes (left box: 199.9 $\pm$ 16.6 lx,  $N=66$ ; right box: 200.2 $\pm$ 13.8 lx,  $N=66$ ;  $t=-0.01$ , d.f.=61.81,  $P=0.99$ ). Before each experiment, we ensured that the cage was oriented such that the birds never faced the sun while flying. To do so, we tested the birds only when it was cloudy or when the sun was above the birds. Under each monitor box there

was a perch attached to a feeding box with 10 closed compartments. Each compartment contained a piece of raw chicken meat, which could be given as a reward for correct choice behaviour by the experimenter remotely opening the compartment.

### Behavioural experiment

Visual acuity of Harris's hawks and black kites was measured using an operant conditioning technique. The birds were required to choose between a positive stimulus (uniform grey) on one screen and a negative stimulus (a grating composed of black and white vertical stripes; Michelson contrast=0.97) on the other screen, which were presented simultaneously. If the bird flew to the perch located under the positive stimulus, it received a food reward (3 g piece of chicken). The reward was presented by opening a compartment of the feeding boxes associated to the positive stimulus, using an electric motor with a remote control. The grey stimulus was randomly either darker or brighter ( $\pm 10\%$ ) than the average brightness of the grating to exclude the possibility that birds could use brightness as a cue. The determination of visual acuity involved two phases, as described below.

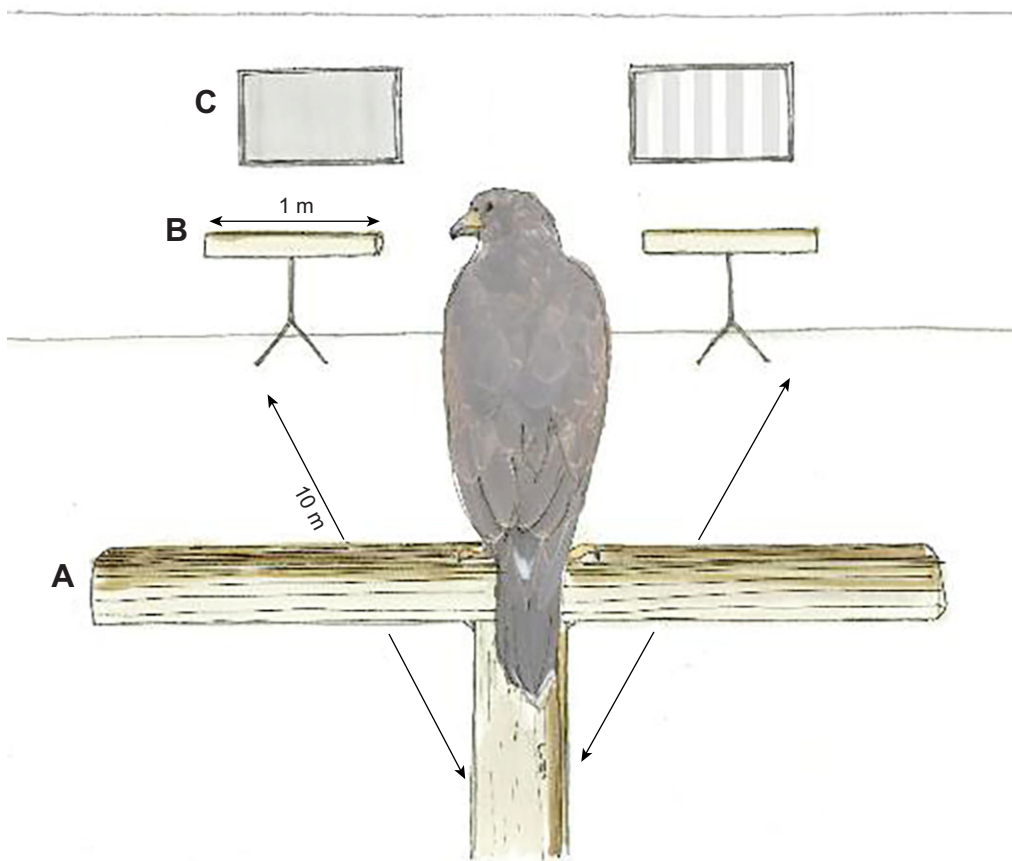
In phase 1 (training and conditioning), the birds learned to fly from the starting perch to the perch under the monitors and choose the monitor displaying the uniform stimulus (rewarded) instead of the monitor displaying the coarse grating (1.71 cycles deg<sup>-1</sup>) corresponding to 5 cycles presented. During the first 2 days, the feeding boxes were rotated at 90 deg so that the birds could look into the opened compartments at the start of each trial. A trial began when the monitors were turned on and the compartment was opened. The birds continuously saw both stimuli during the training phase. The monitors were switched off after 5 s if the bird made an incorrect choice, or after the bird had finished eating if the bird made a correct choice. The observer (S.P.) then attracted the birds to return to the starting perch with a piece of food in his hand, but without giving it to them. Later, the food reward was hidden and the bird returned to the starting perch voluntarily. Two sessions of 30 trials were conducted every day until the birds were conditioned; conditioning was assumed when the bird made more than 80% of correct choices during three consecutive training sessions. For a session of 30 trials, positive and negative stimuli were presented 15 times on each side. The side was changed in a quasi-random order, i.e. to prevent side preferences, the positive stimulus was presented on the same side for a maximum of three consecutive trials (Reymond, 1985).

In phase 2 (test), two sessions were conducted per day for 3 days and one session was conducted on the fourth day. Before each test session, we presented five coarse gratings (1.71 cycles deg<sup>-1</sup>) to ensure that the birds were still conditioned to the grey pattern. We considered that the birds were still conditioned if they made five correct choices. Otherwise, we continued training with coarse gratings until performance returned to 80% (this was not necessary

**Table 2. Experimental subjects and visual acuity**

Species	Individual	Sex	Age (years)	Visual acuity (cycles deg <sup>-1</sup> )	Time to decision (s)	No. head movements before decision
Harris's hawks	A	Female	5	42.8	4.2 $\pm$ 0.1	3.1 $\pm$ 0.2
	B	Female	4	35.3	2.2 $\pm$ 0.1	1.6 $\pm$ 0.1
	C	Male	4	37.2	3.7 $\pm$ 0.3	3.2 $\pm$ 0.2
	D	Female	4	27.4	2.3 $\pm$ 0.1	1.1 $\pm$ 0.1
	E	Male	5	43.7	3.1 $\pm$ 0.1	2.3 $\pm$ 0.1
Black kites	A	Male	1	32.7	27.1 $\pm$ 1.8	17.0 $\pm$ 0.9
	B	Male	1	25.9	15.4 $\pm$ 0.7	17.6 $\pm$ 0.8

Visual acuity was estimated using the operant conditioning method. Data for time to decision and number of head movements are means $\pm$ s.e.m.



