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Selected ocular dimensions of three penguin species

Peter W. Hadden [a], Misha Vorobyev [b], Stephanie B. Cassidy [c], Akilesh Gokul [a], Samantha K. Simkin [a], Henry Tran [d], Charles N.J. McGhee [a], Jie Zhang [a]

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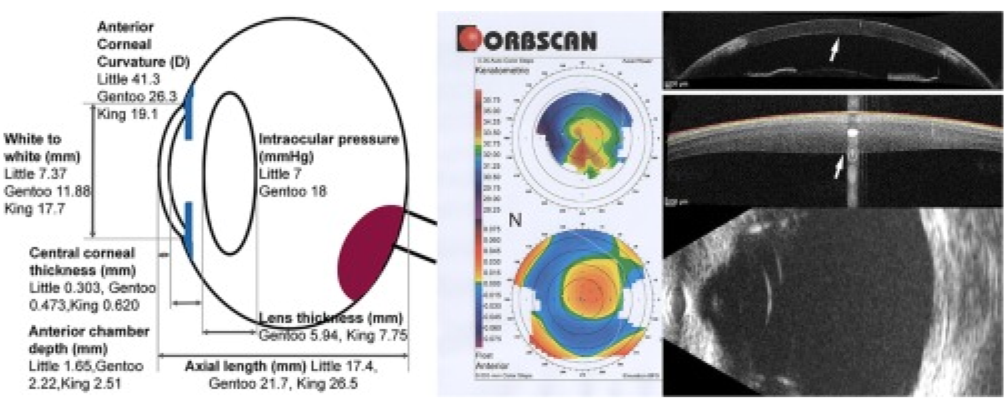
Highlights

- Smaller penguin species have smaller eyes.
- The power of the penguin cornea is inversely proportional to the size of the eye.
- Gentoo, king and little penguins are emmetropic in air.
- Gentoo penguins are emmetropic underwater.
- The little penguin eye gathers less light than do gentoo and king penguin eyes.

Abstract

Penguins (Spheniscidae) are a diverse clade of flightless, marine birds. Their eyes, likely a primary driver of behaviour, have been noted to have anatomic adaptations to their amphibious lifestyle. In particular, they have a relatively flat cornea, which would make the transition from a subaerial to a submarine environment require less accommodative effort. However, the ocular dimensions are not known for many penguin species, despite the diversity within the family, and their accommodative abilities have been the source of some dispute. In this study we undertook to establish the basic dimensions of the eye of the smallest, a mid-sized penguin and the second largest penguin. The power of the front surface of the cornea was inversely related to the size of both the eye and penguin, being 41.3 D in the little penguin (*Eudyptula minor*), a power greater than previously measured in any other penguin species, 26.3 D in the gentoo (*Pygoscelis papua*) and 19.1 D in the king penguin (*Aptenodytes patagonicus*). All other dimensions increased or decreased in line with the size of the eye. All penguins were able to achieve emmetropia in air. The gentoo appeared to be emmetropic underwater. A finding of central corneal thickening in some penguins may be artefactual. Calculations using the ocular dimensions demonstrated that the mean retinal illumination of an extended source of light in the little penguin eye is less than that of its larger, deeper-diving relatives.

Graphical abstract



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Keywords

Gentoo; King penguin; Little penguin; Vision; Cornea; Eye

1. Introduction

Penguins have an amphibious and flightless lifestyle unlike other birds, creating both opportunities and challenges for vision, which in birds is usually the primary driver of behaviour (Martin, 2017). Indeed, penguins may have a relatively underdeveloped sense of smell compared to many other birds (Bang & Cobb, 1968). It has long been recognised that penguin eyes have adaptations, such as a relatively flat cornea, to enable vision both under and above water (Howland and Sivak, 1984, Martin and Young, 1984, Martin, 1999, Sivak and Millodot, 1977, Sivak et al., 1987, Sivak, 1976). Other adaptations consistent with their ecological niche are also likely. For instance, foraging underwater requires the penguin to operate under conditions of low illumination (Martin, 2017, Zielinski, 2013). This has led in other animals to alterations in the shape of the eye, although neural methods of compensating for low light conditions are also important (Warrant, 1999). Moreover, penguins are a diverse clade, with widely different phyletic lines and variation in body size and morphology, and range from the equator to Antarctica, with some penguins diving to less than 100 m deep and others to several hundred metres (Baker et al., 2006, Cole et al., 2022, Croxall et al., 1988, Culik et al., 1996, Kooyman et al., 1992, Montague, 1985, Vargas et al., 2005, Vianna et al., 2020, Wienecke et al., 2007, Zusi, 1975). Thus, it is likely that there is significant variation within the family.

There is disagreement in the literature as to whether penguins are emmetropic on land and underwater. The suggestion that penguins are 'notoriously myopic' in air (Walls, 1942, p. 439) was supported by Martin and Young (1984) with regard to the Humboldt penguin (*Spheniscus humboldti*). However, other authors have found gentoo (*Pygoscelis papua*), Magellanic (*Spheniscus magellanicus*), rockhopper (probably southern rockhopper, as stated to be *Eudyptes crestatus*) and Humboldt penguins to be emmetropic or nearly so in both air and water (Howland and Sivak, 1984, Sivak et al., 1987). Similar studies have found the African penguin (*Spheniscus demersus*) to be slightly hyperopic underwater and emmetropic on land (Sivak, 1976) while gentoo, king and rockhopper penguins have been described elsewhere as being emmetropic or slightly myopic in air but significantly hyperopic underwater (Sivak & Millodot, 1977). A difference between post-mortem studies and those done *in vivo*, as well as an age effect, may explain at least some of this variation (Sivak et al., 1987).

A schematic eye has been constructed for the Humboldt penguin (Martin & Young, 1984) and in that study it was calculated to be myopic in air. Selected ocular dimensions of the Magellanic and king (*Aptenodytes patagonicus*) penguin eyes have also been reported (Martin, 1999, Suburo et al., 1988) and, in a recent electron microscopic study of the cornea of an Australian little penguin, the cornea was found to be 0.38 mm thick (Collin & Collin, 2021). Given the location of specimen collection and recent genetic studies, the latter is likely to be a representative of *Eudyptula novaehollandiae* (Banks, Mitchell, Waas, & Paterson, 2002, Grosser et al., 2017). The antero-posterior and transequatorial diameters of the eye of the New Zealand little penguin (*Eudyptula minor*, henceforth referred to more simply as the little penguin), gentoo and king penguins have also been measured using micro computerised tomography and were found to be 14 mm and 19 mm respectively in the little penguin, 21 mm and 30 mm in the gentoo penguin and 28 and 40 mm in the king penguin (Hadden et al., 2022). However, these results are but a limited selection of the ocular dimensions that are possible to measure. Furthermore, technological advances since the afore-mentioned studies, particularly in anterior segment optical coherence tomography (AS-OCT), ultrasound and corneal topography, have also increased our ability to measure the optical elements of an eye more accurately.

