Review

Visual adaptations of diurnal and nocturnal raptors

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HIGHLIGHTS

- Raptors have large eyes allowing for high absolute sensitivity in nocturnal and high acuity in diurnal species.
- Diurnal hunters have a deep central and a shallow temporal fovea, scavengers only a central and owls only a temporal fovea.
- The spatial resolution of some large raptor species is the highest known among animals, but differs highly among species.
- Visual fields of raptors reflect foraging strategies and depend on the divergence of optical axes and on head structures
- More comparative studies on raptor retinae (preferably with non-invasive methods) and on visual pathways are desirable.

ARTICLE INFO

ABSTRACT

Raptors have always fascinated mankind, owls for their highly sensitive vision, and eagles for their high visual acuity. We summarize what is presently known about the eyes as well as the visual abilities of these birds, and point out knowledge gaps. We discuss visual fields, eye movements, accommodation, ocular media transmittance, spectral sensitivity, retinal anatomy and what is known about visual pathways. The specific adaptations of owls to dim-light vision include large corneal diameters compared to axial (and focal) length, a rod-dominated retina and low spatial and temporal resolution of vision. Adaptations of diurnal raptors to high acuity vision in bright light include rod- and double cone-free foveae, high cone and retinal ganglion cell densities and high temporal resolution. We point out that more studies, preferably using behavioural and non-invasive methods, are desirable.

1. Raptors – an ecologically defined group of birds with large eyes

As Aristotle [1] (350BCE) already knew, "the eagle is very sharp-sighted", a statement often repeated and generalized to all raptors. Here we review what is presently known about eyes and visual adaptations in birds of prey. Raptors, or birds of prey, have been defined in different ways, starting with Aristotle's – "birds of prey, or birds with crooked talons". For the purpose of this review, we follow the definition of raptors by Jarvis et al. [2] and McClure et al. [3], including all birds within the orders Falconiformes (including falcons and caracaras), Accipitriformes (including, for instance, eagles, hawks, Old World vultures), Cathartiformes (New World vultures), Strigiformes (owls) and Cariamiformes (seriemas). Although some species lack sharp talons or are obligate or facultative scavengers, and a few mainly eat plant parts, all of them derive from raptorial landbirds [3].

We are not aware of a single study on eyes or vision of the two species of cariamiforms, but many studies have focused on owls ([4,5],

and references therein) as well as falconiform, accipitriform and cathartiform raptors (examples in [6]). Although some owl species hunt during daytime (*e.g.* the Snowy owl (*Bubo scandiacus*), Burrowing owl (*Athene cunicularia*) and some Barn owls (*Tyto* spp.); [7]) and a third of falconiform and some accipitriform species may have crepuscular habits (see [6] for a review), owls are generally considered a clade with predominantly nocturnal activity [5,8,9], whereas most species in the other orders are mainly diurnal. Accordingly, studies on these groups have focused on different aspects: owls have fascinated researchers by their high absolute sensitivity, whereas diurnal raptors have been studied more vigorously for their high spatial acuity. Here we review literature on both groups. For a summary of original data on raptor eyes and vision from the studies that we were aware of, please consult the supplementary file Potier_et_al_Raptor_eyes.xlsx.

Both high sensitivity and high acuity are facilitated by large eye size that allows for wider pupil diameter and longer axial length. Birds invest in larger eyes relative to body weight than mammals (both in terms
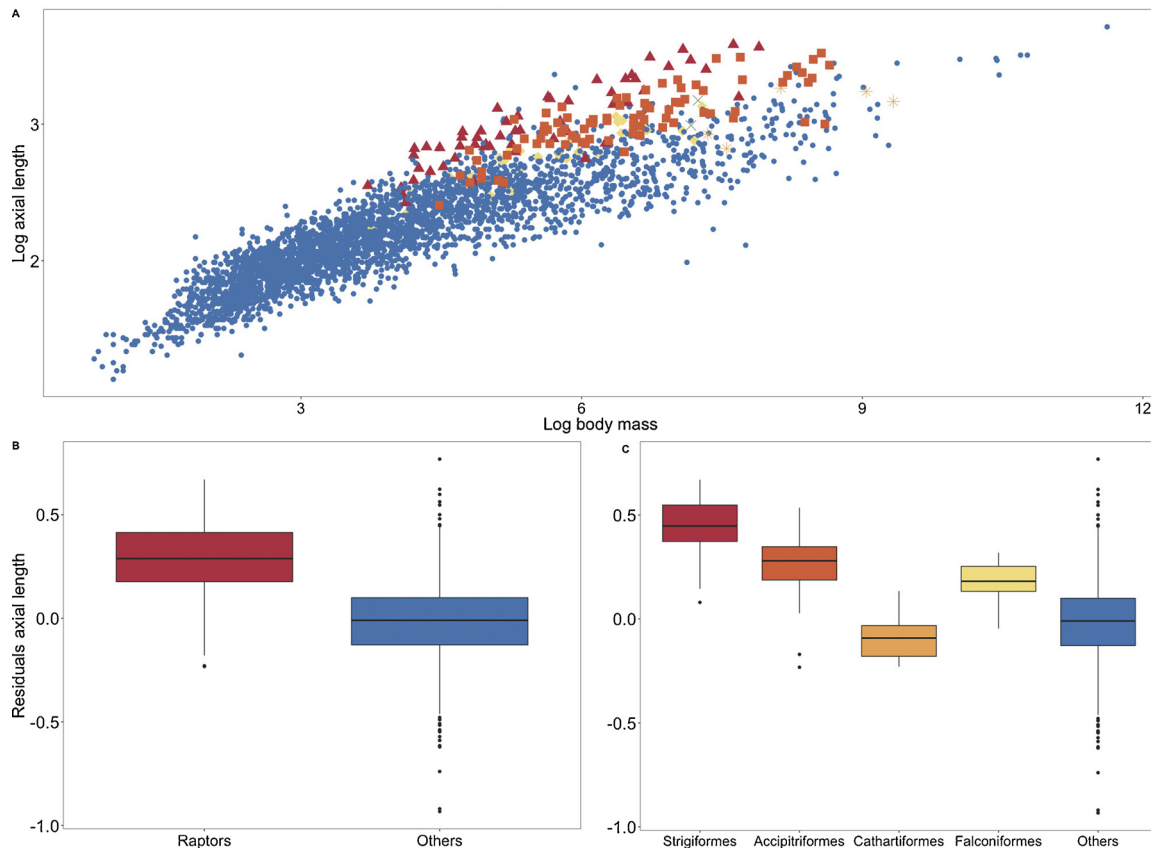