**Fig. 1. Schematic drawing of the experimental setup used to estimate the visual acuity of raptors.** (A) Starting perch, (B) arrival perches with food reward box compartment and (C) screens.

for any of the black kites and was only required for two of the Harris's hawks, individuals C and D). We conducted five sessions of 30 trials and two sessions of 29 trials, with eight different gratings that were presented randomly across trials and sessions. Each grating was presented 26 times. When the bird was about to leave the starting perch (opening the wings before flying), the monitors were switched off (by the observer) to ensure that the bird could not change the decision on the way. The observer (S.P.) was hidden in a cabin to avoid any influence on the bird's choice but he was not blind to the experiment as he needed to command the opening of the food reward compartment. A video camera (GoPro Hero 3+) fixed on the roof of the aviary filmed the bird on the start perch and for each trial the sequence was analysed to determine the number of horizontal head movements (when the bird rotated its head from one side to the other in a horizontal plane) and the time that the bird took before making a decision when monitors were turned on.

#### Physiological measurement

##### Eye size and assessment of visual acuity

Corneal diameter was measured with ImageJ v.1.49 from close-up photographs of three individuals of each species, as proposed by Spiegel et al. (2013). The mean corneal diameter (CD) values for each species were translated to axial length (AL) using the Hall and Ross (2007) formula for diurnal vertebrate eyes:

$$AL = CD / 10^{-0.22}. \quad (1)$$

For black kites, the corneal diameter obtained by close-up photographs ( $10.7 \pm 0.6$  mm) was similar to that reported by Ritland (1982) (10.9 mm). No measurement of corneal diameter was found for Harris's hawks in the literature.

We then calculated the visual acuity (VA) using the allometric function determined by Kiltie (2000):

$$VA = 10^{(1.42 \times \log_{10}(AL) - 0.11)}. \quad (2)$$

We compared the visual acuity obtained by this allometric function with the visual acuity determined experimentally.

#### Foveal and retinal size

We measured retinal thickness at the foveal rim and foveal depth (difference between retinal thickness at the rim and retinal thickness at the foveal pit) using ultra-high resolution spectral-domain optical coherence tomography (OCT; Ruggeri et al., 2010). OCT is a low-coherence interferometric technique based on non-invasive microscopic imaging and provides non-contact, high-resolution, cross-sectional images of biological tissues. The equipment used for this study consisted of a spectral OCT system (OCT/SLO, Group OTI/USA; EDC Vet, Carvin, France) with a specific corneal module. The cornea was not pressed against the device and the observer (S.P.) needed to find a suitable distance between the module and the eye to obtain an image. For each individual, a video sequence was recorded from which the best image was selected to accurately show the retina and the fovea (s). Birds were awake and alert during the entire imaging process, which took less than 10 min. They were held gently by the experienced bird handler (S.P.), and no mechanical device was used to fix the head. For animal welfare, only the right eye was examined in each individual.

## Experiment 2: visual field

We used a non-invasive procedure to measure visual field characteristics in alert birds that has been detailed extensively in publications in >40 species (see Martin, 2007, and Martin and Shaw, 2010, for a list). The procedure was reviewed in 2007 by the UK Home Office.

Each bird was held firmly in a plastic holding tube of the appropriate size to avoid any movement for between 20 and 30 min. The bird's legs were taped lightly together, cushioned by a piece of foam rubber held between them. The head was held in position at the centre of a visual perimeter (a device that allows 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 species to take account of differences in the size and shape of the bills. 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.

Calibrated photographs of the head of each bird when held 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 and bill length.

Visual field parameters were determined using an ophthalmoscopic reflex technique. 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 that divided the head symmetrically into its left and right halves) and this coordinate system is used for the presentation of visual field data. The eyes were examined using an ophthalmoscope mounted against the perimeter arm and its position was read to  $\pm 0.5$  deg. Maximum visual field was measured and the limits were defined by the positions that the eyes spontaneously adopted when they were fully rotated 'forwards' (converged for the front field) and 'backwards' (diverged for the back field). We did not measure eye movements and the projection of the pecten to reduce holding time for the birds.

From these combined data (corrected for viewing from a hypothetical viewing point placed at infinity; this correction is based upon the distance used in the perimeter apparatus and the horizontal separation of the eyes), a topographical map of the visual field and its principal features was constructed. These features were: monocular fields, binocular field, cyclopean field (combination of both monocular fields) and blind area. It was possible to measure the limits of the visual field at 10 deg intervals of elevation in an arc from directly behind the head, to above the head and then down to 60 deg below the horizontal in front of the head. However, depending of the bill shape, the bill holder intruded into the view of the eyes at a specific elevation for each species. Therefore, it was not possible to record visual field data at these elevations and the binocular field width was estimated as the mean value of the binocular field widths above and below these elevations.

## Statistical analysis

All analyses were performed with R.3.1.2 (R Development Core Team 2014) using {lmer} (<http://lme4.r-forge.r-project.org/>), {psyphy} (<http://CRAN.R-project.org/package=psyphy>) and {ggplot2} (<https://cran.r-project.org/web/packages/ggplot2/index.html>) packages. Throughout the paper, means are represented  $\pm$ s.e.m. and statistical significance was assumed for  $P < 0.05$ .

To determine the threshold of visual acuity (72.5% correct choices, binomial test,  $N=26$ ,  $P < 0.05$ ), we fitted a psychometric function to the data of each individual using generalized linear

models (GLMs). We used a mixed model with Gaussian error distribution to test for an effect of the time spent by the bird attending to the stimulus panels before making a choice in the visual acuity tests. To test the relationship between the number of horizontal head movements and visual acuity, we used a mixed model with Poisson error distribution, which is most appropriate for count data (Zuur et al., 2009). We used GLMs to test for a difference between individuals in the number of horizontal head movements (Poisson error distribution) and the delay (Gaussian error distribution) before taking a decision.

We used Mann–Whitney to test for differences in retinal thickness and depth of fovea(s) and the ratio of these between species. We also used Mann–Whitney to test for a difference in the size of the two foveas for the Harris's hawks and difference in eye size between the two species.

We used Mann–Whitney to test for a difference in binocular area (maximum binocular field width and binocular overlap at rest) and blind area (at rest behind and above the head) between species.

## RESULTS

### Experiment 1: visual acuity

#### Behavioural experiment

For experiment 1, we used six Harris's hawks and six black kites. Only two black kites were ultimately conditioned to the pattern. All Harris's hawks were conditioned, but after veterinary examination (chromatic pupillometry, PupilScan SiemBiomédicale, Nîmes, France), one Harris's hawk was found to be insensitive to red light (S.P. and P.-F.I., personal observation). Because the monitor pixels are made of 3 subpixels (red, blue and green), and we do not really know how this bird perceived the stimuli (Weisman and Spetch, 2010), we decided to stop the experiment with this individual.