Here we aimed to measure as many optical elements as possible of the little, gentoo and king penguins and calculate the relative mean retinal illumination. We used both *in vivo* and ex vivo examination, the latter allowing us to utilize more advanced instrumentation and the two together allowing us to check the consistency of our findings and identify artefactual post-mortem changes. We were also interested in determining the accommodative ability of the penguin. It is not possible to use cadaveric tissue to determine the power of the lens, given that *in vivo* its shape alters. However, given that we knew the power of the other optical elements, we hoped to deduce this by using retinoscopy to determine the overall refractive states of the penguins both above and below water.

2. Material and methods

2.1. Animals and ethics

Permission was obtained for this study from the New Zealand Department of Conservation (permit numbers 70961-ROS and 68003-DOA, 28 November 2018, and 89983-DOA, 27 July 2021), Auckland Zoo and SEA LIFE (SL (G) – AR 001). All little penguins were originally recovered from the wild in the Auckland Region, New Zealand, but unable to be re-released due to a variety of physical disabilities not involving the eye. The exact age for these penguins was unknown, although all were adult birds. The gentoo and king penguins were spending or had spent their life in captivity at SEA LIFE Kelly Tarlton's Aquarium in Auckland, New Zealand and were descended from penguins living in South Georgia. The ARRIVE guidelines were followed, except that sex was unknown in some animals and penguins were not routinely weighed unless undergoing anaesthesia.

2.2. Ocular dimension measurements

Ocular dimensions were obtained from 6 adult little, 8 adult gentoo and 6 adult king penguins, as well as 1 gentoo penguin chick. Both eyes were measured where possible, except where a reliable result could not be expected due a traumatic post-mortem enucleation, as was the case for the right eyes of G6 and G7, or where the instrument could not obtain a reading. Demographic data, specimen preservation and the lens condition before examination are presented in Table 1, excluding those eyes examined solely in regard to pupil diameter (8 eyes of 4 adult gentoo penguins and 2 eyes of 1 adult king penguin). Most post-mortem eyes were examined within six hours of death, except two little penguin eyes (both from L6), which were only examined at 72 h. Both eyes of G5, one eye each of G6 and G7 and both eyes of K6 also underwent further examination at 36 h with instruments not available earlier. Pupil diameters in response to dark (mesopic) and light (photopic) conditions were measured in live penguins not included in Table 1 as they were not otherwise examined, including one little, eight gentoo and one king penguins. Of those penguins examined alive, the little penguins (L1, L2, L3 and L4) were undergoing general anaesthesia at Auckland Zoo for non-ocular reasons, predominantly beak trimming, while the gentoo (G1, G2 and 4 penguins which only underwent pupil examination) and king (1, pupil only) penguins had varying degrees of cataract and were being restrained at the aquarium to exclude other ocular pathology. In all cases the anaesthesia was a combination of midazolam and butorphanol for induction, followed by isofluorane by mask and then intubation. Flumazenil was used for reversal of anaesthesia.

Table 1. Demographic data of penguins used for ocular dimension measurements, excluding those used only for pupil measurement. In brackets are the names and / or identification numbers, where known, for each penguin. The age is in years except where noted. The exact ages of birds recovered from the wild were unknown, but all had passed their first molt and are listed as 'adult'. Fresh means the ocular examination was completed within 6 h of death, without being stored in any medium. The eyes of G5, G6 and G7 were placed in saline immediately after euthanasia and, following initial examination at 1.5 h, were then refrigerated for another 36 h in saline before being re-examined by instruments not available at the earlier time.

Penguin identification	Age at examination (years)	Sex and weight	Preservation prior to examination	Lens transparency
Little penguins (*Eudyptula minor*)				
L1 (Mako)	Approx. 13	Male, 1.13 kg	Alive	Clear
L2 (Marlin, A90018)	Approx. 13	Male, 0.89 kg	Alive	Clear
L3 (Manawa, B6008)	Adult, at least 3	Female, 0.86 kg	Alive	Clear
L4 (Kutai, B80519)	Adult	Female, 0.97 kg (missing left wing)	Alive	Clear
L5 (LP1, B80231)	Adult	Unknown	Fresh	Clear
L6 (LP2)	Adult	Male	72 h refrigeration	Clear
Gentoo penguins (*Pygoscelis papua*)				
G1 (Mean bird, G168)	26	Male	Alive	Mild nuclear cataract
G2 (Ken, G196)	26	Male	Alive	Mild nuclear cataract
G3 (Twinkle, G194)	26	Female	Fresh	Mild nuclear cataract
G4 ('38', G138)	24	Female	Fresh	Mild nuclear cataract
G5 (Stanley, G198)	26	Male	1.5 h in normal saline and 36 h after refrigeration	Mild nuclear cataract
G6 (Horse, G140)	26	Male	1.5 h in normal saline and 36 h after refrigeration	Mild nuclear cataract
G7 (Dennis, G144)	26	Male	1.5 h in normal saline and 36 h after refrigeration	Mild nuclear cataract
Gentoo penguin chick (*Pygoscelis papua*)				

Penguin identification	Age at examination (years)	Sex and weight	Preservation prior to examination	Lens transparency
GC1 (Goose, G120)	7 weeks	Unknown	Fresh	Clear
King penguins (*Aptenodytes patagonicus*)				
K1 (no name, K158)	33	Female	Fresh	Moderate nuclear and mild cortical cataract
K2 (Louise, K206)	23 months	Female	Fresh	Clear
K3 (Maggie, K155)	33	Female	Fresh	Mild nuclear cataract
K4 (Poncho, K120)	28	Male	Fresh	Mild nuclear cataract
K5 (no name, K208)	26	Male	Fresh	Mild nuclear cataract
K6 (Eskie, K055)	13	Female, 11 kg	Approximately 18 h post mortem	Clear

A variety of instruments were used to obtain ocular dimensions, influenced by the ease of access in relation to the time of penguin death and hampered by changing CoVid-19 restrictions. These included B-scan ultrasonography (Scanmate B, DGH Technology, Inc., Exton, Pennsylvannia), A-scan (OcuScan RP, Alcon Laboratories Inc., Fort Worth, Texas), photokeratoscopy (using a combination of a Bolor keratoscope, Spain and a Lumix DC Vario camera, Osaka, Japan), ultrasound pachymetry (Pachmate 2, DGH Technology, Inc., Exton, Pennsylvannia), callipers, ruler, applanation tonometry (Tono-Pen Avia handheld tonometer, Reichert Inc., Buffalo, New York), optical coherence tomography (OCT; Cirrus HD-OCT, Carl Zeiss Meditech Inc., Jena, Germany and REVO NX, OPTOPOL Technology Sp. z o.o., Zawierce, Poland) and keratometry: IOLMaster 700 (Carl Zeiss Meditech Inc., Jena, Germany), LENSTAR Optical Biometer (Haag-Streit, Köniz, Switzerland), Nidek OPD-Scan III (Nidek Co. ltd, Aichi, Japan), Pentacam AXL (OCULUS Optikgeräte GmbH, Wetzlar, Germany) and Orbscan II (Bausch and Lomb, Rochester, New York).

