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Simon Potier, Olivier Duriez, Gregory B Cunningham, Vincent Bonhomme, Colleen O'Rourke, et al..
Visual field shape and foraging ecology in diurnal raptors. *Journal of Experimental Biology*, 2018, 221
(14), pp.jeb177295. 10.1242/jeb.177295 . hal-03132841

HAL Id: hal-03132841

<https://hal.science/hal-03132841>

Submitted on 5 Feb 2021

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RESEARCH ARTICLE

Visual field shape and foraging ecology in diurnal raptors

Simon Potier^{1,2,*}, Olivier Duriez¹, Gregory B. Cunningham³, Vincent Bonhomme⁴, Colleen O'Rourke⁵, Esteban Fernández-Juricic⁶ and Francesco Bonadonna¹

ABSTRACT

Birds, particularly raptors, are believed to forage primarily using visual cues. However, raptor foraging tactics are highly diverse – from chasing mobile prey to scavenging – which may reflect adaptations of their visual systems. To investigate this, we studied the visual field configuration of 15 species of diurnal Accipitriformes that differ in such tactics, first focusing on the binocular field and blind area by using a single-traits approach, and then exploring the shape of the binocular field with a morphometric approach. While the maximum binocular field width did not differ between species with different foraging tactics, the overall shape of their binocular fields did. In particular, raptors chasing terrestrial prey (ground predators) had a more protruding binocular field and a wider blind area above the head than did raptors chasing aerial or aquatic prey and obligate scavengers. Ground predators that forage on mammals from above have a wide but short bill – which increases ingestion rate – and a large suborbital ridge to avoid sun glare. This may explain the protruding binocular field and the wide blind area above the head. By contrast, species from the two other groups have long but narrow bills used to pluck, flake or tear food and may need large visual coverage (and reduced suborbital ridges) to increase their foraging efficiency (e.g. using large visual coverage to follow the escaping prey in three dimensions or detect conspecifics). We propose that binocular field shape is associated with bill and suborbital ridge shape and, ultimately, foraging strategies.

KEY WORDS: Accipitriformes, Bill, Binocular shape, Raptors, Morphometrics, Binocular vision

INTRODUCTION

How a species perceives a given environment depends on how its sensory organs filter information. To prevent information overload, each sensory system must focus on environmental features important for that species' survival and reproduction (Stevens, 2013). Because of adaptive differences, species in the same place and time may live in a different 'sensory world', but this may allow species with a similar diet but different sensory systems to coexist in

separate niches (Safi and Siemers, 2010). Interspecific differences in the visual capacities of birds (Fernández-Juricic, 2012; Jones et al., 2007; Martin, 2014; Moore et al., 2016; Rochon-Duvigneaud, 1943; Walls, 1942) also allow species to respond differently to the range of perceptual challenges they face, such as flight, foraging, predator detection, interactions with conspecifics and breeding (Birkhead, 2012; Martin, 2017).

One of the traits that defines a species' sensory world is the shape of its visual field: the volume of space around the head from which visual information can be gathered. Visual fields vary extensively among species (Martin, 2017), which has been attributed to predator detection, foraging, parental care and gathering of social information (Martin, 2014). Even species that are closely related phylogenetically may vary in their visual field characteristics. For example, in the Threskiornithidae family, the differences in visual fields between northern bald ibises, *Geronticus eremita*, and puna ibises, *Plegadis ridgwayi*, may be due to their different foraging strategies, with a wider binocular field in the more visually guided northern bald ibis compared with the narrower binocular field of the more tactile-guided puna ibis (Martin and Portugal, 2011). Similarly, in congeneric ducks (Anatidae family), Guillemain et al. (2002) found that visual foragers such as the wigeon *Anas penelope* have a narrower visual coverage compared with tactile foragers such as northern shovelers, *Anas clypeata*. Among Emberizidae passerines (finches), differences in visual field configuration have been linked to visual acuity differences, with a higher visual acuity in species with broader visual fields (Moore et al., 2015).

Most of the research showing substantial interspecific variation in visual field configuration has been based on single traits: binocular field width in the plane of the bill, the vertical extent of the binocular field, the blind area width above and behind the head, the lateral field width, or the width of the binocular and lateral fields (i.e. cyclopean field) (Fernandez-Juricic et al., 2008; Fernández-Juricic et al., 2010; Martin, 2007). One of the problems with this unidimensional approach is that it does not allow for the characterization of interspecific variation in the overall shape of the visual fields. A multidimensional approach – which to our knowledge has never been adopted – may highlight differences in the overall shape of the visual field and uncover patterns heretofore undetectable via comparisons of unidimensional parameters (Zelditch et al., 2012).

Interspecific variation in visual field shape can be studied by considering the geometrical relationships among multiple parameters (Rohlf and Marcus, 1993). Morphometrics, the study of shape variation and its covariation with other variables of interest (Bookstein, 1997; Dryden and Mardia, 1998), aims to turn shapes into quantitative variables and then analyse variations between these variables (Bonhomme et al., 2014). This morphometric approach can enable the description and comparison of the visual field shapes of organisms (Rohlf and Marcus, 1993).

In this study, we focused on understanding the interspecific variation in the binocular field configuration of 15 diurnal raptor species. This approach also allowed us to test some functional

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hypotheses about the link between binocular vision and the associated behaviours. Binocular vision in birds has been hypothesized to function primarily in guiding the position of the bill and/or the feet, and estimating the time of arrival at a target when foraging (Martin, 2009). Additionally, a recent study pointed out that the length of the blind area in front of the bill is associated with the width of the binocular field, and may be functionally important for visualizing the bill tip and enhancing binocular vision at close distances in species with specific foraging tactics (Tyrrell and Fernández-Juricic, 2017a).

Among diurnal raptors, Accipitriformes are a monophyletic order (Prum et al., 2015), including eagles, vultures, and hawks, which forage using mainly visual cues (Jones et al., 2007). Accipitriformes share a common carnivorous diet, with the exception of the frugivorous palm-nut vulture, *Gypohierax angolensis*. Accipitriformes can also be classified using three main foraging tactics: ground predators (chasing prey moving on the ground), aerial and aquatic predators (chasing for prey moving in three dimensions: in the air or under the water film), and obligate scavengers (seeking for carrion only). Accipitriformes' visual fields have been studied in only a limited number of species (Martin and Katzir, 1999; Martin et al., 2012; O'Rourke et al., 2010a; Portugal et al., 2017; Potier et al., 2016).