The visual acuity determined in the behavioural test ranged from 27.4 to 43.7 cycles  $\text{deg}^{-1}$  ( $N=5$ , mean  $37.3 \pm 2.9$  cycles  $\text{deg}^{-1}$ ) for the Harris's hawks and from 25.9 to 32.9 cycles  $\text{deg}^{-1}$  ( $N=2$ , mean  $29.3 \pm 3.4$  cycles  $\text{deg}^{-1}$ ) for the black kites (Fig. 2, Table 2).

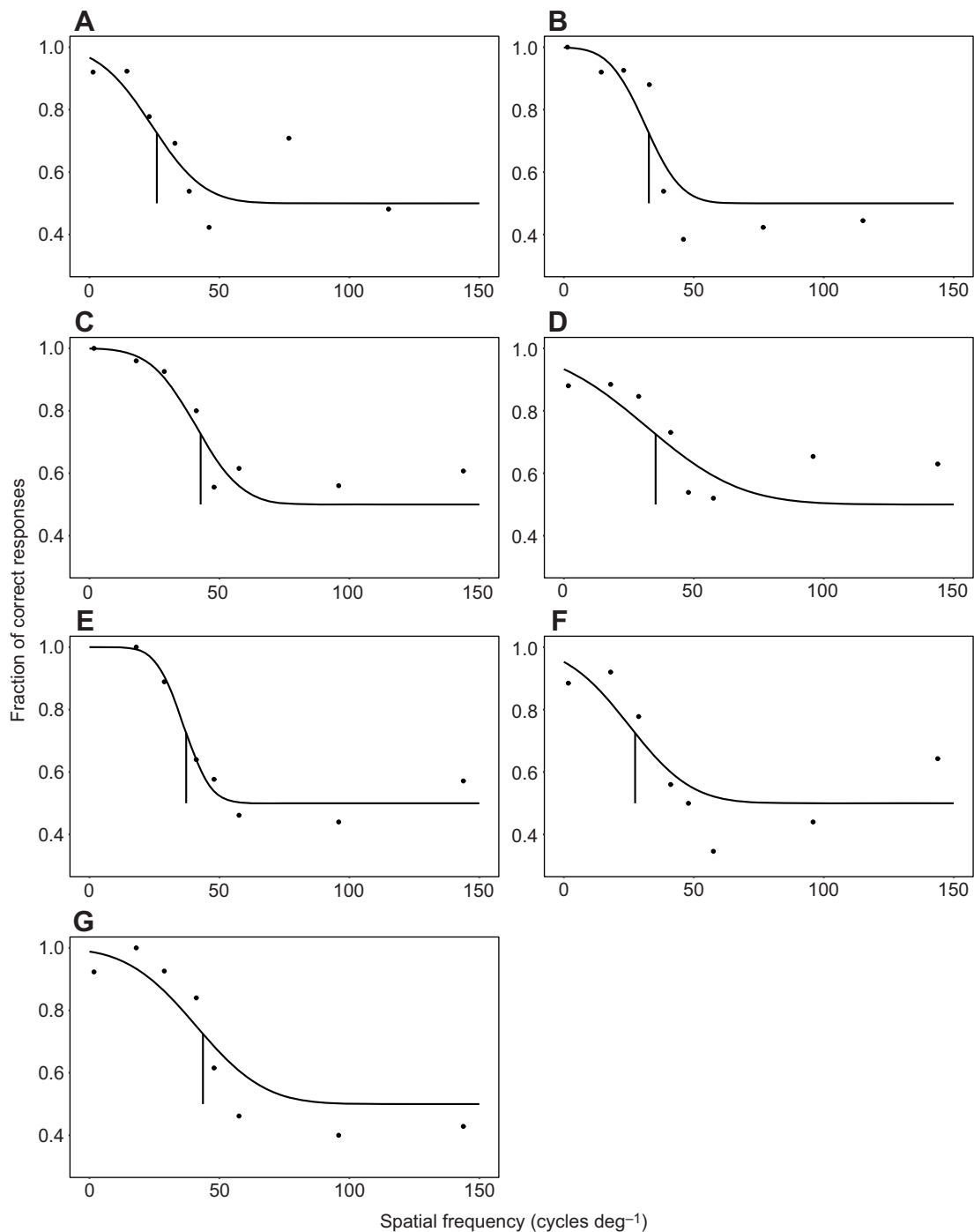
Black kites spent more time ( $21.3 \pm 1.3$  versus  $3.1 \pm 0.1$  s) attending to the stimuli and made more horizontal head movements ( $17.3 \pm 0.9$  versus  $2.3 \pm 0.1$ ) before making a decision than Harris's hawks (Table 2). We found differences between individual Harris's hawks in the time they spent attending to the stimuli (d.f.=4, residual deviance=501.11,  $P < 0.001$ ) and the number of horizontal head movements (d.f.=4, residual deviance=269.66,  $P < 0.001$ ) before making a decision (Table 2). We found that visual acuity was higher in individuals displaying more numerous horizontal head movements ( $t=2.76$ ,  $P=0.006$ ), while there was no link between visual acuity and the time spent attending to the stimuli ( $t=2.02$ ,  $P=0.084$ ).

#### Eye size and assessment of visual acuity

The corneal diameter was  $10.3 \pm 0.5$  mm for Harris's hawks ( $N=6$ ) and  $10.7 \pm 0.6$  mm for black kites ( $N=3$ ). The visual acuity estimated by the allometric function from the corneal diameter measurement was 43.8 and 46.2 cycles  $\text{deg}^{-1}$  for the Harris's hawks and black kites, respectively.

#### Foveal and retinal size

We found two foveas in Harris's hawk retinas (one positioned in a central location and one positioned in the temporal portion of the retina) but only one, centrally positioned fovea in black kite retinas (Fig. 3). Black kites have only a thickened temporal area but no