To calculate the anterior corneal curvature using photokeratoscopy, the image projected onto the cornea through the central 25 D lens of the illuminated keratoscope was photographed. The size of the object (O), being the illuminated concentric rings on the keratoscope, was measured using a ruler. The size of the image (I) was determined by comparing the relative size of the image visible on the photograph with the size of the eye visible on the photograph and scaled to a true measurement by comparing the latter with a photograph of the head taken with a ruler placed adjacent to the eye. Given the keratoscope had a 25 D central lens, when the camera was in focus for infinity the image would be 40 mm from the object (d). This distance was also checked using a ruler. The radius of curvature (r) was calculated using the formula $r=2\ d\ I\ /\ O$. On some occasions the anterior segment OCT was also unable to determine the power of one or other surface of the cornea or lens automatically. In those cases, the chord (c) and arc height (h) of the portion of cornea or lens visible on the scan were measured. The radius of curvature was calculated using the formula $r=h\ /\ 2+c^2\ /\ 8\ /\ h$. In both instances, to determine the dioptric power (D) from r the formula $D=337.5\ /\ r$ was used, 337.5 being the standard keratometric refractive index used by optical equipment. All distance measurements were done in millimetres (mm). Post-mortem eyes undergoing corneal topography were inflated to an intraocular pressure of approximately 15 mmHg (measured digitally by an experienced ophthalmologist, PWH) immediately prior to measurement.

2.3. Refraction and refractive indices

A variety of standard halogen spot retinoscopes and trial lenses were used to refract 14 eyes of gentoo and 11 eyes of king adult penguins while they were fully conscious, either at rest or being restrained to have their toenails cut. Retinoscopy was also attempted while the penguins were feeding underwater, through a flat vertical window at SEA LIFE Kelly Tarlton's Aquarium. This was difficult and only possible with the slower gentoo penguins. Following the example of other authors (Howland and Sivak, 1984, Sivak et al., 1987), the penguins were tempted with food to swim as close as possible and parallel to the window. Retinoscopy was then completed at approximately 50 cm from the eye (thus a+2 D working distance), through the glass; because the penguins were swimming very close to the wall the true working distance was very similar to the distance between the window and the retinoscope and could thus be measured. Lenses were held up to the wall to approximate the focus of the eye and the refraction was completed by an experienced retinoscopy user (SKS). The little penguins that were refracted in air included L1, L2, L3 and L4 referred to above, plus one extra (L7, Merlin B90018); all were anaesthetized as described above and then retinoscopy was performed in the usual manner. Refractive indices were measured using an icoe iPDA B1 digital refractometer (NINGBO ICOE COMMODITY CO., ltd, Ningbo, China) and an Abbe refractometer. To measure the refractive index of solid tissue using the icoe refractometer, the tissue in question was placed on the instrument so that it completely covered the glass prism; this required a large and intact section of tissue and we found it impossible to measure more local issue areas; in particular, we were unable to measure the refractive index of individual layers of the lens. As others have found (Matthiessen, 1882, English translation in Supplementary Material 1), measuring the refractive index of solid tissue using the Abbe refractometer is difficult and the critical borderline was blurred. We were only able to reliably measure the cornea using this latter instrument.

3. Results

3.1. Ocular dimensions

The ocular dimension findings are summarised in Table 2. Using these data, the results are summarised in the form of schematic eyes of an adult little penguin (Fig. 1), adult gentoo (Fig. 2) and adult king (Fig. 3) penguin. Where there was a choice of data between live and post-mortem eyes when drawing these eyes, we used data from the live animals. Failing that, we used the data from the largest number of cadaveric eyes. All raw data is available in the online open access repository https://doi.org/10.17608/k6.auckland.c.5844161.v1 ↗ (Digital Science, London, UK).

Table 2. Ocular dimensions in Spheniscidae, mean±standard deviation (sample size). These dimensions were obtained from the eyes of adult little penguins (*Eudyptula minor*), adult gentoo penguins (*Pygoscelis papua*), a 7-week gentoo penguin chick and adult king penguins (*Aptenodytes patagonicus*). Where no result was obtained, a dash (hyphen) is used.

Parameter	Instrument / method	Little penguin	Gentoo penguin	Gentoo chick	King penguin
Anterior corneal curvature (mm)	Keratoscopy (live)	8.28±1.04 (n=8)	12.0±2.8 (n=4)	–	–
Anterior corneal power in air (D)	Keratoscopy (live)	41.3±5.0 (n=8)	26.3±5.5 (n=4)[1]	–	–
	Nidek (post-mortem)	40.25±0 (n=2)	22.0±1.4 (n=4)	–	19.1±1.95 (n=4)
	IOLMaster (post-mortem)	41.25±1.41 (n=2)	–	33.80 (n=1)	–

Parameter	Instrument / method	Little penguin	Gentoo penguin	Gentoo chick	King penguin
	Pentacam (post-mortem)	–	22.9±3.0 (n=4)[2]	–	–
	Orbscan (post-mortem)	–	–	30.6 (n=1)	–
	Anterior segment OCT (post-mortem)	36.7 (n=1)	24.5±0.5 (n=4)[2]	–	–
Posterior corneal curvature (mm)	Anterior segment OCT (post-mortem)	10.69±2.03 (n=3) mm	−70±96 (n=4) 2, 3	8.1±0.8 (n=2)	−38±11 (n=2) [3]
Central corneal thickness (mm)	Ultrasound pachymetry (live)	0.303±0.042 (n=6)	0.473±0.027 (n=3)	–	–
	Ultrasound pachymetry (post-mortem)	–	–	–	0.605±0.033 (n=2)
	Anterior segment OCT (post-mortem)	0.478±0.058 (n=4)	0.816±0.130 (n=3)	0.541±0.3 (n=2)[4]	0.620±0.084 (n=4)
	Anterior segment OCT (post-mortem)[2]	–	0.870±0.054 (n=4)[2]	–	–
	IOLMaster (post-mortem)	–	–	0.867 (n=1)	–
	Lenstar (post-mortem)	–	0.600±0.092 (n=4)	–	–
Anterior chamber depth (mm)	A scan (live)	–	2.22±0.27 (n=3)	–	–
	Anterior segment OCT (post-mortem)	1.65±0.32 (n=3)	1.46±0.34 (n=4)[2]	2.07±0.43 (n=2)	2.51±0.21 (n=2)