Fig. 1. The eye size of raptors compared to other birds. (A) Logarithmic relation between eye size and body mass in birds (Estimate = 0.22 ± 0.002, t = 114.30, p < 0.001). Red triangles: Strigiformes, orange squares: Accipitriformes, light yellow diamonds: Falconiformes, green crosses: Cariamiformes, dark yellow asterisk: Cathartiformes, other birds: blue dots. Difference in residual axial length between (B) raptorial and non-raptorial species and (C) raptor orders and non-raptor orders was tested using phylogenetic generalized least squares models (PGLS). Residual axial length was calculated from axial length scaled to body mass. Cariamiformes were not included in this analysis as only two species were available. Phylogeny was obtained for 3316 species using a consensus tree based on 1000 randomly selected trees from www.BirdTree.org [124] using Ericson tree distribution. Data were analysed on R 3.6.2 using ggplot 2 [125], ape [126], phytools [127], nlme [128] and emmeans [129]. Edge lengths were obtained by computing the mean edge length for each edge in the consensus tree. Controlling for body size, raptors have larger eyes (axial length) than other birds (Pagel's lambda = 0.92, Estimate = 0.17 ± 0.06, t = 2.96, p = 0.003). At a specific order scale, Strigiformes have significantly larger eyes than Cathartiformes (Estimate = −0.49 ± 0.15, t = −3.23, p = 0.011) and non-raptorial species (Estimate = −0.34 ± 0.09, t = −3.63, p = 0.003), but do not differ from Falconiformes (Estimate = −0.19 ± 0.09, t = −1.20, p = 0.75) and Accipitriformes (Estimate = −0.15 ± 0.13, t = −1.11, p = 0.80). There is no difference within diurnal raptor orders (all p > 0.17) nor between diurnal raptor orders and non-raptorial species (all p > 0.33). Body masses were taken from [130], axial lengths from [131].

of axial length and volume; [10,11]), and raptor eyes are large compared to those of other birds (Fig. 1; [12]), indicating that vision is an important sensory modality for them. Among raptors, the eyes of owls are often said to be larger than the eyes of predominantly diurnal raptors ([12,13]), but a significant difference is found only to Cathartiformes (Fig. 1). The high sensitivity of owl eyes is partly due to their low F-numbers [14,15] or, anatomically, large corneal diameters relative to axial lengths (Fig. 2; [13,16]). In diurnal raptors, smaller corneal diameters and large axial lengths lead to large retinal images and thus, high spatial resolution, but lower sensitivity (Fig. 2; [4,17]).

2. Visual fields and eye movements

Large variation among raptors is found in the visual fields (Fig. 3) and eye movements. Owls are always perceived as having rather frontally placed eyes allowing for large frontal binocular fields. In the Tawny owl (*Strix aluco*), each of the tubular eyes has a relatively narrow visual field of ≈120° width, and the visual axes of the eyes diverge by 55° ([18]; Fig. 3) – a large angle compared to humans, which have parallel visual axes, but smaller than many other birds (see [9]). This results in a cyclopean field (horizontal extension of the visual fields of the two eyes) of 201°, a frontal binocular field of 71° vertical and

maximally 48° horizontal extension, and a blind sector of 159° horizontal extension behind the head [18]. These visual fields are fixed, because the large eyes of owls are positioned partly outside the skull, and the orbital muscles that mainly hold them in place, can only move them within the socket by less than 1.5° (Great horned owl (*Bubo virginianus*); [19]). Unfortunately, visual fields have not been determined in any other species of owl.

Diurnal raptors have larger divergences of the optical axes, for instance 112° in the Short-toed snake eagle (*Circaetus gallicus*), and larger horizontal extensions of the monocular visual fields (139° in *C. gallicus*). This results in a wider cyclopean visual field (259° in *C. gallicus*) and often a narrower binocular visual field (20°) and blind sector behind the head (101°; [20]).

Visual fields are influenced by structures such as the beak and eyebrows [21], and likely also by feathers. Specifically eyebrows that serve as sunshades leave the birds with a large blind sector above the head [21,22]. Visual fields also strongly depend on the size of eye movements. By contrast to owls, many diurnal raptors can move their eyes to various degrees. They make independent eye movements when focusing on objects in the monocular visual field, or coordinated movements of both eyes when viewing frontally positioned objects binocularly [23]. The Little eagle (*Hieraaetus morphnoides*), the only
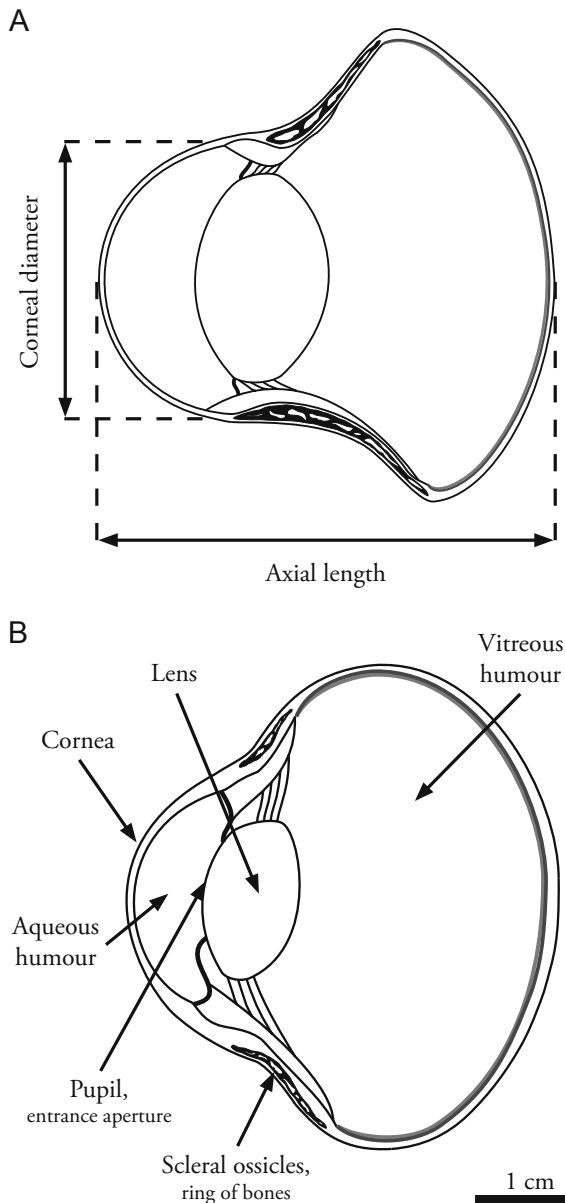
A

B

Fig. 2. Schematic drawings through the transverse plane of eyes of (A) the Eurasian eagle-owl (*Bubo bubo*) and (B) the White-tailed eagle (*Haliaeetus albicilla*). The ratio between posterior nodal distance (or anterior focal length) and pupil diameter, which can be approximated by axial length and corneal diameter, respectively, is an important parameter in the trade-off between resolution and sensitivity.

species in which eye movements have been studied in detail, can move its eyes by 24° in the horizontal plane [24]. In the resting position, the temporal foveae look at ± 13° from the midsagittal plane, placing them just within the binocular visual field. The eagle can converge the eyes such that both temporal foveae are aligned and looking forward. It makes frequent saccadic eye movements, most often moving both eyes in the same direction, with a mean interval of 2.5 s and often with different amplitudes, usually below 5°. O'Rourke et al. [25] recorded eye movements of less than 1° in the American kestrel (*Falco sparverius*), ≈5° in Red-tailed hawk (*Buteo jamaicensis*) and ≈8° in Cooper's hawk (*Accipiter cooperi*). Thus, raptors have smaller eye movements than birds such as corvids (up to 39° in the horizontal plane; [26]), but data on additional species would be highly interesting.