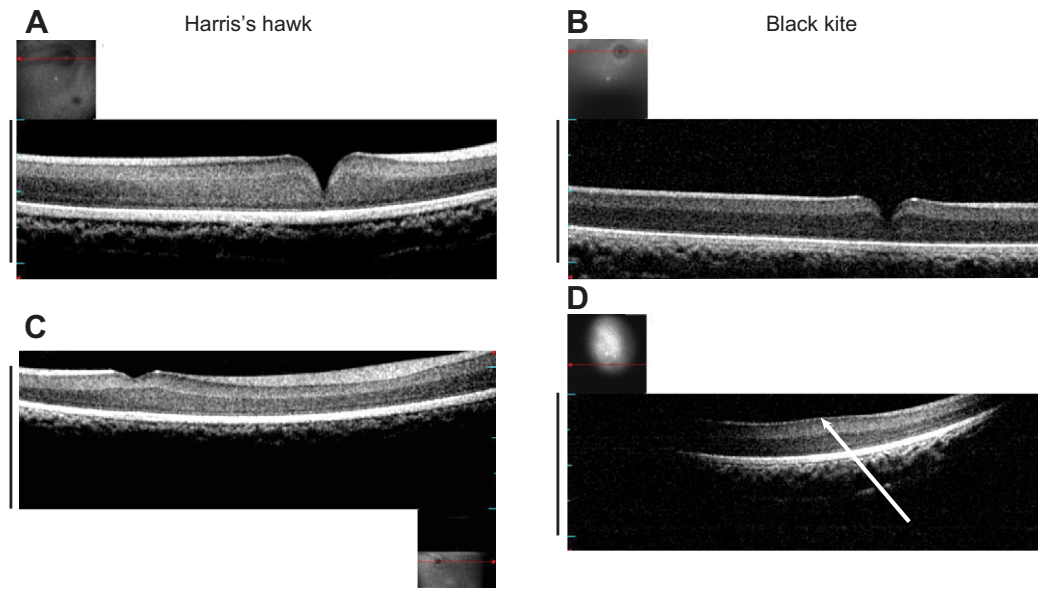


**Fig. 2. Psychometric functions for black kites and Harris's hawks used to determine visual acuity.** Data were obtained from two black kites (A,B; kites A and B, respectively) and five Harris's hawks (C–G; hawks A–E, respectively). Vertical lines represent the estimated visual acuity at the threshold of 72.5% correct choices.

'true' fovea in this region. Harris's hawks have a deeper central fovea than black kites ( $177.8 \pm 15.0$  versus  $115.7 \pm 22.0$   $\mu\text{m}$ , respectively,  $W=21$ ,  $P=0.017$ ; Fig. 4A). The retina was thicker in Harris's hawks than in black kites (respectively,  $268.1 \pm 2.3$  versus  $229.0 \pm 14.4$   $\mu\text{m}$ ,  $V=28$ ,  $P=0.016$ ; Fig. 4B). Moreover, the ratio of fovea depth to retina thickness was higher in Harris's hawks than in black kites ( $0.7 \pm 0.1$  versus  $0.5 \pm 0.1$ , respectively,  $W=20$ ,  $P=0.033$ ; Fig. 4C). The central fovea was significantly deeper than the temporal fovea in Harris's hawks ( $177.8 \pm 15.0$  versus  $19.9 \pm 9.8$   $\mu\text{m}$ ,  $W=49$ ,  $P<0.001$ ).

#### Experiment 2: visual field

The maximum width of the binocular field occurred at a mean elevation of 26 and 7 deg above the eye bill-tip direction in Harris's hawks and black kites, respectively (Fig. 5). The maximum width of the binocular field was  $45 \pm 2$  and  $39 \pm 2$  deg ( $W=15$ ,  $P=0.15$ ) for Harris's hawks and black kites, respectively (Fig. 5). The blind area was larger for Harris's hawks than for black kites above ( $75 \pm 5$  versus  $36 \pm 1$  deg,  $W=18$ ,  $P=0.024$ ) and behind ( $83 \pm 3$  versus  $73 \pm 2$  deg,  $W=17$ ,  $P=0.048$ ) the head (Figs 5 and 6).



**Fig. 3. Sectional and plan view (small image) of the fovea in Harris's hawks and black kites.** (A,B) Central fovea and (C,D) temporal fovea/area for Harris's hawks (A,C) and black kites (B,D) obtained by ultra-high resolution spectral-domain optical coherence tomography (OCT). For black kites, the temporal area was thickened but there was no true fovea (indicated by the white arrow). Scale bars: 1000  $\mu\text{m}$ .

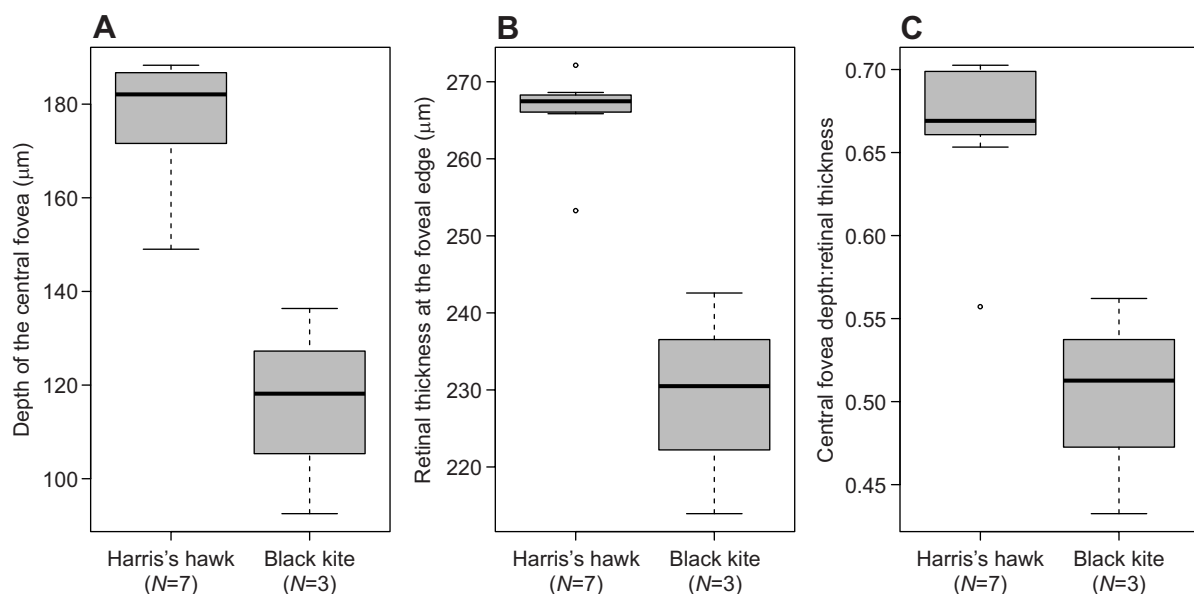
## DISCUSSION

In this study, we combined, for the first time, three complementary methods to investigate visual capabilities in two species of raptor that are morphologically similar but differ in their ecology. We estimated the visual acuity, the foveal shape and the visual fields of Harris's hawks and black kites. We found that Harris's hawks have a slightly higher visual acuity than black kites. The species differ in their retinal morphology, with two foveas (central and temporal) in Harris's hawks but only one central fovea in black kites. Finally, the species differ in their visual fields, with a wider visual field in black kites than in Harris's hawks. These differences in visual capabilities

may reflect different perceptual demands of the foraging behaviours of the two species.