Parameter	Instrument / method	Little penguin	Gentoo penguin	Gentoo chick	King penguin
Lens thickness (mm)	A scan (live)	–	5.94±0.51 (n=4)	–	–
	IOLMaster (post-mortem)	–	–	5.55 (n=1)	–
	Callipers (post-mortem)	4±0 (n=2)	7.14±0.21 (n=6)	–	7.75±1.98 (n=3)[5]
Transequatorial lens diameter (mm)	Callipers (post-mortem)	6±0 (n=2)	9.88±0.41 (n=6)	–	11.08±1.66 (n=3)[6]
Posterior lens to retina (mm)	A scan (live)	–	13.2±0.7 (n=3)	–	–
	B scan (live)	10.53±0.33 (n=6)	–	–	16.42±0.33 (n=6)
Anterior lens radius of curvature (mm)	Anterior segment OCT (post-mortem)	–	–	5.09±0.03 (n=2)	14±8 (n=2)
Axial length (mm)	B scan (live)	17.4±0.7 (n=8)	–	–	–
Axial length (mm)	A scan (live)	–	21.66±0.7 (n=4)	–	–
Axial length (mm)	Lenstar (post-mortem)	–	21.7±0.53 (n=4)	–	–
	IOLMaster (post-mortem)	–	–	19.14 (n=1)	–
Transequatorial eye diameter (mm)	Callipers (post-mortem)	21.5±0.7 (n=2)	30.34±0.36 (n=6)	=	37.3±1.2 (n=3)
Intraocular Pressure (mmHg)	Tono-Pen (live)	7±2 (n=8)	18±2 (n=4)	–	–
White to white diameter (mm)	Ruler (live)	7.37±0.16 (n=4)	11.88±0.25 (n=4)	–	–

Parameter	Instrument / method	Little penguin	Gentoo penguin	Gentoo chick	King penguin
	Callipers (post-mortem)	–	12.47±0.23 (n=4)	–	17.7±4.2 (n=3)
	IOL Master (post-mortem)	–	–	12.0 (n=1)	–
Pupil diameter mesopic (mm)[7]	Ruler (live)	3.5 (n=2)	6 (n=8)	–	6.5 (n=2)
Pupil diameter photopic (mm)[7]	Ruler (live)	1.5 (n=2)	2.5 (n=8)	–	3.5 (n=2)

Notes:

1

The four gentoo eyes had markedly different anterior corneal powers in air. Both eyes of G1 had an average anterior corneal power of 21.7 D while those of G2 had 30.8 D.

2

These examinations were performed 36h post-mortem.

3

The negative sign indicates a negative posterior corneal curvature; this was the case in all adult gentoo and in two of three king penguin eyes, the third being flat. Because a flat surface has an infinite radius of curvature, it was excluded from calculation of the mean.

4

There was a large difference between the central corneal thickness measurements in these two eyes using anterior segment OCT, as one had a central corneal thickness of 0.329mm and another 0.754mm.

5

One of these lenses had a dense nuclear cataract and was 10mm thick; the less cataractous lenses were thinner.

6

One lens was cataractous and had a transequatorial diameter of 13mm; the other two measured 10.25 and 10mm.

7

Individual numbers were not collected as pupil size constantly fluctuated. Instead, the reported numbers are representative pupil sizes under mesopic and photopic conditions for all the penguins combined.

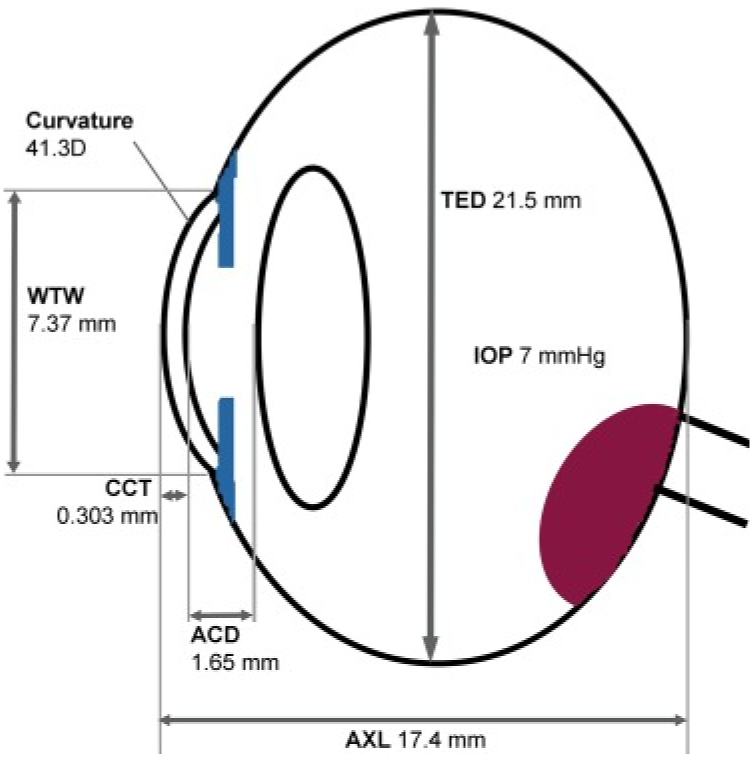

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Fig. 1. The eye of the adult little penguin (*Eudyptula minor*). Dimensions shown include the anterior corneal curvature (41.3 D), the central corneal thickness (CCT, 0.303 mm), the anterior chamber depth (ACD, 1.65 mm), the axial length (AL, 17.4 mm), the white-to-white measurement (WTW, 7.37 mm) and the transequatorial diameter (TED, 21.5 mm). The intraocular pressure is also displayed (IOP, 7 mmHg).