We investigated the interspecific variation in binocular field configuration in members of the order Accipitriformes using both unidimensional (binocular overlap width in the horizontal plane, maximum binocular overlap width and its position) and multidimensional (shape of the binocular fields using a geometric morphometric analysis) approaches. Additionally, we characterized two parameters associated with the blind area (width above the head, and width behind the head in the horizontal plane) as they have been shown to be associated with variations in the width of the binocular field (Tyrrell and Fernández-Juricic, 2017a).

In the present study, we considered the previously published data on seven species from which raw data were obtained, and we added new data measuring the visual field in eight more species. This sample size allowed us to control for the potential confounding effects of phylogenetic relatedness.

The present study has two main parts. First, we compared the visual field parameters of species with different foraging behaviour and tactics. Because wider binocular fields would enhance the accuracy of contacting active prey, we hypothesized that predatory species should have a wider overall binocular overlap in the horizontal plane than carrion-feeding species. Other studies, especially on raptors, have not supported this assumption (see Martin, 2009, for review) but it has never been tested while controlling for the effects of shared ancestry. We also predicted that the blind area above and behind the head would be narrower in carrion foragers as this would increase visual coverage (i.e. wider lateral fields) to detect social information from conspecifics and hence enhance carrion detection (Houston, 1974). Finally, we describe for the first time the actual overall shape of the binocular fields for these species, allowing us to use a multidimensional approach to interpret the results obtained in the first part of the study.

MATERIALS AND METHODS

Subjects

We compared the visual fields of 15 raptor species, using published data from seven species (Martin and Katzir, 1999; Martin et al., 2012; O'Rourke et al., 2010a; Potier et al., 2016) and new data from eight species (see Table 1). The eight species of birds were under the care of a handler from two French falconry parks: Le Grand Parc du Puy du Fou and Les Ailes de l'Urga (see Table 1 for details). Birds at both parks are kept in good health and fly regularly. The individual birds we worked with were measured close to their

Table 1. Species used and ecological affiliation

Family	Species	Common name	No. of individuals (sex)	Age (years)	Foraging behaviour	Foraging tactics	Reference
Accipitridae	<i>Gypohierax angolensis</i>	Palm-nut vulture	2 (1M & 1F)	5	Carrion eater	Obligate scavenger	Present study
	<i>Neophron percnopterus</i>	Egyptian vulture	3 (2F & 1 unknown)	1–4	Carrion eater	Obligate scavenger	Present study
	<i>Circaetus galliacus</i>	Short-toed snake eagle	1 (unknown)	Unknown	Predator	Ground predator	Martin and Katzir, 1999
	<i>Necrosyrtes monachus</i>	Hooded vulture	1 (M)	14	Carrion eater	Obligate scavenger	Present study
	<i>Gyps fulvus</i>	Griffon vulture	1 (F)	10	Carrion eater	Obligate scavenger	Martin et al., 2012
	<i>Gyps africanus</i>	White-backed vulture	2 (1M & 1 unknown)	5	Carrion eater	Obligate scavenger	Martin et al., 2012
	<i>Aquila chrysaetos</i>	Golden eagle	3 (2M & 1F)	4–11	Predator	Ground predator	Present study
	<i>Aquila nipalensis</i>	Steppe eagle	1 (M)	6	Predator	Ground predator	Present study
	<i>Milvus migrans</i>	Black kite	3 (3M)	1	Carrion eater	Aerial and aquatic predator	Potier et al., 2016
	<i>Haliaeetus leucocephalus</i>	Bald eagle	2 (1M & 1F)	6–10	Predator	Aerial and aquatic predator	Present study
	<i>Buteo jamaicensis</i>	Red-tailed hawk	3 (unknown)	1	Predator	Ground predator	O'Rourke et al. 2010a
	<i>Geranoaetus melanoleucus</i>	Black-chested buzzard-eagle	1 (1F)	2	Predator	Ground predator	Present study
	<i>Parabuteo unicinctus</i>	Harris's hawk	6 (3M & 3F)	1–5	Predator	Ground predator	Potier et al., 2016
	<i>Accipiter cooperii</i>	Cooper's hawk	7 (4M & 3F)	1	Predator	Aerial and aquatic predator	O'Rourke et al. 2010a
	Cathartidae	<i>Cathartes aura</i>	Turkey vulture	3 (unknown)	5–12	Carrion eater	Obligate scavenger

holding aviaries and were returned to them promptly after the data were collected.

Species were categorized by their foraging behaviour (predators, carrion eaters) and by their foraging tactics (ground predators: predators that chase prey moving on the ground; aerial and aquatic predators: predators that chase prey moving in three dimensions; obligate scavengers: species that exclusively seek carrion), based on De Graaf et al. (1985) (Table 1).

Ethics

We used the same procedure and apparatus of Prof. Graham Martin with his permission. The procedure was reviewed in 2007 by the UK Home Office. 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 the 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). Both trainers were present during the experiments.

Visual field measurements

We used a non-invasive procedure to measure visual field characteristics in alert birds. This protocol has been described extensively in multiple previous papers (e.g. Fernandez-Juricic et al., 2008; Martin, 2007; Potier et al., 2016; Potier et al., 2017a). In summary, each bird was held firmly for 20–30 min in a plastic restraining tube of the appropriate size to avoid any movement. The bird's legs were lightly taped (Micropore Surgical tape 1530/1B) together and cushioned by foam rubber held between them. The head was held at the centre of a visual field apparatus (a device that permits the eyes to be examined from known positions around the head) by specially manufactured steel and aluminium bill holders. The head was maintained in the visual field apparatus following the natural head position of the birds. Different bill holders were used for each species to account for differences in bill size and shape. The surfaces of the holders were coated in cured silicone sealant to provide a non-slip cushioned surface. We held the bill in place with Micropore tape, being sure not to cover the nostrils to allow the birds to breathe. We took calibrated photographs of the head of each bird while held in the apparatus to determine eye position within the skull, the horizontal separation between the centre of the two eyes, the distance between the centre of the eye and the bill tip, and the bill length.