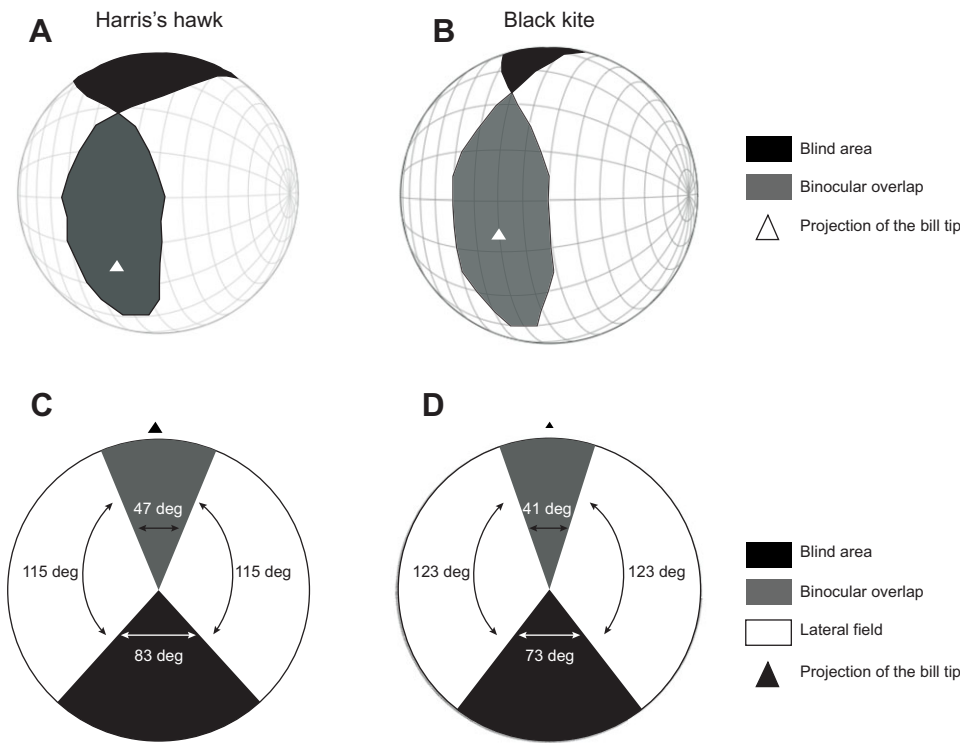
## Visual acuity

In birds in general, visual acuity is correlated with eye size (Kiltie, 2000; but see Boire et al., 2001). As we did not find any difference in corneal diameter between the two species, the theoretically estimated visual acuity according to the axial length did not differ between the two species (43.8 and 46.2 cycles  $\text{deg}^{-1}$  for the Harris's hawks and black kites, respectively, although the sample size was too small to use appropriate statistical tests). Our behavioural experiments



**Fig. 4. Foveal and retinal characteristics of Harris's hawks and black kites.** (A) Depth of the central fovea (Wilcoxon test,  $W=21$ ,  $P=0.017$ ). (B) Retinal thickness at the foveal edge (Wilcoxon test,  $V=28$ ,  $P=0.016$ ). (C) Ratio of the depth of the central fovea and retinal thickness (Wilcoxon test,  $W=20$ ,  $P=0.033$ ).



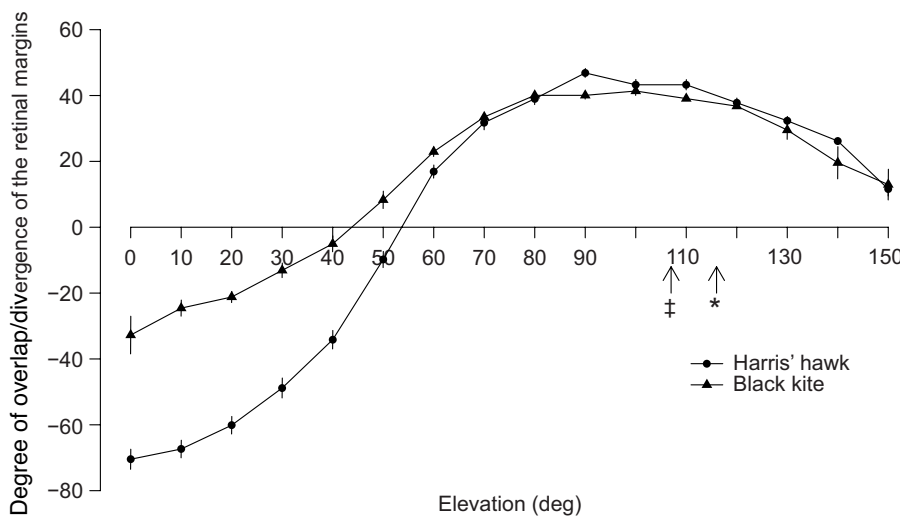


**Fig. 5. Visual field of Harris's hawks and black kites with the eye at rest.** Two views of the visual field of Harris's hawks ( $N=6$ ; A,C) and black kites ( $N=3$ ; B,D). (A,B) Orthographic projection of the boundaries of the retinal fields of the two eyes. A latitude and longitude coordinate system was used with the equator aligned vertically in the median sagittal plane. The bird's head is imagined to be at the centre of the globe (grid is at 20 deg intervals in latitude and 10 deg in longitude). (C,D) Horizontal sections through the horizontal plane (90–270 deg) showing the visual field configuration of each species. Each chart represents the average retinal visual field when the eyes were at rest.

showed an overlap between the two species, but with a slight tendency for Harris's hawks to have a higher visual acuity than black kites [if we refer to the best bird (43.7 versus 32.7 cycles  $\text{deg}^{-1}$ ) and the mean (37.3 versus 29.3 cycles  $\text{deg}^{-1}$ ) in both species]. The visual acuity estimated from the corneal diameter was higher than the visual acuity estimated by behavioural measurements for both species, with a greater difference for black kites (about 85% of the theoretical estimate for Harris's hawks and 63% for black kites). This slightly higher acuity may be due to differences in the ecology of the two species. From an anatomical point of view, differences in visual acuity could be due to a higher retinal ganglion cell density in the central fovea of predatory birds compared with carrion-eating birds (Inzunza et al., 1991). For example, predatory birds (red-tailed hawk, *Buteo jamaicensis*; goshawk, *Accipiter gentilis*; sparrow hawk, *Accipiter nisus*; and black-chested buzzard-eagle, *Geranoetus melanoleucus*) are known to have a higher ganglion

cell density than carrion eaters (chimango caracara; Andean condor, *Vultur gryphus*; black vulture, *Coragyps atratus*; and turkey vulture, *Cathartes aura*) (Fite and Rosenfield-Wessels, 1975; Inzunza et al., 1991; Lisney et al., 2013). Cone photoreceptor density limits spatial resolution more than ganglion cell density in birds with a fovea (Coimbra et al., 2015); unfortunately, to our knowledge, no data on this are available for our two species.