Potier et al. [21] found that ground predators, which are unlikely to use the dorsal visual field to search for conspecifics or prey, have larger

blind sectors above the head than aerial predators or scavengers. Generally, many raptors forage flying, while bending the head and looking downwards, such that the dorsal blind field is pointing into the direction of forward flight, which may explain why raptors are particularly prone to collisions with artefacts such as wind turbines and power lines [27].

3. Ocular media transmittance

Before reaching the retina, light passes the ocular media (Figs. 2 and 4), of which the cornea and lens absorb all UVB radiation (of 280–315 nm wavelength), and to some degree also UVA (315–400 nm), while the aqueous and vitreous humours are mostly transparent [28]. Ocular media transmittance (OMT) is described by λt_{50}, the wavelength at which 50% of incoming light is transmitted, and varies considerably: most species of diurnal raptors (λt_{50} 380 ± 10 nm) appear to have UV-absorbing pigments in their lenses, just like humans, allowing less than 30% of UVA radiation to reach the retina. The Western marsh harrier (*Circus aeruginosus*) is the only exception among nine studied species, in which the lens probably is not pigmented (λt_{50} of 352 nm; Fig. 4; [29,30]; Peter Olsson, MM, AK, unpublished data). In owl eyes, despite the thick lenses, more than 40% of UVA radiation reaches the retina, with λt_{50} between 340 and 360 nm [31]. In a starlit night, UV contributes only a small proportion of all light, but during dusk, it contributes significantly [32]. Rods have a beta sensitivity peak around 350 nm, thus UV-transmitting ocular media may contribute significantly to the absolute sensitivity of many owl eyes [31]. On the negative side, UV light is also scattered most, and contributes most to chromatic aberration, impairing eyes with high visual acuity (see below) – a potentially important reason why many diurnal, but not nocturnal raptors strongly limit the UV radiation reaching the retina [29].

4. Accommodation

The main function of the cornea and the lens (apart from eye protection and filtering the incoming light) is to focus the image on the retina. In falcons (American kestrel), emmetropia (well focused vision) develops from severe myopia (short-sightedness) during the first two weeks after hatching, a process that requires visual feedback [33]. Barn owl juveniles have mixed refractive errors after eyelid opening (two weeks post-hatching); some are hyperopic (long-sighted) and some are myopic (short-sighted), but achieve near emmetropia within two weeks [15].

Many birds can accommodate by changing the curvature of both cornea and lens [34,35]. By contrast, mammals can only change lens curvature, allowing, for instance, young humans to accommodate by 8.6 Diopters (D), while older humans loose accommodation completely [36]. The Red-tailed hawk can totally accommodate up to 28 D [37], and other studied species of diurnal raptors accommodate between 4 D (Sharp-shinned hawk *Accipiter striatus*) and 16 D (American kestrel; [37]). Small species do not have corneal accommodation, but in the Turkey vulture (*Cathartes aura*), African fish eagle (*Haliaeetus vocifer*), Bald eagle (*Haliaeetus leucocephalus*), Golden eagle (*Aquila chrysaetos*) and Red-tailed hawk it ranges between 3 and 9 D [37].

Diurnal raptors accommodate symmetrically when focusing objects in the binocular field of view, but monocularly when viewing objects in the monocular field [37]. Differently, at least in Barn owls, accommodation is symmetrical in both eyes [38].

Most owls likely lack corneal accommodation [34]. The American barn owl (*Tyto furcata*) can accommodate more than 10 D [37], but for other owl species, accommodation ranges between 0.6 and 6 D [39,40]. The difference in accommodation power between diurnal and most nocturnal raptors may be related to the feeding habits. While owls feed their young and swallow whole prey items, diurnal raptors tear the flesh, thus need a focused image for precise beak-talon coordination [37].
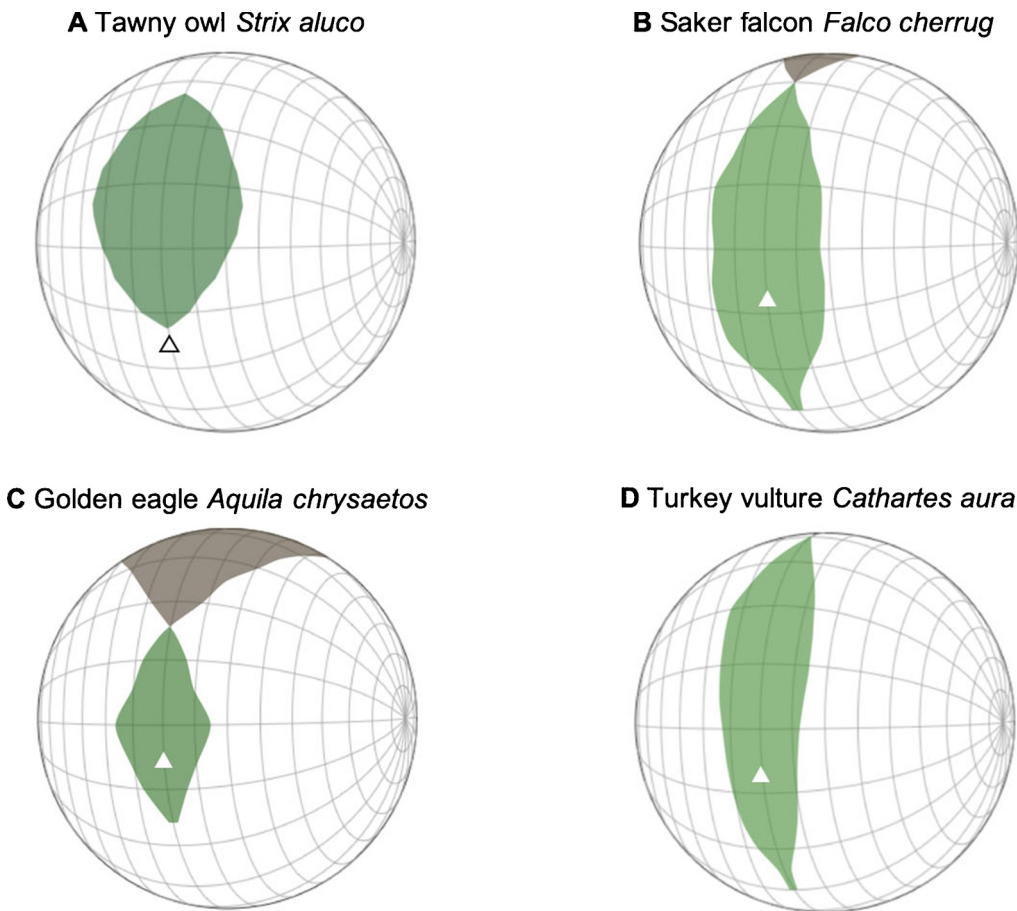
A Tawny owl *Strix aluco*

B Saker falcon *Falco cherrug*

Fig. 3. Orthographic projections of retinal field boundaries of the eyes of four raptor species. A latitude and longitude coordinate system was used with the equator aligned vertically in the median sagittal plane (20 deg intervals in latitude and 10 deg intervals in longitude). The bird's head is at the centre of the globe. Green areas represent the binocular sectors, white areas the monocular sectors and brown areas the blind sectors. Triangles: direction of bill projection. Figure modified from [18,132] and [21]. Unfortunately, the blind sector was not estimated in the Tawny owl.