Visual field parameters were measured using an ophthalmoscopic reflex technique. The perimeter's coordinate system followed conventional latitude and longitude measures, with the equator aligned vertically in the median sagittal plane of the head (i.e. a vertical plane that divides the head symmetrically into left and right hemispheres). We used this coordinate system in the presentation of the results. We examined the eyes using an ophthalmoscope mounted against the perimeter arm with an accuracy of ± 0.5 deg. We measured the boundaries of the retina projection by the positions that the eyes spontaneously adopted when they were fully rotated 'forwards' (converged for estimation of binocular area boundaries) and 'backwards' (diverged for estimation of blind sector boundaries) for the blind area behind the head. We did not measure the degree of eye movements or the projection of the pecten to reduce the time the animals were restrained.

We corrected our data for viewing from a hypothetical viewing point placed at infinity (this correction is based upon the distance

used in the measurements taken with the visual field apparatus and the horizontal separation of the eyes; Martin, 1984). After the corrections, we constructed a topographical map of the visual field and its different components. These features included: lateral field, binocular field, cyclopean field (the total field around the head produced by the combination of the monocular fields of both eyes) and blind areas above and behind the head. The limits of the visual field were determined 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 on the bill shape of a given species, the bill holder intruded to different extents into our view of the eyes at a specific elevation. Therefore, we did not record data at elevations where the bill holder was blocking our view and instead estimated the binocular field width as the mean value of the binocular field widths immediately above and below these elevations (Martin and Portugal, 2011).

Bill morphology measurements

We measured (and averaged) (1) the length of the bill from the bill base to the bill tip and (2) the width of the bill at the commissure, using callipers (Fig. S2) of three individuals per species (except one individual for the golden eagle, *Aquila chrysaetos*, the red-tailed hawk, *Buteo jamaicensis*, and the steppe eagle, *Aquila nipalensis*, and two individuals for the white-backed vulture, *Gyps africanus*, and the palm-nut vulture, *Gypohierax angolensis*, because three individuals were not available). We obtained the bill morphology for every species used in the study, except the Cooper's hawk, *Accipiter cooperii*, which was not available in the French falconry parks.

Statistical analysis

We collected visual field data from three individuals per species (when possible) and used averaged values for each species for the statistical analyses. When comparing the shapes of the visual fields in birds, we were limited to analysing the shape of the binocular field; we could not estimate the limits of the lateral and blind portions because of the aforementioned visual obstruction of the visual field apparatus (Martin, 2007).

Analyses were carried out using R 3.1.4 (R Development Core Team 2016) using Momocs (<https://www.r-project.org/>), ape (<https://CRAN.R-project.org/package=ape>), phytools (Revell, 2012), geiger (<https://CRAN.R-project.org/package=geiger>) and nlme (<http://CRAN.R-project.org/package=nlme>) packages. We compared the five following parameters across species: (a) width of the binocular field at the horizontal plane (i.e. eyes converged at the 90 deg elevation), (b) width of maximum binocular overlap (eyes converged), (c) elevation at which maximum binocular overlap occurred (eyes converged), (d) width of the blind area behind the head at the horizontal plane (eyes diverged at 270 deg elevation) and (e) width of the blind area perpendicularly above the head (eyes diverged at 0 deg elevation), as commonly measured in birds (Martin, 2007).

In addition, we compared the shape of the binocular field across species with a morphometric approach using outline analysis that aimed at translating shapes into quantitative variables to allow comparative analyses in a common multivariate framework (Bonhomme et al., 2014). The shape was defined as 'the total of all information invariant under translations, rotations and isotropic rescaling' (Small, 2012). From a visual field perspective, the morphometric analysis allowed the identification of variation in the shape of the binocular fields.

For the morphometric analysis, we calculated an elliptic Fourier transform (EFT) on the (x, y) coordinates of the binocular field

outlines projected on a Cartesian plane. EFT turns the (x, y) outline coordinates in two harmonic sums of trigonometric functions (one for the x coordinate, and one for the y coordinate). Each harmonic is described by four harmonic coefficients (amplitude and phase for x , and the same for y). The EFT principle has been summarized elsewhere (Bonhomme et al., 2014) and has been found to be the best approximation of an outline of a shape, in a least-squares sense (Crampton, 1995). For Fourier-based approaches in morphometry, some rules are commonly used for the choice of the number of harmonics. Here, we followed: (1) the cumulated sum of squared harmonic coefficient as the harmonic power, (2) the Euclidean distance between every two points of the reconstructed shape to the best possible reconstructed shape and (3) visual inspection. Some minor editing (estimation of the lower bounds) was necessary to reconstruct the bottom section of the visual fields of three species because the apparatus did not allow observation of the eyes at the lowest elevations. In morphometric analyses, such minor editing has been shown to not affect the analysis (Bonhomme et al., 2013).

We used phylogenetic analyses of variance (ANOVA, 100,000 permutations) to compare the visual field parameters. The phylogenetic ANOVA were run on a single data point per species (averaged values per species). Phylogenetic ANOVA gave the probability of rejecting the null hypothesis without considering the phylogeny (P -value) and also corrected for phylogenetic signals [$P(\text{phy})$]. For the shape analysis, we first performed a principal component analysis (hereafter, PCA) on the matrix of Fourier coefficients. The PC factors were utilized to discriminate between shape variations and to test differences between ecological groups. Then, phylogenetic ANOVA were calculated on the PC factor 1 and 2 scores. Tree topology followed Jiang et al. (2015) with turkey vulture, *Cathartes aura*, as the outgroup (Fig. S1).

We compared the bill morphology between ground predators and obligate scavengers using Wilcoxon tests. Then, to understand whether the bill morphology impacted the binocular field shape, we fitted a phylogenetic linear regression. In particular, we estimated the relationship between the two first axes of the PCA obtained from the binocular field shape and (1) the length of the bill, (2) the width of the bill and (3) the length:width ratio of the bill.