Raptors are usually considered to have a high resolving power, based on extrapolations from data collected on one specimen of wedge-tailed eagle, *Aquila audax*, that had a visual acuity of 142 cycles  $\text{deg}^{-1}$  (i.e. 2.5 times higher than that of humans; Reymond, 1985). Nevertheless, some other raptor species have been shown not to have a higher acuity than humans (Table 1). It is likely that the distance from which raptors search for food and the type of prey are linked to their visual acuity. Indeed, species that search for prey on the ground or at low/medium altitude, such as chimango



**Fig. 6. Binocular overlap and blind area across elevations around the head of Harris's hawks ( $N=6$ ) and black kites ( $N=3$ ).** Mean ( $\pm$ s.e.m.) angular separation of the retinal field margins as a function of elevation in the median sagittal plane. Binocular fields are indicated by positive values of overlap of the visual field margins, whereas blind areas are indicated by negative values. The coordinate system is such that the horizontal plane is defined by an elevation of 90 deg (in front of the head) and 0 deg lies directly above the head. Arrows indicate projection of the bill tip (\*Harris's hawks; †black kites).

caracaras (visual acuity of 37–39 cycles  $\text{deg}^{-1}$ ; Potier et al., 2016), red-tailed hawks (visual acuity of 16.8 cycles  $\text{deg}^{-1}$ ; McIsaac, 2001), Harris's hawks (visual acuity of 27.4–43.7 cycles  $\text{deg}^{-1}$ , present data), black kites (visual acuity of 25.9–32.9 cycles  $\text{deg}^{-1}$ , present data) and American kestrels (visual acuity of 42 cycles  $\text{deg}^{-1}$ ; Hirsch, 1982), have a much lower visual acuity than eagles and Old World vultures (visual acuity of 108–135 cycles  $\text{deg}^{-1}$ ; Fischer, 1968) that search for prey when flying at high altitude. The visual acuity may also differ because of diet, and it has been suggested that, among mammals, active predators have a higher visual acuity than herbivores (Veilleux and Kirk, 2014). Results on visual acuity in birds in general seem to emphasise this finding, with raptors having a higher visual acuity than non-raptorial birds (Kiltie, 2000). In our study, while no statistics can be used because of the small number of black kites tested, we observed a slightly higher visual acuity in Harris's hawk. Nevertheless, in general, there is no behavioural evidence of any differences in terms of spatial resolution between raptors that chase living prey and carrion eaters (Fischer, 1968; Hirsch, 1982; McIsaac, 2001; Reymond, 1985, 1987) although differences in retinal cell density have been found (Inzunza et al., 1991).

In Harris's hawk, we found inter-individual differences in the estimates of visual acuity. Individual differences have previously been found in American kestrels, independent of sex (Gaffney and Hodos, 2003). In our operant conditioning experiments, we noticed that some birds made a number of horizontal head movements before making a decision. We found a significant relationship between the number of horizontal head movements and visual acuity in Harris's hawks; individuals that made more horizontal head movements (sometimes 3 times more) had a higher visual acuity than those making fewer movements. It is known that head movements rather than eye movements are associated with gaze changes in birds (Land, 2015), and this has been found in Indian peafowls, *Pavo cristatus*, where most head turns were horizontal (Yorzinski et al., 2015). In our experiment, when individuals did not make any horizontal head movements, video analysis suggested that they held the stimulus in the frontal visual field (binocular field: S.P., personal observation), which may be correlated with the use of the temporal area in black kites or the temporal fovea in Harris's hawks (as the temporal fovea is assumed to project into the frontal view). Increasing the number of horizontal head movements may mean increased use of the central fovea associated with monocular field vision (Jones et al., 2007; Tucker, 2000). Because the central fovea is generally associated with the highest visual acuity (Jones et al., 2007), mainly because of higher cone density (Reymond, 1985), increasing the number of horizontal head movements could allow for better discrimination of the two stimuli and thus a different estimation of visual acuity in our operant conditioning experiment.

All earlier studies that estimated visual acuity by operant conditioning in raptors have tested fewer than three individuals (Fischer, 1968; Fox et al., 1976; Hirsch, 1982; McIsaac, 2001; Potier et al., 2016; Reymond, 1985, 1987). We showed here that the operant conditioning method might give different results that could be linked to behavioural (as suggested here) or anatomical differences between individuals, suggesting the necessity to test as many individuals as possible to correctly estimate the mean visual acuity of a given species.

### Foveal characteristics

We found that Harris's hawks have two foveas (one central and one temporal), as commonly assumed for raptors, while black kites had

only one central fovea and one temporal thickened area. A previous study also showed that carrion-eating and opportunist raptors have only one central fovea, while predators have two (Inzunza et al., 1991). Nevertheless, black kites had a thickened area located in the temporal retina, which could suggest an area of high retinal ganglion cell density, as found in Leach's storm petrel *Oceanodroma leucorhoa* (M. Mitkus, Spatial vision in birds: anatomical investigation of spatial resolving power, PhD thesis, Lund University, 2015; M. Mitkus, G. A. Nevitt, J. Danielsen and A.K., submitted). This could be an area of higher resolution, similar in function but not associated with a fovea. These differences in foveal development probably relate to different styles of living and hunting. Indeed, falcons and hawks that look for and chase moving prey may use their central fovea for long-distance vision (monocular side vision) and their temporal fovea for short-distance vision (binocular front vision) to catch their prey with their claws (Jones et al., 2007; Tucker, 2000). The lack of a temporal fovea in kites is also reflected by their behaviour in our experiments. In general, black kites showed more horizontal head movements than Harris's hawks when performing the discrimination task; this may be because they could use only monocular side vision (central fovea) to choose between the two screens. Because Harris's hawks have two foveas, individuals can use different strategies to choose between the two monitors; they can look using their temporal or central fovea to discriminate the stripes. Moreover, because Harris's hawks eat mainly mobile prey, they may need to be quick in their decision, resulting in fewer horizontal head movements. In Harris's hawks, we found a relationship between horizontal head movements and visual acuity. This suggests that individuals that choose the 'temporal fovea strategy' use an area with lower cell density compared with individuals that choose the 'central fovea strategy', resulting in different estimates of visual acuity. Note that we used captive raptors that are fed daily by falconers. Thus, it seems that making errors in discriminating between visual stimuli does not have fitness costs for these individual birds. This may influence the different strategies used by these birds, because they know that they will receive their daily food rations afterwards, regardless of whether they make an incorrect choice during the experiments. Harris's hawks had a deeper central fovea than black kites, and it has been suggested that the shape of the fovea could also enhance spatial resolution by magnifying the image (Snyder and Miller, 1978; but see Sillman, 1973). Indeed, in the bottom-most region of the pit, the fovea may serve as a convex lens that could magnify the image without distortion (Snyder and Miller, 1978). In addition, we found that the ratio between foveal depth and retinal thickness was higher in Harris's hawks than in black kites. As the scattering of light making up the retinal image by the neuronal layers of the inner retina may reduce the contrast of the image, a relatively deep fovea in which superficial neuronal layers are displaced could increase spatial resolution (Weale, 1966). A detailed understanding of the link between visual acuity and foveal characteristics has not been developed to date, as very few studies have explored foveal shape and visual acuity in raptors (but see Sillman, 1973). It is possible that interspecific differences in the foveal and retinal characteristics may also be important in accounting for interspecific differences in visual acuity.

### Visual field

We found a difference between the visual fields of the two species that may suggest a difference in sensory specializations for gathering information from their environment. While the two species do not differ in the width of their maximum binocular field, they do differ in the width of the blind area (above and behind the head).