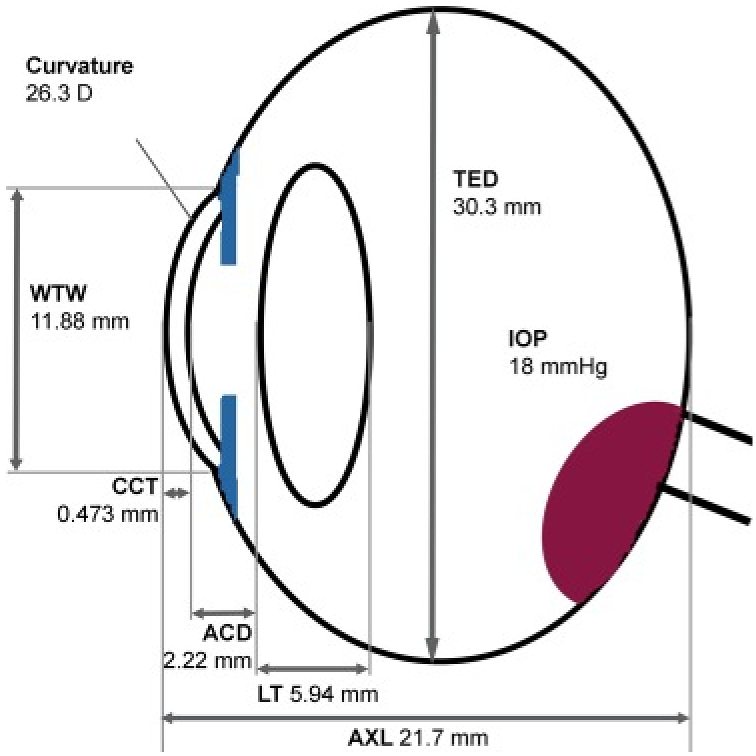

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Fig. 2. The eye of the adult gentoo penguin (*Pygoscelis papua*). Dimensions shown include the anterior corneal curvature (26.3 D), the central corneal thickness (CCT, 0.473 mm), the anterior chamber depth (ACD, 2.22 mm), the lens thickness (LT, 5.94 mm), the axial length (AXL, 21.7 mm), the white-to-white measurement (WTW, 11.88 mm) and the transequatorial diameter (TEQ, 30.3 mm). The intraocular pressure is also displayed (IOP, 18 mmHg).

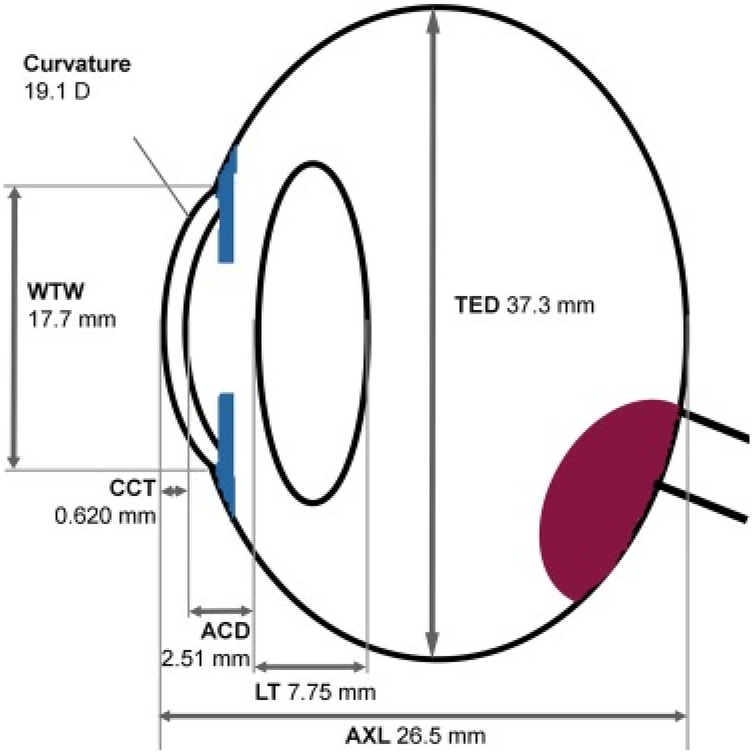

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Fig. 3. The eye of the adult king penguin (*Aptenodytes patagonicus*). Dimensions shown include the anterior corneal curvature (19.1 D), the central corneal thickness (CCT, 0.620 mm), the anterior chamber depth (ACD, 2.51 mm), the lens thickness (LT, 7.75 mm), the axial length (AXL, 26.5 mm), the white-to-white measurement (WTW, 17.7 mm) and the transequatorial diameter (TEQ, 37.3 mm).

3.2. Refraction and refractive indices

Eight little penguin eyes (L1, L2, L3 and L4) had a retinoscopic refraction of between 0 and +3 D under anaesthesia, while 14 gentoo and 11 king penguin eyes were within 1D of emmetropia when refracted roaming freely in the aquarium above water (Table 3). 14 gentoo penguin eyes were also able to be refracted underwater while swimming and were within 1D of emmetropia. However, when refracted near the start of anaesthesia five little penguin eyes (L1 both eyes, L2 right eye and L7 both eyes) recorded a refraction between −11 and −15 D; in three (L1 both eyes and L2 right eye), the refraction changed to between 0 and +3 D later in the procedure or when under anaesthesia on a different day. Similarly, when refracted while being physically restrained to have their toenails clipped, six gentoo eyes had an average refraction of −5.4 D (±1.0 D, standard deviation) and three king penguin eyes all had a refraction of −3 D. We suspect that the penguins were accommodating when we recorded the myopic refractions. Post-mortem autorefraction of eyes in air revealed an average refraction of −4.5 D for little penguins and −5.4 D for king penguins.

Table 3. Refractive state and refractive index of penguin eyes, mean±standard deviation (sample size) or range (sample size). Where no result was obtained, a dash (hyphen) is used.

Parameter	Instrument / method	Little penguin	Gentoo	King
Refraction above water (D)[1]	Retinoscopy (live, under deep anaesthesia)	Between 0 and +3 (n=8)	–	–
	Retinoscopy (live, unrestrained)	–	Between −1 and +1 (n=14)	Between −1 and +1 (n=11)
	Nidek OPD-Scan III (post-mortem)	−4.5±0.5 (n=2)	–	−5.4±0.9 (n=2)
	Retinoscopy (live, physically restrained)	–	−5.4±1.0 (n=6)	−3 (n=3)
	Retinoscopy (live, under light anaesthesia)	Between −15±3 (n=5)	–	–
Refraction under water (D)[1]	Retinoscopy (live, unrestrained)	–	Between −1 and +1 (n=14)	–
Refractive index of cornea	Digital refractometer	1.3690±0.0004 (n=2)	1.37±0.01 (n=4)	–
Refractive index of cornea	Abbe refractometer	1.3694 (n=1)	–	–
Refractive index of lens[2]	Digital refractometer	1.4075 (n=1)	1.39±0.01 (n=4)	–
Refractive index of vitreous	Digital refractometer	1.33635±0.0000007 (n=2)	1.3364±0.0005 (n=5)	–

Note:

1

Only the spherical equivalent is noted as it was too difficult to accurately measure cylinder.

2

This was measured at the surface of the lens; we were unable to measure individual layers of the lens.

3.3. Corneal asphericity

Topographical maps of the cornea were obtained from L6, G5, G6, G7, GC1, K2, K3 and K6. The Orbscan results summary of the left eye of GC1, the only chick in the series, showed significant peripheral corneal flattening (Fig. 4A). There seemed to be less difference between centre and periphery in the adult gentoo penguins (Fig. 4B, for example). There was also a tendency for adult little and king penguin corneas to have a higher power centrally than more peripherally (Fig. 5A and B), K6 being a possible exception (Fig. 5C), and some corneas were more irregular than others. Note that the axial topographical maps of Fig. 4 are not directly comparable to the instantaneous topography shown in Fig. 5; the former tends to reduce extremes.