RESULTS

Visual field parameters

The new data on the visual fields of eight species of Accipitriformes (listed in Table 1) are presented in Figs 1 and 2. The width of the binocular field at the horizontal plane across all 15 species varied

from 17.9 deg in the griffon vulture, *Gyps fulvus*, to 55.5 deg in the black-chested buzzard-eagle, *Geranoaetus melanoleucus* (Table 1, Fig. 1). The width of the maximum binocular overlap ranged from 19.9 deg in the griffon vulture to 55.5 deg in the black-chested buzzard-eagle. The monocular fields at the horizontal plane varied from 107.1 deg in the black-chested buzzard-eagle to 144.5 deg in the turkey vulture, *Cathartes aura* (Fig. 1). The width of the blind area above the head (0 deg elevation) varied from 75.5 deg in Harris's hawk, *Parabuteo unicinctus*, to 1 deg in the turkey vulture. The width of the blind area behind the head (270 deg elevation) varied from 101.5 deg in the short-toed snake eagle, *Circaetus gallicus*, to 45.1 deg in the turkey vulture (Fig. 1).

Visual field of predators versus carrion eaters

We found no significant differences between predators and carrion eaters in each of the following binocular field parameters: (a) width of the binocular field at the horizontal plane [carrion eaters: 33.3 ± 4.2 deg; predators: 37.2 ± 3.6 deg; d.f.=1,13, $F=0.50$, $P=0.492$, $P(\text{phy})=0.583$], (b) maximum (eyes converged) binocular field width [carrion eaters: 35.6 ± 4.3 deg; predators: 38.6 ± 3.3 deg; d.f.=1,13, $F=0.33$, $P=0.575$, $P(\text{phy})=0.650$] and (c) elevation at which maximum binocular field width occurred [carrion eaters: 87.1 ± 4.7 deg; predators: 87.5 ± 3.1 deg; d.f.=1,13, $F=0.004$, $P=0.950$, $P(\text{phy})=0.960$].

The width of the blind area above (carrion eaters: 25.8 ± 7.5 deg; predators: 52.8 ± 8.4 deg; d.f.=1,13, $F=5.56$, $P=0.035$, $P(\text{phy})=0.082$) and behind (carrion eaters: 59.6 ± 5.1 deg; predators: 74.2 ± 6.8 deg; d.f.=1,13, $F=2.79$, $P=0.119$, $P(\text{phy})=0.203$) the head (eyes diverged) did not differ significantly between carrion eaters and predators.

Visual fields and foraging tactics

We found no significant differences between species that engaged in different foraging tactics (ground predators, aerial and aquatic predators, obligate scavengers) in each of the following visual field parameters: (a) width of the binocular field in the horizontal plane [d.f.=2,12, $F=0.28$, $P=0.757$, $P(\text{phy})=0.839$; Fig. 3A], (b) maximum binocular (eyes converged) field width [d.f.=2,12, $F=0.25$, $P=0.782$, $P(\text{phy})=0.854$; Fig. 3B], (c) elevation at which maximum binocular field width occurred [d.f.=2,12, $F=0.89$, $P=0.435$, $P(\text{phy})=0.586$; Fig. 3C] and (d) width of the blind area behind the head (eyes diverged) [d.f.=2,12, $F=5.36$, $P=0.022$, $P(\text{phy})=0.077$; Fig. 3D].

However, we found a significant difference in the width of the blind area above the head between species with different foraging tactics [d.f.=2,12, $F=11.82$, $P=0.001$, $P(\text{phy})=0.011$; Fig. 3E].

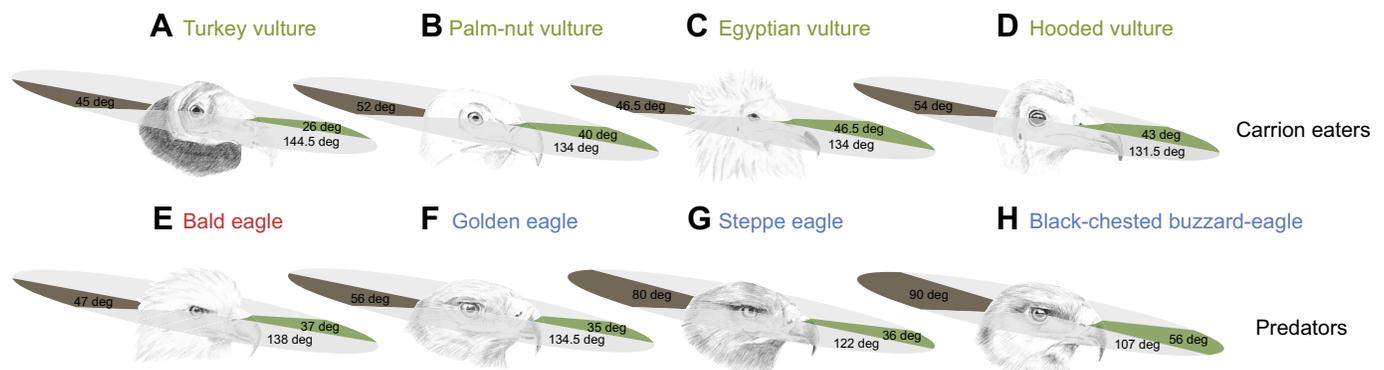


Fig. 1. Schematic representation of the visual fields in the horizontal plane. Green areas represent the binocular sector, grey areas the monocular sectors and brown areas the blind sectors. Species names are coloured according to foraging tactic (green: obligate scavengers; red: aerial/aquatic predators; blue: ground predators).