The maximum binocular field of black kites and Harris's hawks ( $39\pm 2$  versus  $45\pm 2$  deg, respectively) is wider than the narrow range typically found in birds (15–30 deg; Martin, 2007, 2009). The binocular field is proposed to be involved in the capture of prey at close distances by controlling the position of the feet and the timing of claw opening while approaching a target (Martin, 2009). Harris's hawks are pursuit predators that may need to maintain prey at a certain visual angle, like other raptors, and use their binocular field when approaching their prey (Kane et al., 2015; Kane and Zamani, 2014; Tucker, 2000). In this case, binocular vision, i.e. vision that achieves simultaneous views of the same object from slightly different positions, is important when the bird is near to catching its prey (Martin, 2009). While black kites are mainly carrion eaters on the ground, they also forage on the wing, such as scavenging for food remains (e.g. kleptoparasitism on vultures) and catching flying insects or fishes near the surface (Del Hoyo and Elliot, 1994). Thus, as for Harris's hawks, binocular overlap is certainly important for them to catch prey.

The two species also differ in the elevation of the maximum width of the binocular field, which could be linked to their feeding behaviour, as suggested by O'Rourke et al. (2010a). The maximum width of the binocular field is much greater above the eye bill-tip direction in Harris's hawks (26 deg) than in black kites (7 deg). The maximum width of the binocular field is, in both species, in the direction of their feet when they grab the prey (see Fig. S1 for Harris's hawk example).

Black kites have a narrower blind area than Harris' hawks, leading to a wider lateral field. This suggests that the lateral field may be essential in this species for gathering information about prey or social information about predators or conspecifics (Martin, 2009). Indeed, this raptor uses public information to estimate food availability (Sergio, 2003) and to travel in large groups on migration. The larger blind area above and behind the head in Harris's hawks results from a larger supraorbital ridge (see Fig. S2), which may act as a sun-shade, blocking the dazzling sun (Martin and Katzir, 2000). Because black kites also catch small prey, such as insects, when flying, while Harris's hawks search mainly for mammals, they probably need to scan all directions to search for insects and, thus, having a smaller eyebrow may aid in finding insects above their head.

## Conclusions

Raptor vision has always interested scientists (Jones et al., 2007), with the conclusion that raptors have extraordinary eyes (relatively large size, high acuity and the presence of two foveas and large binocular fields compared with other birds). Here, we have shown that two similarly sized species of raptor differ in their visual field, as found by O'Rourke et al. (2010a) in other raptor species (red-tailed hawk; Cooper's hawk, *Accipiter cooperi*; and American kestrel), and slightly in their visual acuity. These differences may be biologically significant and reflect adaptations to the differences in the perceptual challenges faced by these birds in their foraging behaviour.

In conclusion, we found that: (1) the two tested species differ in their visual traits, which may reflect different demands of gathering information about prey and conspecifics; (2) visual acuity differs slightly between the species (if we refer to maximum and mean visual acuity estimated), which may be linked to their ecology; (3) the two species differ in the number of foveas (one central and one temporal in Harris's hawk but only one central fovea in black kites and a temporal area) and in the physical characteristics of their fovea(s); (4) the two species differ in their number of head movements they make before taking a decision, with more

horizontal head movements for the uni-foveate species (black kites); and (5) the two species differ in their visual field, which also may be linked to their ecology. Improving our knowledge on visual traits in raptors will improve insight into the evolution of anti-predator tactics and will also increase the efficiency of conservation programmes for raptors through a better understanding of their collisions with human-made devices (Martin, 2011; Martin et al., 2012; McIsaac, 2001).

## Acknowledgements

We thank N. De Villiers, L. Albert, J.-L. Liegeois and T. Bouchet of Le Grand Parc du Puy du Fou, and P. Potier and N. Descarsin of Les Ailes de l'Urga for allowing us to perform the experiments. We also thank H. Billaud, S. Campagna, A. Celerier, G. B. Cunningham, J. Barrier, A. Sahnoune and M. Mentek, for their help with the fieldwork. Thank you to M. Mitkus for fruitful discussions on raptor vision. Finally, thank you to D. Deguedre for the construction of experimental devices for the behavioural acuity test.

## Competing interests

The authors declare no competing or financial interests.

## Author contributions

S.P., F.B., A.K., G.R.M., P.-F.I., T.D. and O.D. designed the study. S.P. and P.-F.I. performed the experiments. S.P. analysed the data. S.P. wrote the manuscript, with contributions from all authors.

## Funding

S.P. was supported by a PhD fellowship from the Labex Cemeb and the Association Française des Parcs Zoologiques (AFdPZ). In particular, 13 raptor parks gave funding to AFdPZ for this study: Le Grand Parc du Puy du Fou, Le Rocher des Aigles, Les Ailes de l'Urga, Le Zoo d'Amnéville, La Volerie des Aigles, Le Donjon des Aigles, Le Bois des Aigles, Les Géants du Ciel, Le Zoo de la Bourbansais, Le Zoo de la boissière du Doré, Le Zoo de la Barben, Le Zoo du Pal and Le Parc des Oiseaux.

## Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.142083.supplemental>

## References

- Biondi, L. M., Bó, M. S. and Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Anim. Cogn.* **13**, 701–710.
- Boire, D., Dufour, J.-S., Theoret, H. and Ptitto, M. (2001). Quantitative analysis of the retinal ganglion cell layer in the ostrich, *Struthio camelus*. *Brain Behav. Evol.* **58**, 343–355.
- Coimbra, J. P., Collin, S. P. and Hart, N. S. (2015). Variations in retinal photoreceptor topography and the organization of the rod-free zone reflect behavioral diversity in Australian passerines. *J. Comp. Neurol.* **523**, 1073–1094.
- Del Hoyo, J. and Elliot, A. (1994). *Handbook of the Birds of the World. New World Vultures to Guinea-fowl*, Vol. 2 (ed. A. and J. Sargatal). Barcelona: Lynx Edicions.
- Fernández-Juricic, E. (2012). Sensory basis of vigilance behavior in birds: synthesis and future prospects. *Behav. Processes* **89**, 143–152.
- Fischer, A. B. (1968). Laboruntersuchungen und Freilandbeobachtungen zum Sehvermögen und Verhalten von Altweltgeiern. *Zool. Jb. Syst.* **96**, 81–132.
- Fite, K. V. and Rosenfield-Wessels, S. (1975). A comparative study of deep avian foveas. *Brain Behav. Evol.* **12**, 97–115.
- Fox, R., Lehmkuhle, S. W. and Westendorf, D. H. (1976). Falcon visual acuity. *Science* **192**, 263–265.
- Gaffney, M. F. and Hodos, W. (2003). The visual acuity and refractive state of the American kestrel (*Falco sparverius*). *Vision Res.* **43**, 2053–2059.
- Guillemain, M., Martin, G. R. and Fritz, H. (2002). Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). *Funct. Ecol.* **16**, 522–529.
- Hall, M. I. and Ross, C. F. (2007). Eye shape and activity pattern in birds. *J. Zool.* **271**, 437–444.
- Hart, N. S. (2001). Variations in cone photoreceptor abundance and the visual ecology of birds. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **187**, 685–697.
- Hirsch, J. (1982). Falcon visual sensitivity to grating contrast. *Nature* **300**, 57–58.
- Inzunza, O., Bravo, H., Smith, R. L. and Angel, M. (1991). Topography and morphology of retinal ganglion cells in Falconiforms: a study on predatory and carrion-eating birds. *Anat. Rec.* **229**, 271–277.
- Jones, M. P., Pierce, K. E. and Ward, D. (2007). Avian vision: a review of form and function with special consideration to birds of prey. *J. Exot. Pet Med.* **16**, 69–87.
- Kane, S. A. and Zamani, M. (2014). Falcons pursue prey using visual motion cues: new perspectives from animal-borne cameras. *J. Exp. Biol.* **217**, 225–234.