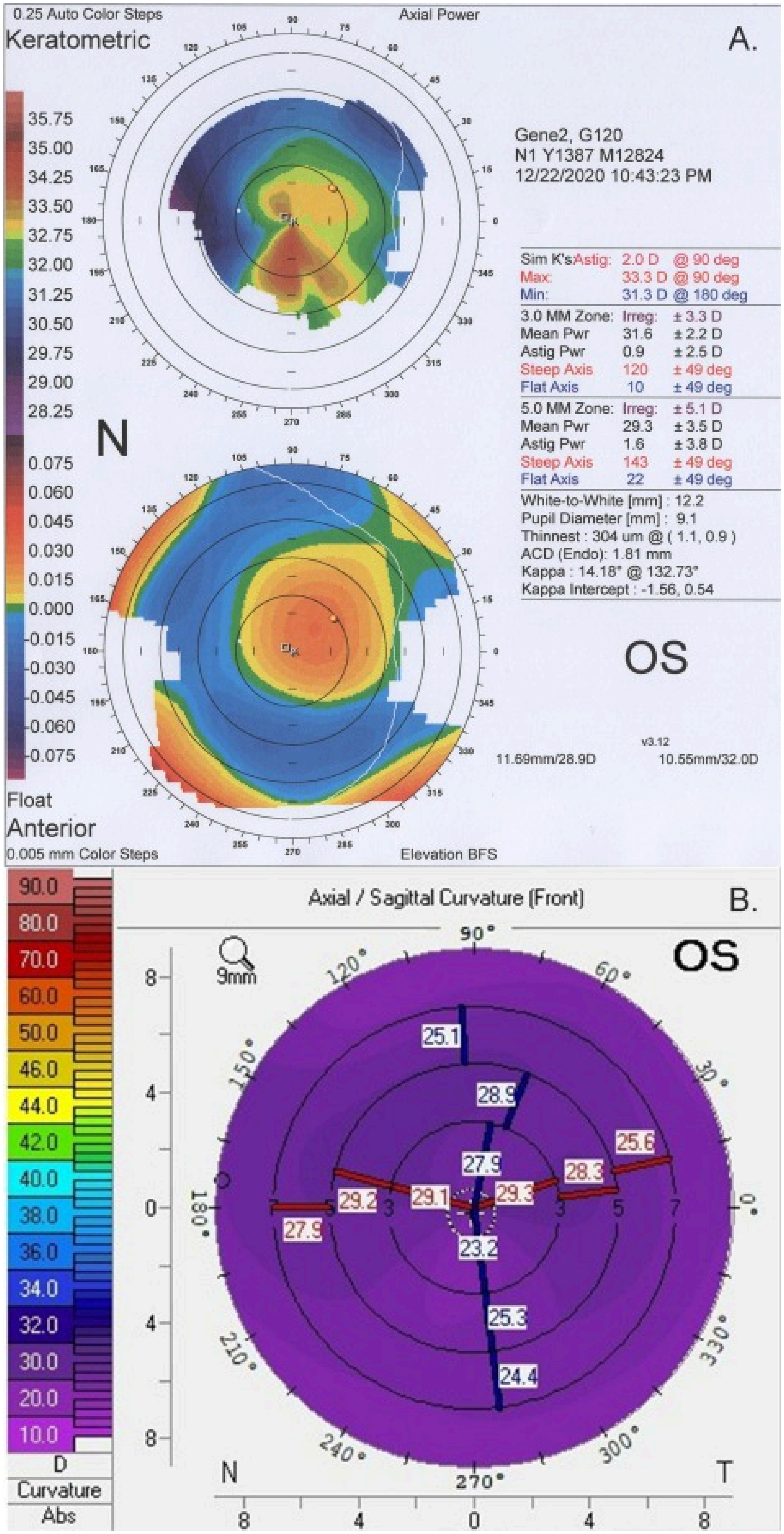
0.25 Auto Color Steps
Keratometric
Axial Power
A.
Gene2, G120
N1 Y1387 M12824
12/22/2020 10:43:23 PM
Sim K's Astig: 2.0 D @ 90 deg
Max: 33.3 D @ 90 deg
Min: 31.3 D @ 180 deg
3.0 MM Zone: Irreg: ± 3.3 D
Mean Pwr 31.6 ± 2.2 D
Astig Pwr 0.9 ± 2.5 D
Steep Axis 120 ± 49 deg
Flat Axis 10 ± 49 deg
5.0 MM Zone: Irreg: ± 5.1 D
Mean Pwr 29.3 ± 3.5 D
Astig Pwr 1.6 ± 3.8 D
Steep Axis 143 ± 49 deg
Flat Axis 22 ± 49 deg
White-to-White [mm] : 12.2
Pupil Diameter [mm] : 9.1
Thinnest : 304 um @ (1.1, 0.9)
ACD (Endo): 1.81 mm
Kappa : 14.18° @ 132.73°
Kappa Intercept : -1.56, 0.54
N
OS
v3.12
11.69mm/28.9D
10.55mm/32.0D
Float
Anterior
0.005 mm Color Steps
Elevation BFS
Axial / Sagittal Curvature (Front)
B.
OS
9mm
D
Curvature
Abs
N
T

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Fig. 4. Axial corneal topography of gentoo penguins (*Pygoscelis papua*). A. Orbscan image of the left cornea of gentoo penguin GC1, a 7-week-old chick, demonstrating a steeper central cornea with peripheral flattening. Warmer colours (red, orange) represent steeper areas and cooler colours (blue, green) represent flatter areas. B. 26-year-old gentoo penguin G6, left cornea, imaged with Oculus Pentacam AXL (axial map). Dioptric power is displayed; the difference between centre and periphery is less pronounced than in the gentoo chick.