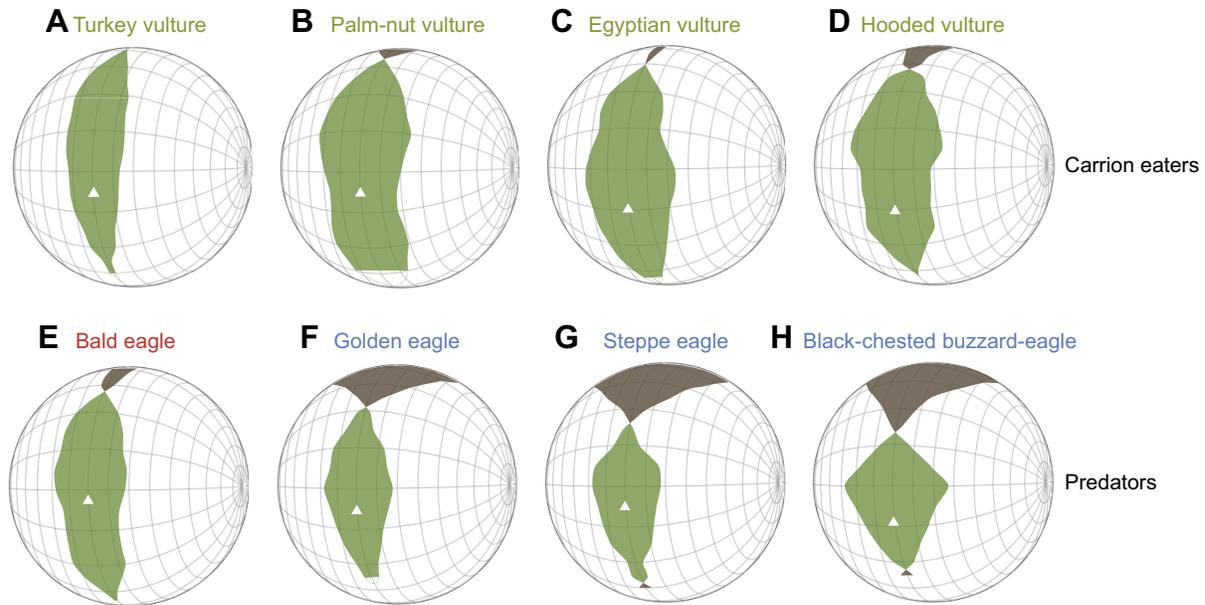


Fig. 2. Orthographic projection of the boundaries of the retinal fields of the two eyes of birds investigated in the current study. A latitude and longitude coordinate system was used with the equator aligned vertically in the median sagittal plane. The bird's head is imagined to be at the centre of the globe (grid is at 20 deg intervals in latitude and 10 deg intervals in longitude). Green areas represent the binocular sector, white areas the monocular sectors and brown areas the blind sectors. The triangle indicates the direction of bill projection. Species names are coloured according to foraging tactic (green: obligate scavengers; red: aerial/aquatic predators; blue: ground predators).

Ground predators had a larger blind area above the head than aerial and aquatic predators [d.f.=1,7, $F=30.20$, $P<0.001$, $P(\text{phy})=0.004$] and obligate scavengers [d.f.=1,10, $F=17.67$, $P=0.002$, $P(\text{phy})=0.017$]. However, width of the blind area above the head for scavengers did not differ significantly from that of aerial and aquatic predators [d.f.=1,7, $F=0.005$, $P=0.947$, $P(\text{phy})=0.955$].

Shape of the binocular field

The first two principal components (PC) gathered 93.1% of the total variance (77.4% for PC1, eigenvalue: 0.132; 15.7% for PC2, eigenvalue: 0.059) and are discussed below. Positive PC1 scores represent a narrower binocular field just below the horizontal plane, while positive PC2 scores represent a protrusion shape (at the lower and upper edge) of the binocular field (Fig. 4A).

For PC1, we did not find any significant difference among species with different foraging behaviour [d.f.=1,13, $F=2.03$, $P=0.178$, $P(\text{phy})=0.276$; Fig. 4A,B] or foraging tactics [d.f.=2,12, $F=1.31$, $P=0.307$, $P(\text{phy})=0.464$; Fig. 4A,C].

For PC2, we did not find any significant difference among species with different foraging behaviour [d.f.=1,13, $F=4.68$, $P=0.050$, $P(\text{phy})=0.108$; Fig. 4A,B]. However, species with different foraging tactics did vary significantly in PC2 score [d.f.=2,12, $F=7.60$, $P=0.007$, $P(\text{phy})=0.037$; Fig. 4C,D]. Ground predators had a protruding binocular field shape at the upper and lower edges, whereas obligate scavengers [d.f.=1,10, $F=14.24$, $P=0.004$, $P(\text{phy})=0.028$] and aerial and aquatic predators [d.f.=1,7, $F=11.08$, $P=0.013$, $P(\text{phy})=0.036$] had a relative rectilinear binocular field shape (Fig. 4A,C,D). Finally, obligate scavengers and aerial and aquatic predators did not differ significantly in PC2 score [d.f.=1,7, $F=0.48$, $P=0.640$, $P(\text{phy})=0.734$; Fig. 4A,C,D].

Shape of the binocular field and bill morphology

Because we did not get any measurements of the Cooper's hawk, we were not able to compare the bill morphology of the aerial and aquatic predators with that of the ground predators and obligate

scavengers. However, ground predators and obligate scavengers differ significantly in their bill length (ground predators: 45.88 ± 3.56 mm; obligate scavengers: 60.4 ± 3.96 mm; $W=4$, $P=0.026$; Fig. S3A), bill width (ground predators: 45.45 ± 4.03 mm; obligate scavengers: 31.78 ± 1.59 mm, $W=33$, $P=0.015$; Fig. S3B) and the length:width ratio of the bill ($W=0$, $P=0.002$; Fig. S3C).

We found no relationship between the first axis of the PCA and the bill length ($N=14$, d.f.=12,14, $t=0.23$, $P=0.82$), bill width ($N=14$, d.f.=12,14, $t=-0.56$, $P=0.59$) and the length:width ratio of the bill ($N=14$, d.f.=12,14, $t=0.28$, $P=0.79$). There was also no relationship between the second axis of the PCA and bill length ($N=14$, d.f.=12,14, $t=-0.33$, $P=0.75$) and bill width ($N=14$, d.f.=12,14, $t=1.36$, $P=0.20$). However, a significant relationship was found between the second axis of the PCA and the length:width ratio of the bill ($N=14$, d.f.=12,14, $t=-2.22$, $P=0.047$; Fig. S4). Species with a short but large bill had a higher PC2 score, i.e. they had a more protruding binocular field shape at the lower and upper edges.