C Golden eagle *Aquila chrysaetos*

D Turkey vulture *Cathartes aura*

Owls may partly compensate for their inability to focus very near objects by pupil constriction, which increases depth of focus [39]. Pupil response to light has rarely been studied in owls (*e.g.* [38,41]). In birds, the pupil reacts to changes in light intensity faster, but with a smaller change in area than in mammals ([42] and references therein); it also strongly responds to specific visual stimuli [42]. More research is needed to understand the relevance of accommodation and pupil size for visually guided behaviour in different raptor groups.

5. The retina and the pecten

Diurnal raptors have thicker retinae than other birds, including owls (Fig. 5; *e.g.* [43–47]). For example, the central retina of the Short-toed snake eagle can be as thick as 630 μm [46,48], significantly thicker than that of the Eurasian eagle-owl (*Bubo bubo*; 360 μm; [48]) or non-raptorial species such as the chicken (*Gallus gallus*; < 200 μm; [49]), or Turquoise-fronted parrot (*Amazona aestiva;* 280 μm; [50]). As birds lack retinal blood vessels [44], the retina receives nutrients and oxygen *via* the lamina choriocapillaris and the pecten [51]. The latter is a fan-like pigmented and highly vascularized structure projecting into the vitreous from below the optic nerve head in ventro-temporal quadrant of the fundus. According to Pettigrew et al. [44], it oscillates in saccades orthogonally to its long axis, likely to optimize retinal perfusion, but several other potential functions of the pecten have been discussed [51].

The pleated pecten of raptors and owls consists of a single accordion-folded lamina. In the Red-tailed hawk it has 17–18 pleats held together apically by a heavily pigmented bridge. The pecten is $12-14$ mm long at its base and projects 7–8 mm into the vitreous chamber [52]. The pecten of the Common buzzard (*Buteo buteo*) has 17–18 [53], and that of the Black kite (*Milvus migrans*) 12–13 folds [54].

The pectens of owls are generally smaller than those of diurnal raptors (Fig. 6; [55,56]), that of the Barn owl has 7–8-folds, is 4.4 mm wide at the base, 1.4 mm at the apical tip, and 2.7 mm long [57]. That of the Spotted eagle-owl (*Bubo africanus*) has 5–6 [54], and that of the Great horned owl 7–8 folds [58]. Thus, the size of the pecten is not correlated with eye size, but strongly depends on phylogeny and differs between diurnal or nocturnal species (Fig. 6).

Even though light does not have to pass through retinal blood vessels, it has to pass through several neuronal layers before reaching the outer segments of the photoreceptors (see Fig. 5). The distribution of photoreceptors and retinal interneurons varies across the retina, leading to a thicker retina in regions with higher densities of photoreceptors and retinal neurons.

All raptor species studied to date have at least one fovea – an indentation in the vitreal surface of the retina, where inner retinal layers are displaced centrifugally, often creating a surrounding foveal rim (see *e.g.* [46,59,60]). Most actively hunting diurnal raptors have a central deep fovea and a shallower temporal fovea (Fig. 5; *e.g.* [23,45,46,60–63]). Due to their retinal positions, the refractive status of these two foveae differs, with the temporal fovea (used for viewing near-by objects) being myopic compared to the central deep fovea (primarily used to look at distant objects) [64]. Carrion feeding raptors only have one central deep fovea (Fig. 5; [46,63]). Owls, by contrast, only have a temporal (Fig. 5) usually very shallow fovea (*e.g.* in the Barn owl, [16] could not find it while [65] did). Most raptor species investigated so far also have a more or less well defined visual streak, a linear area of increased cell density, thickness and spatial resolution, either extending horizontally from the single fovea or connecting both foveae ([16,63,66]).

The function of the deep fovea of diurnal raptors has been discussed widely beginning with Walls [67], but has never been determined
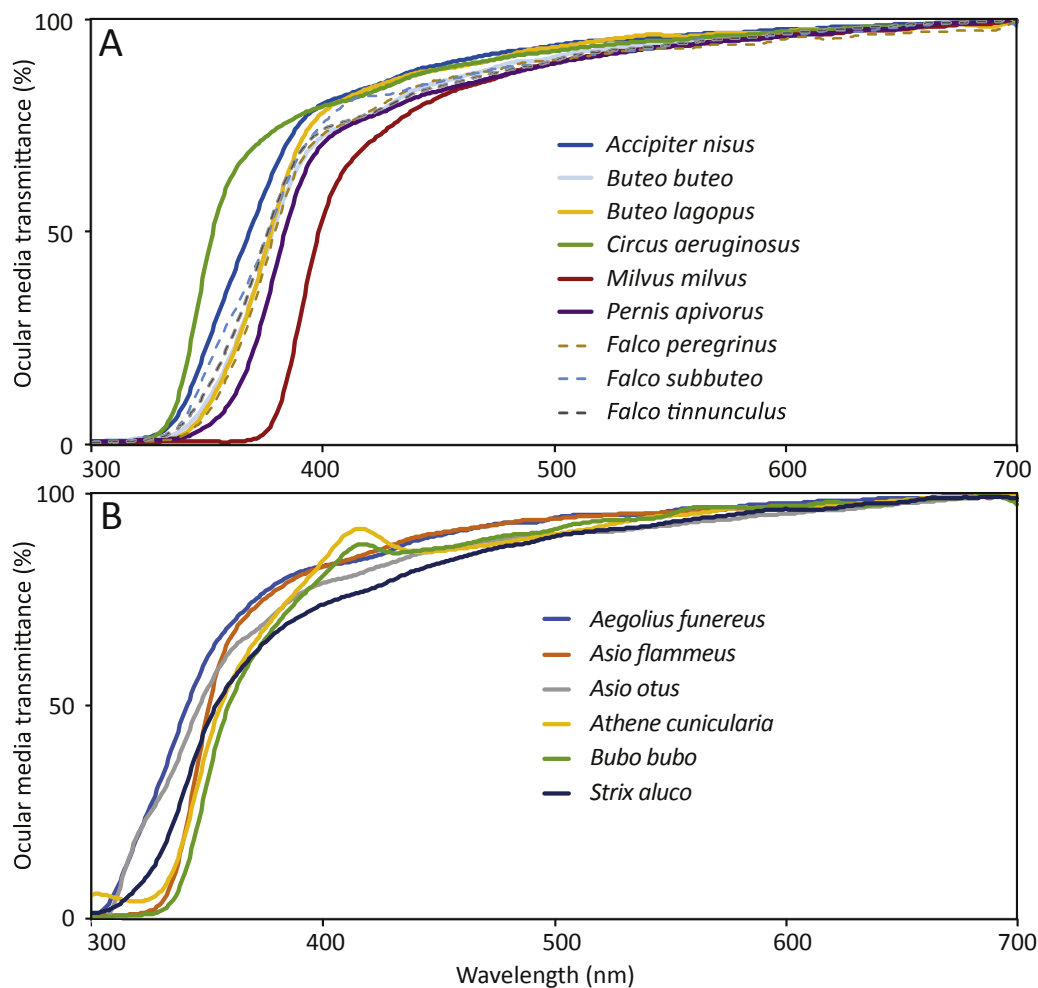
Fig. 4. Ocular media transmittance of diurnal raptors (A) and owls (B). Data from [29,31] and Olsson, Mitkus, Lind, and Kelber, unpublished data.