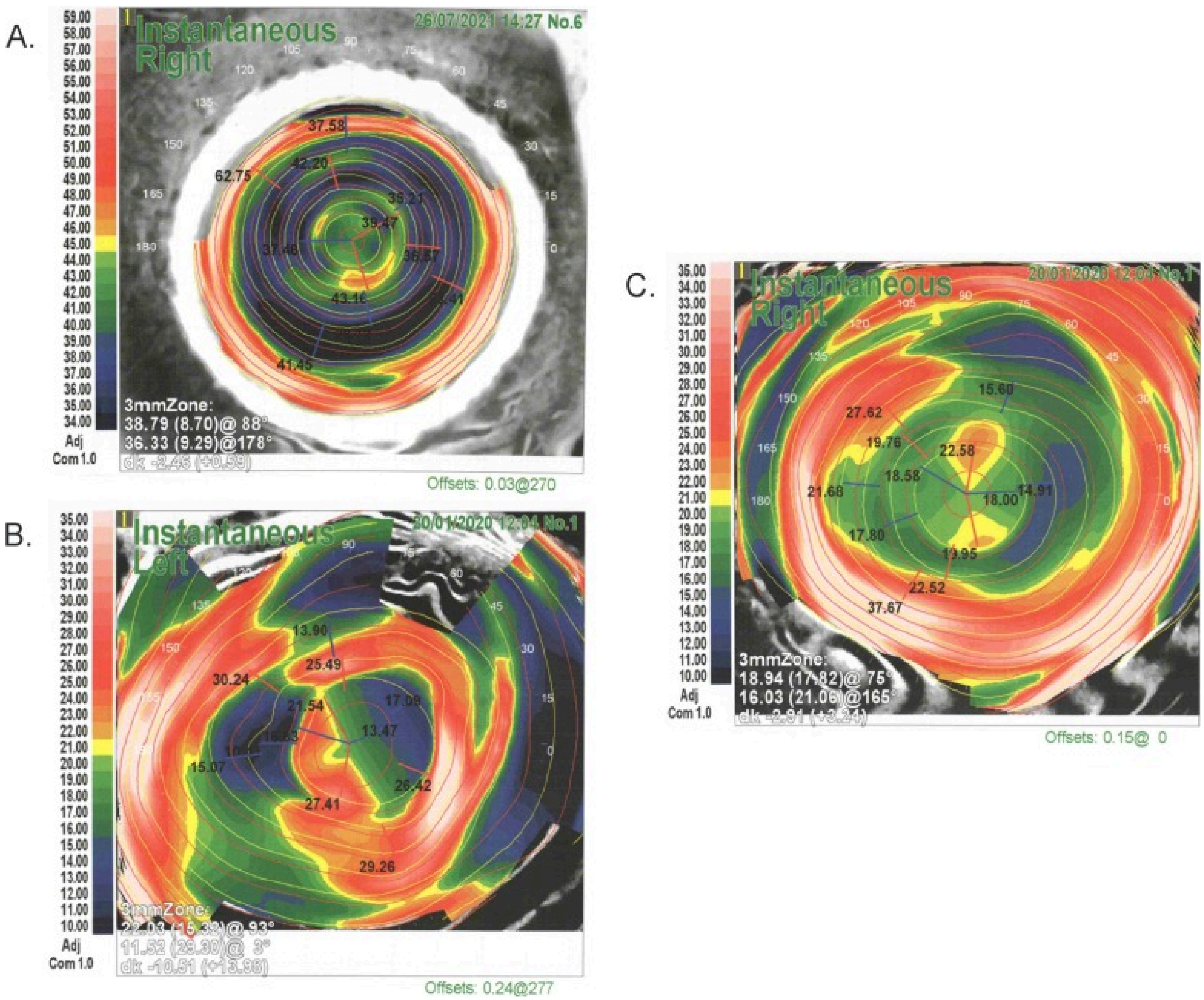

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Fig. 5. Instantaneous corneal topography using the Nidek OPD-Scan III, showing anterior corneal dioptric powers. A. Little penguin (*Eudyptula minor*) L6, right eye, B. King penguin

(*Aptenodytes patagonicus*) K2, left eye and C. King penguin K6, right eye. Warmer colours (red, orange) represent steeper areas and cooler colours (blue, green) represent flatter areas. Although variable, most adult little and king penguins seemed to have a steeper central cornea and a less steep mid-periphery.

4. Discussion

4.1. Corneal curvature

Photokeratoscopy has been used both in this study and others to measure the anterior corneal curvature of penguin eyes and the *in vivo* measurements presented here appear to align closely with those taken post-mortem, giving us more confidence of the validity of each technique. Howland and Sivak (1984) previously found an average anterior corneal power of 30.36 D in six rockhopper and 29.3 D in two Magellanic penguin eyes while Sivak et al. (1987) found a power of 31.25 D to 33.5 D in the Humboldt penguin. These penguins are slightly smaller than gentoo and much smaller than king penguins (Shirihai, 2007), which we found to have slightly less powerful corneas (26.3 D) and much less powerful corneas (19.1 D) respectively, but larger than the little penguin, which had a more powerful cornea (41.3 D). The shorter eye of the gentoo chick GC1 also had a more powerful cornea (30.6 to 33.8 D) than those of the adult gentoo penguins. Assuming similarly sized penguins have similarly shaped corneas, the afore-mentioned studies appear to have produced results consistent with this one and increasing corneal power appears to correlate with decreasing body size and decreasing axial length.

However, both our results and those mentioned above show significantly more powerful corneas than those published by Sivak and Millodot (1977), which were 17.0 to 18.2 D in rockhopper, 14.9 and 15.3 D in gentoo and 11.1 and 11.5 D in king penguins. Anterior corneal powers of 10.2 D in king penguins and 21–22 D (15–16mm radius of curvature) in African penguins (*Spheniscus demersus*) have also been reported (Martin, 1999, Sivak, 1976). All were measured using photokeratoscopy. Nevertheless, the trend for more powerful corneas in smaller penguins remains and, in this context, our results align with these studies also. A possible explanation for these variances is corneal accommodation, which in the pigeon is around 15 D (Gundlach, Chard, & Skahen, 1945). However, this ability has not been demonstrated in penguins. For ease of reference, other authors' results can be found summarized in Supplementary Material 2.

With regard to posterior corneal curvature, optical topography did not appear reliable because of a more intense reflection from the front surface of the cornea than is usual in human eyes; this was most obvious when using the Orbscan but also a problem when using the PentaCam. Further, the shape of the posterior corneal surface appeared to differ even between individuals of the same species, when examined by anterior segment OCT (Fig. 6). In particular, the posterior cornea of all four adult gentoo penguin eyes measured (G5 both eyes, G6 and G7 left eyes) had a negative posterior radius of curvature, as did those of two king penguin eyes (both eyes of K6). Conversely, one king penguin eye (K2 left eye) had a flat posterior cornea and all little penguins as well as the gentoo chick (GC1 both eyes) had posterior corneas with a positive radius of curvature. In those eyes where the posterior cornea was found to have a negative radius of curvature, it was only the central area that had this contour and the shape was due to thickening of the central cornea. A possible explanation is artefactual post-mortem swelling, perhaps exacerbated by the transportation of the cornea in saline in the case of the adult gentoo penguins or, in the case of K6, a delay between death and examination of 18 h. The latter hypothesis is supported by the observation that in general post-mortem eyes had a greater corneal thickness than those measured *in vivo*. Furthermore, the posterior half of these corneas appeared less dense on OCT (Fig. 6B), suggesting post-mortem entry of water into the posterior cornea due to endothelial pump failure, forcing the corneal lamellae apart and thus reducing keratocyte density, keratocytes being primarily responsible for the back scatter that OCT records. The greater swelling of the posterior cornea could reflect a difference between anterior and posterior proteoglycan molecules that link the corneal collagen fibrils and inhibit such swelling. Further investigation of corneal structure may be rewarding. Another potential explanation is thickening of the cornea with age as G5, G6 and G6 were 26 years old but GC1 only 7 weeks. Unfortunately, OCT was unable to be performed on live penguins because of an inability to restrain and position them adequately and an inability to transport the OCT scanner to the operating theatre for those that were anaesthetised and thus resolve this issue.