DISCUSSION

Our results show that species of Accipitriformes that differ in foraging tactics did not differ in their maximum or at-rest binocular overlap, but they did differ in the shape of their binocular field (i.e. ground predators had a more protruding binocular field shape at the upper and lower edges compared with obligate scavengers and aquatic and terrestrial predators). This pattern, not apparent when using the classic unidimensional approach, was revealed by our multi-dimensional assessment (morphometric analysis). Additionally, the blind sector above – but not behind – the head was significantly different among Accipitriformes with different foraging tactics (i.e. ground predators had a larger blind area than aerial and aquatic predators as well as obligate scavengers; Fig. 3).

For all species considered, we found on average wider binocular fields (17.9–55.5 deg) in the horizontal plane compared with those of other non-passerine birds (usually between 20 and 30 deg;

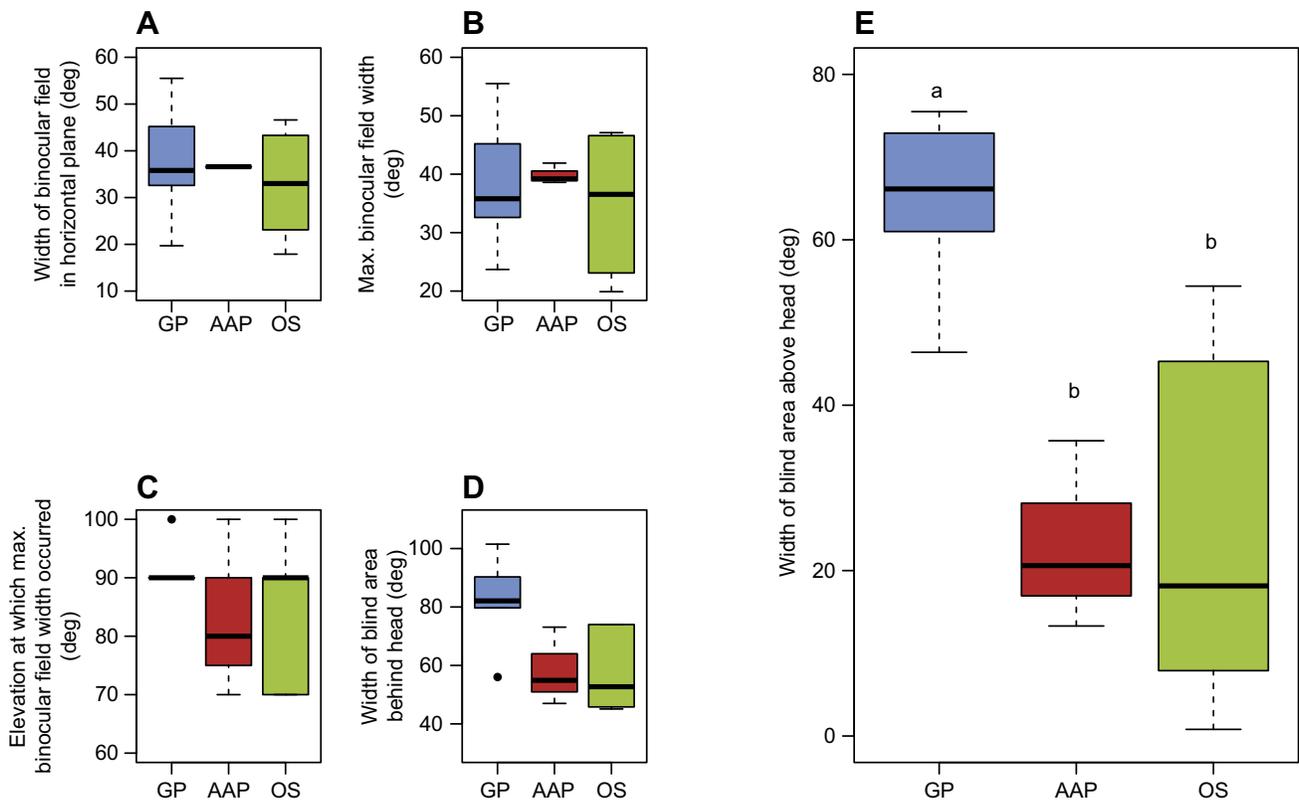


Fig. 3. Visual field parameters with respect to foraging tactic. (A) Width of the binocular field in the horizontal plane, (B) maximum binocular (eyes converged) field width, (C) elevation at which maximum binocular field width occurred, (D) width of the blind area behind the head (eyes diverged) and (E) width of the blind area above the head. GP, ground predators; AAP, aerial and aquatic predators; OS, obligate scavengers. Different letters reflect significant differences ($P < 0.05$).

Martin, 2009). Our findings suggest that species with a carnivorous diet – which mainly search for their prey visually (Jones et al., 2007) – may have increased binocularity compared with that of other birds (except passerines and owls), as already shown for carnivorous mammals versus non-carnivorous mammals (Heesy, 2007). From a functional perspective, Accipitriformes species may use these wide binocular fields for the accurate positioning and timing of the arrival of their bill or feet with respect to a prey target (Martin, 2009).

We hypothesized that predators' binocular fields would differ from those of carrion eaters because they may need wider binocular fields for the accurate positioning and timing of the arrival of their feet at the moment of prey capture. However, we did not find significant differences in the binocular field between predators and carrion eaters. Because predators – but not carrion eaters – have a second centre of acute vision (the temporal fovea) that is probably linked to the binocular field (Inzunza et al., 1991; Potier et al., 2016; Potier et al., 2017a, b), a wider binocular field would have been expected. The tree swallow, *Tracycineta bicolor*, a non-raptor species that similarly pursues mobile aerial prey, has been shown to have a similar visual configuration (retinal topography and visual fields) to that of other diurnal raptors (Tyrrell and Fernández-Juricic, 2017b), suggesting that species with predatory habits may have converged on similar visual system configurations. The lack of a significant result is thus difficult to explain, although we cannot exclude a possible low statistical power given the number of species studied. However, this could also suggest that no general binocular imperative is associated with predation (Martin, 2009).