conclusively (for review see [68]). An undisputed effect is the thinner layer of retinal tissue that light has to pass before being absorbed by visual pigments in the photoreceptor outer segments, leading to a lower degree of scattering. The photoreceptor packing density in the fovea of some accipitriform raptors is close to the maximum predicted by the limitations of waveguide optics ([43,61,62,69]). This allows for high spatial resolution, but limits absolute sensitivity. If the shape of the fovea, due to the refractive index difference between retina and vitreous, acts as a magnifying lens as Snyder and Miller [70] have suggested, this effect is very likely insignificant ([61,62,71]). On the other hand, Pumphrey's [72] hypothesis that the distortion of the image in the foveal region may help to fixate moving prey, still awaits experimental tests. The finding of large intraspecific differences in foveal shape [73] has made the picture even more complicated.

6. Photoreceptors

The duplex retinae of raptors house rods (expressing RH1 opsin, with a peak sensitivity to light of 500 nm wavelength), unequal double cones (LWS) and, in most raptors, four types of single cones [74]. The single cones express visual pigments sensitive to violet (SWS1 opsin-based pigments), blue (SWS2), green (RH2) and red (LWS) light [74], but photoreceptor complement and the spectral sensitivity of opsins in diurnal raptors have barely been studied. The SWS1 opsin, which is violet-sensitive in raptors [75], has been lost in at least two species of Accipitriformes (Cinereous vulture (*Aegypius monachus*); Black-winged kite (*Elanus caeruleus*); [76]), but spectral sensitivities of diurnal raptor cones have never been directly recorded.

All owls have lost functional SWS1 opsin, and owls of the genus *Tyto* also lost functional RH2 [31,76]. Microspectrophotometric (MSP) investigations in the Tawny owl and transcriptomes in several species of owls indicate a short-wavelength shift of the LWS (λ_{max} 555 nm) and a long-wavelength shift of SWS2 (λ_{max} 463 nm), compared to other birds [76,77].

In bird cones, oil droplets situated immediately prior to the outer segment in the light path influence the light that is available for vision [78]. In all except the violet-sensitive cones, the oil droplets contain carotenoid pigments, which reduce the absolute sensitivity by 70–90% and shift the sensitivity peak by $20-40$ nm to longer wavelengths, compared to the visual pigment [74]. Galloxanthin and dihydrogalloxanthin stain oil droplets in blue-sensitive cones, zeaxanthin in green-sensitive cones, and astaxanthin in red-sensitive cones. The sensitivity of violet-sensitive cones depends on OMT directly [29,30]. Birds take up zeaxanthin with food, but produce the other carotenoids by modifying zeaxanthin in enzymatic pathways [79,80]. Owls have lost the gene coding for the enzyme required to produce astaxanthin, thus their red-sensitive cones likely retain a higher and less red-shifted sensitivity (Höglund et al. 2017) than those of other birds. Diurnal raptors have all four types of oil droplets [81,82], but the Eurasian hobby (*Falco subbuteo*), the American kestrel and the Common buzzard have been found to lack red oil droplets in the fovea [81].

The relative densities of single cones, double cones and rods differ drastically between owls and diurnal raptors, but also within the retina in those species, in which this has been investigated.

Double cones make up between ≈ 20 and $\approx 60\%$ of all photoreceptors [45,52,83] outside the foveae of diurnal raptor retinae. They
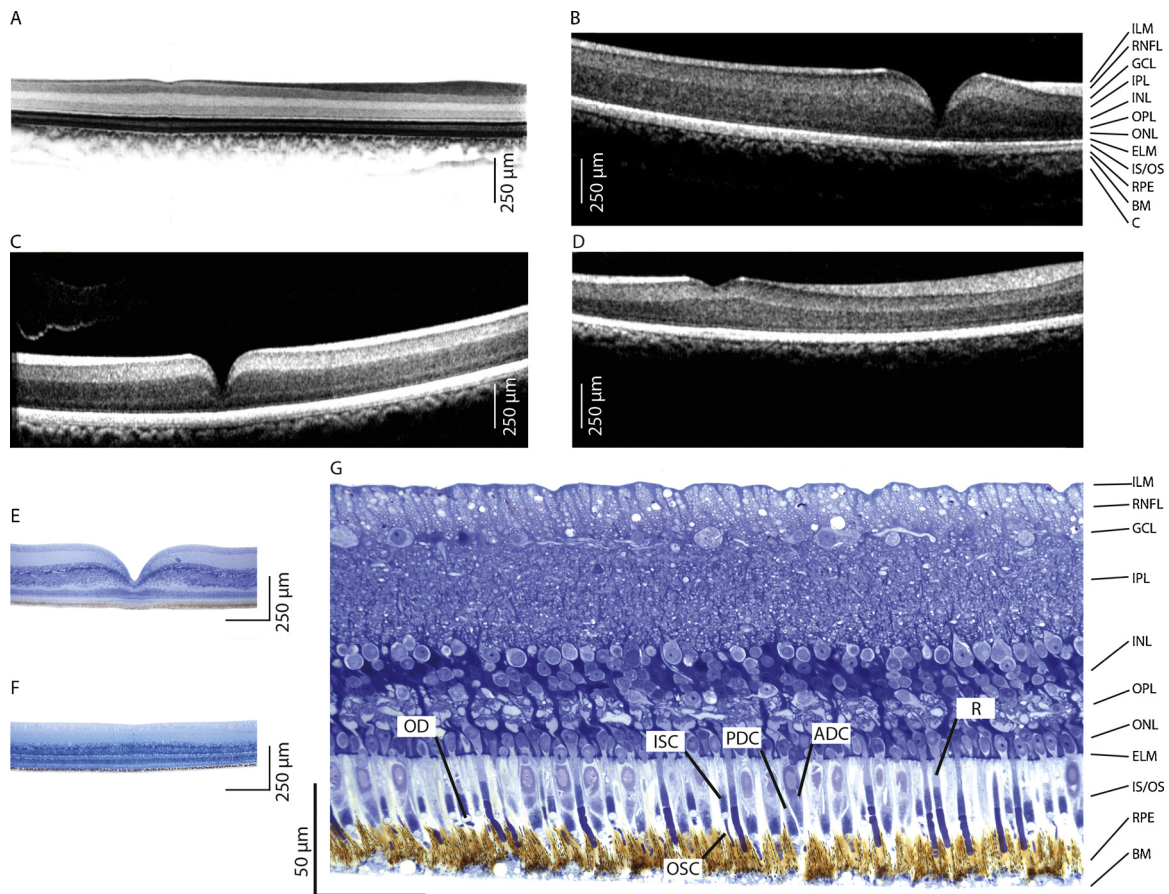
Fig. 5. Retinae and foveae of different raptor species. SD−OCT images (B-scans) of (A) temporal fovea of the Tawny owl (*Strix aluco*; Strigiformes), (B) deep central and (D) shallow temporal fovea of the Harris's hawk (*Parabuteo unicinctus*; Accipitriformes), (C) deep temporal fovea of the Southern caracara (*Caracara plancus*; Falconiformes) taken in living animals. Histological sections (2 μm thick, stained with Azure II – Methylene Blue) of (E) deep central fovea, (F) shallow temporal fovea, and (G) peripheral temporal retina of the Red kite (*Milvus milvus*; Accipitriformes). Note, that in (E)–(G) scale bar applies to both x and y axis of the picture, whereas in (A)–(D) the scale bar is available only for the y axis of the picture due to specific reasons of the imaging technique (for detailed explanation see *e.g.* [46]). (E) and (F) are adjusted in size to match the y axis scale bar of (A)–(D). (A) is modified from Velasco Gallego [133], using a different OCT apparatus and other capturing parameters than in (B)–(D), which are unpublished scans by SP. (E) and (F) are modified from Mitkus et al. [45], and (G) is an unpublished picture by M Mitkus. Abbreviations: ILM, inner limiting membrane; RNFL, retinal nerve fiber layer; GCL, ganglion cell layer; IPL, inner plexiform layer; INL, inner nuclear layer; OPL, outer plexiform layer; ONL, outer nuclear layer; ELM, external limiting membrane; IS/OS, photoreceptor inner/outer segments; RPE, retinal pigment epithelium; BM, Bruch's membrane; C, choroid; OD, oil droplet; ISC, inner segment of the single cone; OSC, outer segment of the single cone; PDC, principle member of the double cone; ADC, accessory member of the double cone; R, rod.