- Kane, S. A., Fulton, A. H. and Rosenthal, L. J. (2015). When hawks attack: animal-borne video studies of goshawk pursuit and prey-evasion strategies. *J. Exp. Biol.* **218**, 212–222.
- Kiltie, R. (2000). Scaling of visual acuity with body size in mammals and birds. *Funct. Ecol.* **14**, 226–234.
- Land, M. F. (2015). Eye movements of vertebrates and their relation to eye form and function. *J. Comp. Physiol. A* **201**, 195–214.
- Land, M. F. and Nilsson, D.-E. (2012). *Animal Eyes*. Oxford: Oxford University Press.
- Lisney, T. J., Stecyk, K., Kolominsky, J., Graves, G. R., Wylie, D. R. and Iwaniuk, A. N. (2013). Comparison of eye morphology and retinal topography in two species of new world vultures (Aves: Cathartidae). *Anat. Rec.* **296**, 1954–1970.
- Martin, G. R. (2007). Visual fields and their functions in birds. *J. Ornithol.* **148**, 547–562.
- Martin, G. R. (2009). What is binocular vision for? A birds' eye view. *J. Vis.* **9**, 14.
- Martin, G. R. (2011). Understanding bird collisions with man-made objects: a sensory ecology approach. *Ibis* **153**, 239–254.
- Martin, G. R. and Katzir, G. (1999). Visual fields in short-toed eagles, *Circus gallicus* (Accipitridae), and the function of binocularity in birds. *Brain Behav. Evol.* **53**, 55–66.
- Martin, G. R. and Katzir, G. (2000). Sun shades and eye size in birds. *Brain Behav. Evol.* **56**, 340–344.
- Martin, G. R. and 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. and Shaw, J. (2010). Bird collisions with power lines: failing to see the way ahead? *Biol. Conserv.* **143**, 2695–2702.
- Martin, G. R. and 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., Portugal, S. J. and Murn, C. P. (2012). Visual fields, foraging and collision vulnerability in Gyps vultures. *Ibis* **154**, 626–631.
- McIsaac, H. P. (2001). Raptor acuity and wind turbine blade conspicuity. In National Avian-Wind Power Planning Meeting IV, Proceedings. Prepared by Resolve, Inc., Washington, DC, pp. 59–87.
- O'Rourke, C. T., Hall, M. I., Pitlik, T. and Fernández-Juricic, E. (2010a). Hawk eyes I: diurnal raptors differ in visual fields and degree of eye movement. *PLoS ONE* **5**, e12802.
- O'Rourke, C. T., Pitlik, T., Hoover, M. and Fernández-Juricic, E. (2010b). Hawk eyes II: diurnal raptors differ in head movement strategies when scanning from perches. *PLoS ONE* **5**, e12169.
- Potier, S., Bonadonna, F., Kelber, A. and Duriez, O. (2016). Visual acuity in an opportunistic raptor, the chimango caracara (*Milvago chimango*). *Physiol. Behav.* **157**, 125–128.
- Remsen, J. and Robinson, S. K. (1990). A classification scheme for foraging behavior of birds in terrestrial habitats. *Stud. Avian Biol.* **13**, 144–160.
- Reymond, L. (1985). Spatial visual acuity of the eagle *Aquila audax*: a behavioural, optical and anatomical investigation. *Vis. Res.* **25**, 1477–1491.
- Reymond, L. (1987). Spatial visual acuity of the falcon, *Falco berigora*: a behavioural, optical and anatomical investigation. *Vis. Res.* **27**, 1859–1874.
- Ritland, S. M. (1982). *The Allometry of the Vertebrate Eye*. Chicago: University of Chicago, Department of Biology.
- Robinson, S. K. and Holmes, R. T. (1982). Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* **63**, 1918–1931.
- Ruggeri, M., Major, J. C., Jr, McKeown, C., Knighton, R. W., Puliafito, C. A. and Jiao, S. (2010). Retinal structure of birds of prey revealed by ultra-high resolution spectral-domain optical coherence tomography. *Invest. Ophthalmol. Vis. Sci.* **51**, 5789–5795.
- Schwab, I. R., Dubielzig, R. R. and Schobert, C. (2012). *Evolution's Witness: How Eyes Evolved*. Oxford: Oxford University Press.
- Sergio, F. (2003). From individual behaviour to population pattern: weather-dependent foraging and breeding performance in black kites. *Anim. Behav.* **66**, 1109–1117.
- Shlaer, R. (1972). An eagle's eye: quality of the retinal image. *Science* **176**, 920–922.
- Sillman, A. J. (1973). Avian vision. *Avian Biol.* **3**, 349–387.
- Snyder, A. W. and Miller, W. H. (1978). Telephoto lens system of falconiform eyes. *Nature* **275**, 127–129.
- Spiegel, O., Getz, W. M. and Nathan, R. (2013). Factors influencing foraging search efficiency: why do scarce lappet-faced vultures outperform ubiquitous white-backed vultures? *Am. Nat.* **181**, E102–E115.
- Tucker, V. A. (2000). The deep fovea, sideways vision and spiral flight paths in raptors. *J. Exp. Biol.* **203**, 3745–3754.
- Veilleux, C. C. and Kirk, E. C. (2014). Visual acuity in mammals: effects of eye size and ecology. *Brain Behav. Evol.* **83**, 43–53.
- Weale, R. (1966). Why does the human retina possess a fovea? *Nature* **212**, 255–256.
- Weisman, R. G. and Spetch, M. L. (2010). Determining when birds perceive correspondence between pictures and objects: a critique. *Comp. Cogn. Behav. Rev.* **5**, 117–131.
- Yorzinski, J. L., Patricelli, G. L., Platt, M. L. and Land, M. F. (2015). Eye and head movements shape gaze shifts in Indian peafowl. *J. Exp. Biol.* **218**, 3771–3776.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer Science and Business Media.