We did not find differences in the maximal binocular field width or its position across species with different foraging tactics. This may reflect a degree of ecological convergence upon an optimal

binocular field width for the production of symmetrically expanding optical flow fields. This is probably used to guide bill or feet position, which has been proposed to be traded off against requirements for an extended vision (Martin, 2009, 2014).

Nevertheless, we found that the shape of the binocular field protrudes much more at the upper and lower edges in ground predators than in aerial and aquatic predators or obligate scavengers (PC2). We propose three non-mutually exclusive functional hypotheses to explain the shape difference of the binocular fields: (1) hunting moving prey, (2) reducing sun dazzling and optimizing target detection, and (3) bill-shape constraints.

Hunting moving prey

One of the major visual differences between aerial and aquatic versus ground predators is in the number of spatial dimensions in which their prey can move to escape. Ground predators search for prey that move in a 2D plane, while aerial and aquatic predators search for prey that move in a 3D world. Binocular vision has been proposed as necessary to control the position of the feet (Martin, 2009, 2014). Aerial and aquatic predators may need to keep a constant large width of the binocular field along the vertical axis in front of the head in response to the 3D movements of their prey. The relative rectilinear shape of the binocular field (i.e. similar width along the vertical axis) may be advantageous to control feet position for catching a prey escaping in three dimensions with the elongated and narrow toes and legs of Falconids and *Accipiters* (Einoder et al., 2007; Fowler et al., 2009). Indeed, for these species, the distance from the eye to the toes will thus be larger than in birds with short toes.

By contrast, ground predators would only need a large binocular overlap in the middle of their binocular field to control feet position

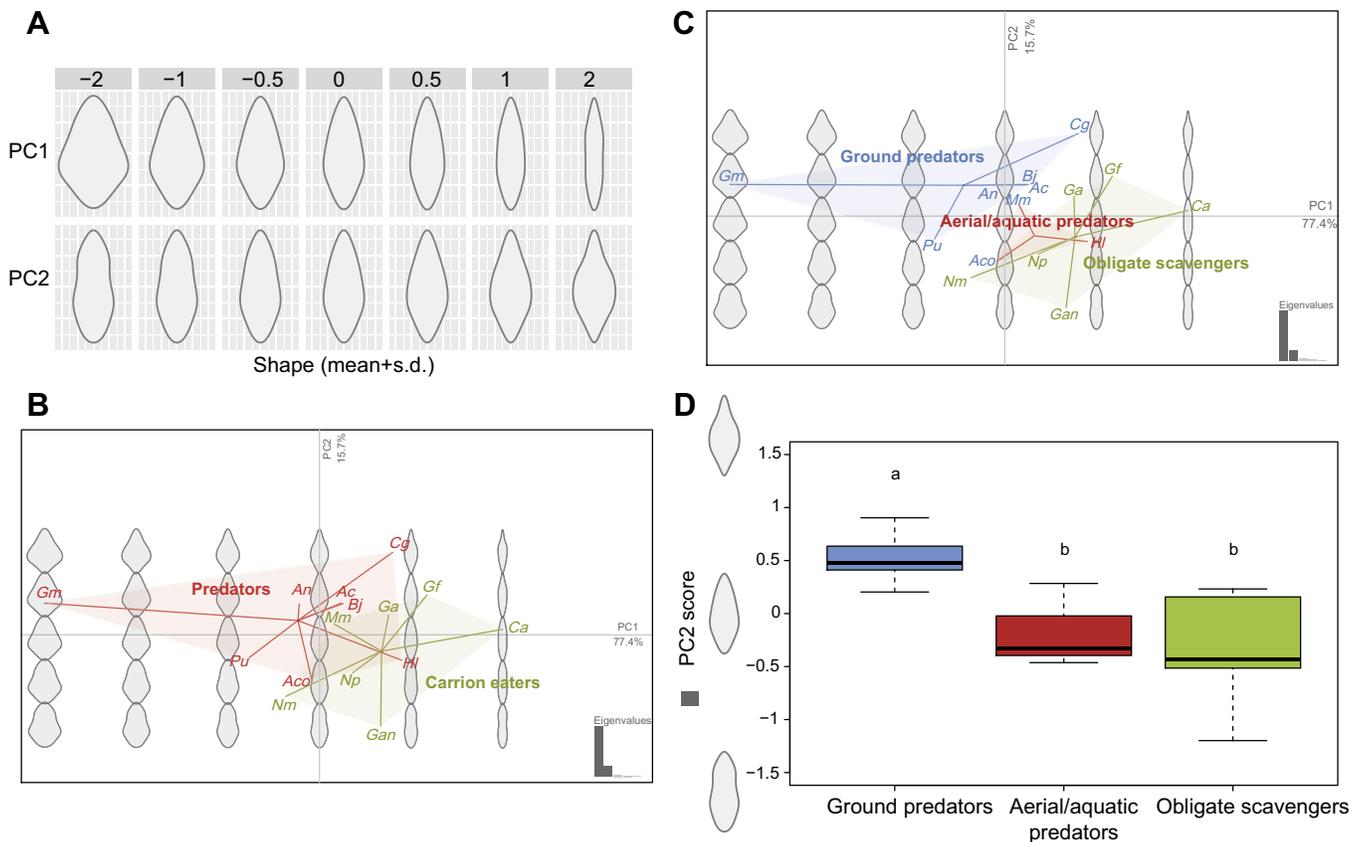


Fig. 4. Results of principal component analysis. (A) Aspects of binocular field shapes captured by the first two principal components. (B,C) Binocular field shape with respect to (B) diet and (C) foraging tactic. (D) Difference in PC2 scores among species with different foraging tactics. Different letters reflect significant differences ($P < 0.05$). Species: *Accipiter cooperii* (Aco), *Aquila chrysaetos* (Ac), *Aquila nipalensis* (An), *Buteo jamaicensis* (Bj), *Cathartes aura* (Ca), *Circus galliacus* (Cg), *Geranoaetus melanoleucus* (Gm), *Gypohierax angolensis* (Gan), *Gyps africanus* (Ga), *Gyps fulvus* (Gf), *Haliaeetus leucocephalus* (Hl), *Milvus migrans* (Mm), *Necrosyrtes monachus* (Nm), *Neophron percnopterus* (Np), *Parabuteo unicinctus* (Pu).

while catching a prey item moving in a horizontal plane. A large binocular overlap in the middle of the binocular field may also be associated with an enhanced grip (compared with that of aerial predators) and shorter toes (Fowler et al., 2009) and tarsi (Einoder et al., 2007), as the angular width of the talons spread out from the bird's eye will be larger than for species with elongated toes and a weak grip. O'Rourke et al. (2010a) also showed that species that chase moving prey in three dimensions differ in the position of the maximum binocular overlap. The Cooper's hawk, *Accipiter cooperii*, (which chases birds) has a maximum binocular field enlarged much more above the eye–bill tip direction compared with that of two ground predators, the red-tailed hawk, *Buteo jamaicensis*, and the American kestrel, *Falco sparverius* (O'Rourke et al., 2010a).