have a broader spectral sensitivity than single cones and have been thought to mediate achromatic vision and motion detection in birds [84]. However, their large cross-sectional diameters and absence from the deep foveae of most species, where this has been studied [45,62], indicate that they may not be the optimal or only receptors mediating high-resolution vision of raptors.

Rods make up only ≈ 20 to 25% of the photoreceptors of diurnal raptors ([52]; J–P Coimbra and A Kelber, unpublished data). They tend to be absent from the foveae of diurnal raptor species [43,45,61,62], allowing for higher cone densities and thus higher spatial resolution of vision in bright light. In owl foveae, by contrast, rods are by far the most frequent receptor type. They make up 90% or more of all receptors in owl retinae [58,65,85,86], and in retinal transcriptomes, rod opsin RH1 stands for over 98% of all opsin RNA [31]. Braekevelt [58,86] found double cones to be more frequent than single cones in owls, and accordingly LWS opsin is most highly expressed of all cone opsins [31].

7. Retinal neurons and visual pathways

The signals from photoreceptors are sent to the retinal ganglion cells (RGCs) *via* bipolar cells, with horizontal and amacrine cells providing intra-retinal interactions [36]. However, information on structure and

components of inner retinal layers of raptors, or any other birds, is very limited. The axons of RGCs form the optic nerve, which sends partly processed information to the visual centres of the brain. In the central fovea of the Common buzzard and the Common kestrel (*Falco tinnunculus*), Oehme [43] found RGC:cone ratios of 1:1, indicating that cone density, not RGC density, limits spatial resolution. Outside the fovea, the RGCs are the bottleneck for the information capacity of the eyes [36]. RGC topography maps exist for two falconiform (American kestrel and Chimango caracara *Milvago chimango*), one accipitriform (Black-chested buzzard-eagle *Geranoaetus melanoleucus*), three cathartiform (Andean condor *Vultur gryphus*, Black vulture *Coragyps atratus*, Turkey vulture) [63,66] and nine strigiform species [16].

Birds have a complete optic nerve crossing, and RGCs project to the brain *via* the tectofugal pathway (to the tectum opticum), the thalamofugal pathway (to thalamic nuclei and then the visual Wulst, the putative homologue to the mammalian primary visual cortex) and the accessory optic system (AOS; [87,88]). In the American kestrel, the retinotopic map of the optic tectum represents the entire retina. The visual fields of tectal neurons are small in the foveal regions, and increasingly larger towards the periphery [64,89]. By contrast, cells in the visual Wulst represent the binocular visual field, but lack representation of the central retina, including the central fovea. This mapping is
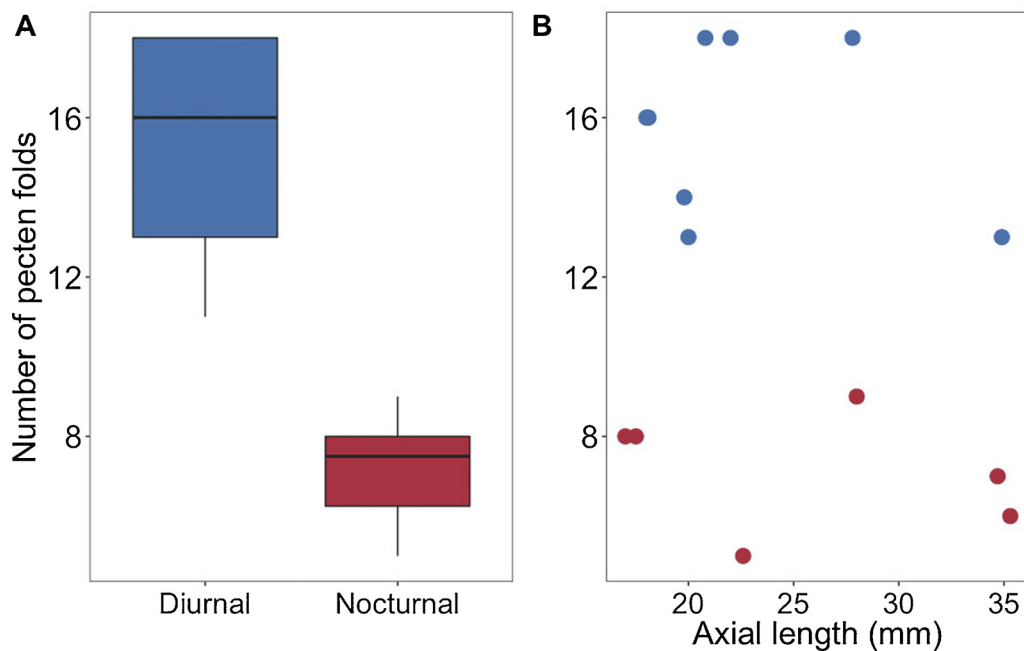
Fig. 6. Number of pecten folds in relation to (A) lifestyle and (B) axial length of the eye. Phylogenetic generalized linear model following a Poisson error distribution. Phylogeny was obtained using a consensus tree based on 100 randomly selected trees from www.BirdTree.org [124] using Ericson tree distribution. Data were analysed on R 3.6.2 using ggplot 2 [125], ape [126], phytools [127] and phylolm [134]. Edge lengths were obtained by computing the mean edge length for each edge in the consensus tree. Number of pecten folds is highly dependent on phylogeny (Pagel's lambda = 1). While the number of pecten folds is not related to axial length (Estimate = $-3.99e^{-3} \pm 4.16e^{-3}$, z = -0.96, p = 0.34), diurnal and nocturnal species differ significantly in the number of pecten folds when phylogeny is taken into account (Estimate = -0.74 ± 0.17, z = -4.37, p < 0.001). For original data and references please consult the supplementary file Potier_et_al_Raptor_eyes.xlsx.

similar in the Barn owl and the Black vulture [23]. Some cells in the visual Wulst of the Burrowing owl respond to sine wave gratings of contrast as low as 2.5% [90] – this is remarkable as most birds, including the Barn owl [91] and several diurnal raptors [92], do not respond to contrasts lower than 10%, in behavioural tests.

Finally, the accessory optic system analyses the optic flow resulting from the bird moving through the visual world [93]. Not much is known about the AOS in raptors, but Davies and Green [94] found that Harris' hawks (*Parabuteo unicinctus*) use the self-induced rate of motion expansion to time their landing.

8. Binocular depth perception

Little is known about binocular depth perception of raptors. The binocular cells in the visual Wulst, which get input from the ipsilateral eye *via* the supraoptic decussation [95,96], in addition to the input from the contralateral eye, are selective for binocular disparity [97] and involved in stereopsis, both in the American kestrel [98] and the Barn owl (e.g [99]). The binocular representation of the frontal visual field might be related to the need of precise object fixation in the last moments of prey capture [87].

9. Spatial resolution and contrast sensitivity

Spatial resolution, or visual acuity, of raptor eyes builds on their large focal length, receptor and retinal neuron spacing, and optics (*e.g.* [36,100]). In raptors, it has been estimated anatomically, measured by electroretinograms (ERGs) or determined in behavioural tests in several species (Table 1). The anatomical estimate builds on the spacing of cones or RGCs. Diurnal raptors, with cone-dominated retinae, have RGC:cone ratios of 1:1 or possibly even higher, in their rod- and double cone-free central foveae [43]. Therefore, and because RGCs are centrifugally displaced from the fovea, cone density is the best anatomical estimate of spatial resolution.

In diurnal raptor species, in which both have been studied, the behaviourally determined resolution is indeed in the same range as the anatomical estimate based on cone density (Table 1). The fovea of the Wedge-tailed eagle (*Aquila audax*) has over 450,000 cones/mm², each with a diameter of ≈1.6 μm, close to the theoretical limit set by waveguide optics [69], allowing for a resolution of ≈140 cycles/degree,

which closely matches the behaviourally obtained value (138 cycles/degree) [61]. Similarly, for the Brown falcon (*Falco berigora*), the anatomical estimate is 76 cycles/degree, and the behavioural result is 73 cycles/degree [62]. Thus, in diurnal raptors, anatomical resolution is a reliable estimate for the maximal behavioural resolution, the resolution achievable in a small foveal area, under optimal conditions: bright light and high contrast.

Other large raptors such as Old World vultures also resolve up to almost 140 cycles/degree [101]. Thus, it is true that some diurnal birds of prey have the highest spatial resolution among extant animal, even though popular claims that their resolution is 8 times as good as that of humans are definitely not true. Medium-sized species like the Common buzzard and Harris's hawk have a similar resolution as humans (40–60 cycles/degree [43,92]). Cathartiforms such as the Turkey vulture have a central fovea [46], but only the RGCs density has been determined [66]. It is therefore hard to judge whether the low spatial resolution estimated from these RGC densities (Table 1; [66]) reflects their actual capabilities.

In owls, with rod-dominated retinae and foveae, RGC density is a better estimate for maximum spatial resolution, because rod signals are generally pooled to improve sensitivity and signal to noise ratio [36]. Surprisingly, in the Great horned owl and the Western barn owl, behavioural resolution is even much lower (four to eight times) than this anatomical estimate (Table 1). It remains to be seen whether this is a general pattern amongst owls, or whether more diurnally active species with a deeper foveae, like the Burrowing owl, are different. Murphy and Howland [39] have mentioned the possibility that the low spatial resolution determined in behavioural tests may, at least to some degree, have been affected by the very close presentation of stimuli (17.5 cm, for the Great horned owl [85]). Due to its small accommodative range, the owl may not have seen a focussed image of the finest gratings. More data are needed to resolve this issue.

Spatial resolution also depends on light intensity and, in diurnal species, decreases steeply with decreasing light levels. At sunset, the resolution of the Wedge-tailed eagle, for instance, is only about a third of its maximum (50 cycles/degree) achieved in ≈1000 times brighter light [61]. Dramatic decreases are also found for vultures [101]. In the Great horned owl, however, the loss of resolution is less steep (1.5 log units over six log units of light intensity difference; [85]). In barn owls resolution is even slightly higher in twilight conditions than in bright

Table 1

Spatial resolution of raptors measured using various methods.

Order, Family, Species	N	Spatial resolution (cyc/deg)	Method	References
Accipitriformes Accipitridae				
Common buzzard *Buteo buteo*	3	64	Receptor spacing	Oehme [43]
Wedge-tailed eagle *Aquila audax*	1	140	Receptor spacing	Reymond [61]
	1	138	Behaviour	Reymond [61]
Griffon vulture *Gyps fulvus*	1	104	Behaviour	Fischer [101]
Egyptian vulture *Neophron percnopterus*	2	108 − 135	Behaviour	Fischer [101]
Indian vulture *Gyps indicus*	1	135	Behaviour	Fischer [101]
Black kite *Milvus migrans*	2	25.9 − 32.7	Behaviour	Potier et al. [102]
Harris's hawk *Parabuteo unicinctus*	5	27.4 − 60	Behaviour	Potier et al. [102]
Falconiformes				
Falconidae				
Common kestrel *Falco tinnunculus*	4	43	Receptor spacing	Oehme [43]
American kestrel *Falco sparverius*	1	46	Receptor spacing	Dvorak et al. [103]
	9	25 − 45	ERG	Gaffney and Hodos [104]
	1	40	Behaviour	Hirsch [105]
Brown falcon *Falco berigora*	1	76.1	Receptor spacing	Reymond [62]
	1	73	Behaviour	Reymond [62]
Chimango caracara *Milvago chimango*	3	15.1 − 39.8	Behaviour	Potier et al. [106]
Cathartiformes Cathartidae				
Turkey vulture *Cathartes aura*	3	15.4	RGC density	Lisney et al. [66]
Black vulture *Coragyps atratus*	3	15.8	RGC density	Lisney et al. [66]
Strigiformes				
Strigidae				
Burrowing owl *Athene cunicularia*	1	14.6	RGC density	Lisney et al. [16]
Snowy owl *Bubo scandiacus*	2	38.3	RGC density	Lisney et al. [16]
Great horned owl *Bubo virginianus*	5	32.0	RGC density	Lisney et al. [16]
	3	50	RGC density	Fite [85]
	3	6 − 7.5	Behaviour	Fite [85]
Great grey owl *Strix nebulosa*	1	24.6	RGC density	Lisney et al. [16]
Barred owl *Strix varia*	2	29.3	RGC density	Lisney et al. [16]
Northern hawk owl *Surnia ulula*	1	19.2	RGC density	Lisney et al. [16]
Little owl *Athene noctua*	3	5 − 8$^\$$	ERG	Porciatti et al. [107]
Tytonidae				
Barn owl *Tyto alba*	3	13.6	RGC density	Lisney et al. [16]
	2	2.6 − 4	Behaviour	Harmening et al. [100]
Australian masked owl *Tyto novaehollandiae castanops*		10	Behaviour	Reymond [108] cited after Wathey and Pettigrew [109]

For anatomical data, average values are given, for other methods, the range when available. ERG: Electroretinogram. RGC: Retinal Ganglion Cell. $^\$$ recorded in the visual Wulst, the lower value for monocular, the higher for binocular stimulation.

sunlight [91].