Reducing sun dazzling and optimizing target detection

Predatory species have a larger eye size than carrion eaters after controlling for body mass (Potier et al., 2017b). This finding seems to be particularly true for ground predators (Potier et al., 2017b). Predatory species need a large eye for improving the visual acuity to detect their prey (Kiltie, 2000; Land and Nilsson, 2012). Yet, an increasingly larger eye may also be subject to higher levels of 'disability glare' (i.e. reduction of visual acuity or contrast sensitivity as a result of light scattered within the eye, especially caused by imaging the sun (Aslam et al., 2007; Koch, 1989). Disability glare can be particularly pronounced in large-eyed species (Martin and Coetzee, 2004) such as raptors (Martin and

Katzir, 2000). This disability glare may reduce target detection (Fernández-Juricic and Tran, 2007; Gall and Fernández-Juricic, 2009) especially for objects (e.g. prey) of low visual contrast (LeClaire et al., 1982). Thus, to keep high visual acuity and high contrast sensitivity (Kiltie, 2000; Reymond, 1985), ground predators may have adapted enlarged brows to avoid sun dazzling. However, enlarged brows cause a large blind area over the head (Martin, 2007), which narrows the binocular overlap at the upper edge. By contrast, aerial/aquatic predators benefit from a narrow blind area over the head, enabling them to search for prey that move in three dimensions, which requires large visual coverage to follow the escaping prey. Similarly, obligate scavengers, having a narrow blind area over the head, can detect and use conspecific information to find food (Houston, 1974). Large visual coverage may be important for social foraging in birds (Fernández-Juricic et al., 2004; Martin, 2009), especially in species that track the behaviour of conspecifics to gather information about food presence/position (Tisdale and Fernández-Juricic, 2009). For aquatic predators such as the bald eagle, *Haliaeetus leucocephalus*, eyebrows may not be as efficient in terms of avoiding sun dazzling as for ground predators because they mainly search for prey under the water surface, where reflection effects are important from below too (Del Hoyo and Elliot, 1994).

Bill-shape constraints

Avian bill shape varies with diet (Darwin, 1859; Grant and Grant, 2011). In raptors, while the bill shape evolved together with braincase morphology, it also varies with prey type (Bright et al.,

2016), with a wide but short bill in species that forage on mammals (Slagsvold et al., 2010; Figs S2 and S3), and long, narrow bills in obligate scavengers (Hertel, 1994; Figs S2 and S3). This specialized bill morphology in scavengers enhances tearing ability, even if the shape of the bill may vary according to the part of the carcass that is preferentially consumed (Hertel, 1994). This bill morphology may account for the wide lower edge of the binocular field (and thus a less protruding binocular field shape at the lower edge). Raptors that eat birds or fish also have a long and narrow bill shape, which may be advantageous for plucking (Slagsvold and Sonnerud, 2007) or flaking prey, as bald eagles do. The wide but short bill of ground foragers allows them to increase the ingestion rate of mammalian prey (Slagsvold and Sonnerud, 2007). Similar to large brows at the upper edge of the binocular field, this bill morphology may lead to a more protruding binocular field shape at the lower edge compared with that of the two other groups (Fig. S4). We therefore suggest that the shape of the binocular field may be associated with the constraints of the bill shape.

It is important to note that we did not assess between-species differences in head/eye movements, which could have a very important influence on visual field topography and consequently visual perception (e.g. Martin, 2017; Moore et al., 2013; Tyrrell et al., 2015). Although considerable research has been done on eye and head movements in songbirds (e.g. Baumhardt et al., 2014; Moore et al., 2015, 2017), relatively little has been done in raptors. Nevertheless, it has been shown that raptor species can differ in their head and eye movements (O'Rourke et al., 2010a, b). Future work combining eye and head movement information with our novel analytical approach may provide a more functional dimension on visual field shape variation across raptors.

While the link between form and function has been one of the most enduring questions in organismal biology, it is only now possible to use new techniques (morphometrics) to quantitatively compare the shape of the visual fields across species relative to foraging strategies. By using morphometric analyses, we provide novel findings to understand the relationship between visual fields and their potential function in diurnal raptors. This type of analysis may provide novel opportunities to understand the link between visual field shape and ecological niche specialization in vertebrates.

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 carry out these experiments. We also thank H. Billaud, F. Blais, J. Fluhr, J. Barrier, A. Sahnoune, E. Challet, P. Bouffandeau and L. Bouvier for their help with fieldwork. We are grateful to M. Lieuvain for the drawing of raptors in Fig. 1. We sincerely thank Graham R. Martin for comments on the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.P., O.D., F.B.; Methodology: S.P.; Validation: S.P., F.B.; Formal analysis: S.P., V.B.; Data curation: S.P., G.B.C., C.O., E.F.-J., F.B.; Writing - original draft: S.P.; Writing - review & editing: S.P., O.D., G.B.C., V.B., C.O., E.F.-J., F.B.; Supervision: O.D., F.B.

Funding

S.P. was supported by a PhD fellowship from the LabEx CeMEB (Centre Méditerranéen de l'Environnement et de la Biodiversité) 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 La Boissière du Doré, Le Zoo de la Barben, Le Zoo du Pal, Le Parc des Oiseaux.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.177295.supplemental>

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