Even in bright light, spatial resolution is strongly limited by the achromatic contrast of stimuli. The raptors, in which this has been investigated, have contrast sensitivities between ≈ 10 (Wedge-tailed eagle [110]; Harris's hawk [92]; Barn owl [100]) and 30 (American kestrel [105,111]), thus, the lowest contrasts they can detect are between 3 and 10%. For such contrasts, spatial acuity is also far below the absolute limit. The Wedge-tailed eagle, for instance, requires 7% contrast to resolve 10 cycles/degree, the Harris's hawk 8–9% contrast at $5 − 8$ cycles/degree and the Barn owl, which shows more variation, 5–12% at 1 cycle/degree (see [92] for review).

While achromatic contrast sensitivity is considerably lower in raptors than in humans (human contrast sensitivity is > 200, allowing us to see contrasts of 0.4%; [112]), the Harris's hawk can resolve purely chromatic patterns (lacking any contrast for double cones) up to a frequency of over 20 cycles/degree [92], twice the 10 cycles/degree that humans reach [113].

A topic that still awaits investigation in raptors is the influence of the behavioural context, in which visual spatial resolution is determined. As birds have three visual pathways, carrying information with potentially different spatial resolution to different brain centres, it seems likely that resolution differs between visually guided tasks like object detection and flight control.

10. Temporal resolution

The speed of vision is ultimately set by the integration time of the photoreceptors, but may also depend on neuronal mechanisms such as

temporal pooling [36]. Short integration times allow for fast vision but low sensitivity, while longer integration times allow for higher absolute sensitivity. Diurnal, fast-flying raptors such as falcons require fast vision, both to avoid collisions, and for hunting moving prey. Nocturnal species, by contrast, might prioritize slower vision with higher sensitivity.

As a proxy for the speed of vision, the flicker fusion frequency (FFF) is often measured (Table 2). Of only three species of diurnal raptors, in which it has been determined behaviourally, the Peregrine falcon (*Falco peregrinus*) had the highest FFF, 129 Hz, at the highest light intensity used (55,500 cd/m^2), followed by the Saker falcon (*Falco cherrug*) with 102 Hz. The Harris's hawk could resolve flicker up to 81 Hz [114], still higher than humans ($\approx 40 − 60$ Hz). At lower light levels, all species had considerably lower FFFs; at 160 cd/m^2, for instance, the Peregrine falcon could only resolve flicker of less than 60 Hz. No scavenging species have been investigated – as they tend to fly slower, often scan the ground from high altitudes for carrion we would expect them to have slower vision.

In owls, FFF has only been measured using electroretinogram recordings. Even though it is not optimal to compare results obtained with different methods, the FFFs of all tested owls are lower than those of diurnal raptors: the Great horned owl could resolve up to 40 Hz [106], the Little owl (*Athene noctua*) 50 Hz [107] and the Short-eared owl (*Asio flammeus*) up to 67.5 Hz [115].

Table 2
Raptor species in which the flicker fusion frequency (FFF) has been tested.

Species common name	Species scientific name	Method	Mean FFF	Reference
Harris's hawk	*Parabuteo unicinctus*	Behavioural	77.7	Potier et al. [114]
Saker falcon	*Falco cherrug*	Behavioural	102.0	Potier et al. [114]
Peregrine falcon	*Falco peregrinus*	Behavioural	124.5	Potier et al. [114]
Little owl	*Athene noctua*	ERG	50.0[a]	Porciatti et al. [107]
Short-eared owl	*Asio flammeus*	ERG	67.5	Bornschein and Tansley [115]
Great horned owl	*Bubo virginianus*	ERG	40.0[a]	Ault and House [116]

[a] When FFF continuously increased with luminance for some individuals, the highest FFF is given. ERG: Electroretinogram. Behavioural: dual choice tests between a steady and an intermittent stimulus.

11. Absolute sensitivity and its relation to diurnal/nocturnal hunting activity

Many of the features discussed so far influence the absolute sensitivity of raptor eyes. In diurnal species, specifically accipitriforms and falconiforms, the high temporal and spatial resolution, the filtering properties of the cone oil droplets, low rod densities and the absence of double cones and rods in the fovea reduce the potential to see well in dim light. By contrast, the low FFF of owls, together with their large corneal diameters, long rod outer segments and rod-dominated retinae, indicate that their vision is optimized for high sensitivity with good enough acuity in dim light. Unfortunately, absolute sensitivity has only been determined in a single owl species, the Tawny owl, whose eyes are only 2.5 times more sensitive than those of humans [117].

Some species of owls, however, are either diurnally active, for instance Barn owls and the Burrowing owl, or, like the Snowy owl, active in the far north, where there is no shortage of light at night during summer. In such bright light intensities, owls use cone-based vision and can discriminate colours, as demonstrated for the Tawny owl [118,119] and the Little owl [120].

Although a third of falconiform species and about 5% of accipitriforms also show some crepuscular or nocturnal activity [6], no study has determined their absolute sensitivity. Known adaptations to dim light activity include, for instance, relatively large eye size in Pygmy-falcons (genus *Polihierax*) and Forest-falcons (genus *Micrastur*), the loss of the SWS1 opsin in the Black-winged kite [76], and larger cones in the fovea in the Brown falcon [62]. The truly nocturnal Letter-winged kite (*Elanus scriptus*) has a larger eye, a larger pupil relative to axial length (thus, a smaller F-number) than the congeneric Black shouldered kite (*Elanus axillaris*) and other diurnal raptors [55], indications for a convergent evolution between *Elanus* kites and owls [121].

12. Future research directions

The fact that invasive investigations on large, charismatic and often rare raptors have always been uncommon and are even less usual now, is one reason for the relatively scarce knowledge on eye anatomy and visual physiology of birds of prey. While some general features are quite similar among birds, the foraging ecology of many raptors poses special demands and has led to the evolution of extremes such as the highest visual acuity in large eagles and vultures that seek for food at long distance and extremely high sensitivity in owls foraging by night. The comparison between the predominantly diurnal accipitriform, falconiform, cathartiform and cariamiform raptors on one side, and the mostly nocturnal owls, on the other side, has revealed some of the adaptations allowing for their performance. However, it has also shown large knowledge gaps, some of which could potentially be filled by behavioural experiments, specifically using captive, tame and trained birds in falconries (*e.g.* [122]), and non-invasive techniques such as OCT (Fig. 5; [46,59,123]), imaging with adaptive optics, and ultrasound.

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