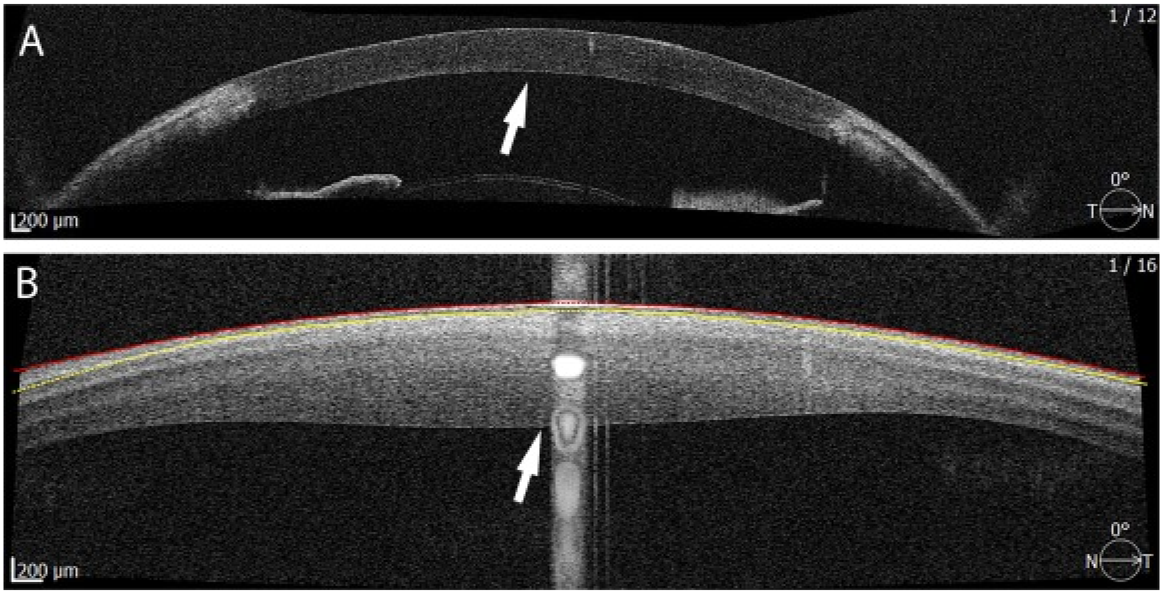

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Fig. 6. Variation in posterior corneal curvature. In some corneas, the posterior surface had a negative radius of curvature on AS-OCT, but this was variable. A. The left cornea of L5 (*Eudyptula minor*), demonstrating a posterior cornea with a positive radius of curvature (arrow). B. The left cornea of G5 (*Pygoscelis papua*), demonstrating the negative radius of curvature of its posterior corneal surface and a reduced density of back scatter in the OCT image of the posterior cornea (arrow), which may represent post-mortem swelling.

4.2. Light gathering ability

The design of the eye, in particular the entrance pupil and axial length, determines the f-number (f), where f=focal length / entrance pupil diameter. A comparison between the relative brightness of the retinal image of an extended source of light in vertebrate eyes can be made by examining the reciprocal of the square of the f number, i.e. $1/(\text{f-number})^2$. The focal length of the penguin eye can be determined using the following formula: focal length=0.71×axial length (Coimbra, Nolan, Collin, & Hart, 2012), based on work by Martin and Young (1984). Using the mesopic pupil measurements, underwater, where the entrance pupil is the same size as the real pupil, $1/(\text{f-number})^2$ was 0.08 in the little, 0.15 in the gentoo and 0.16 in the king penguin. Martin and Young (1984) data suggest a value of 0.15 in the Humboldt penguin. It would appear that the light gathering ability of the smaller and more shallow diving little penguin eye is significantly less than that of other penguins (Bethge et al., 1997, Gales et al., 1990). This is still significantly lower than the value of 0.59 in the eye of another low light forager, the tawny owl (*Strix aluco*), which forages in low light and has a minimum f-number of 1.3 (Martin, 2017). However, it is quite possible that the penguin pupil is able to dilate more than what we were able to observe in very dim illumination. Furthermore, in air the entrance pupil is magnified by the cornea, the power of which is almost completely lost underwater (Martin & Young, 1984). This results in an increase in entrance pupil size of 8.7% in the little, 7.6% in the gentoo and 6.4% in the king penguin, which in turn increases $1/(\text{f-number})^2$ by 18.3%, 15.8% and 13.1% in the respective species.

4.3. Axial length

We note that the published axial lengths of rockhopper (22.7 mm) and Magellanic (27.3 mm) penguin eyes is much longer than their body size would suggest, relative to birds in this study (Howland and Sivak, 1984, Shirihai, 2007). However, those studies measured the external antero-posterior diameter of the globe while we measured from the corneal surface to the inner retinal surface.

4.4. Variation with age

The gentoo chick appeared to have a steeper cornea than the adults, as well as a shorter eye. This would be in keeping with the possibility of further growth yet to come, as gentoo penguins have obtained only approximately 80% of adult mass at 7 weeks (Reilly & Kerle, 1981). Age differences may also affect comparisons between other live and dead eyes in this study, as the latter were obtained from specimens generally euthanised at the end of their lifespan.

4.5. Refractive state and accommodative ability

Our finding that penguins are emmetropic or close to it above water is consistent with those of Howland and Sivak, 1984, Sivak et al., 1987. Even the finding of only mild myopia in cadaveric eyes refutes the suggestion that penguins are ‘notoriously myopic’ (Walls, 1942) in air. We could only confidently determine the refractive status of the gentoo penguin underwater. However, this study’s finding of underwater emmetropia is consistent with the result of other authors (Howland and Sivak, 1984, Sivak et al., 1987) when examining gentoo, Magellanic, Humboldt and southern rockhopper penguins. Underwater emmetropia would seem logical, given that penguins forage when diving and presumably therefore their ocular anatomy would be optimised for that environment. There was an earlier, contrary study involving one of the same authors (Sivak) which found three species of penguins to be hyperopic underwater (Sivak & Millodot, 1977). However, Sivak appears to have retracted that finding to some degree as a later paper (Howland & Sivak, 1984) referred to the 1977 findings as preliminary. He also noted that, rather than refracting the penguins while swimming freely in the aquarium, a more natural environment and the approach we copied, in the 1977 study a water bath was held over the eye and the eye refracted through that. This clearly artificial environment may have caused misleading accommodation, similar to the myopia we found when refracting restrained penguins. Given the diversity of penguins examined over these studies, we think it is likely that other penguins are emmetropic under both conditions also.

If penguins are emmetropic on both land and underwater, their accommodative ability must be impressive. Assuming an index of refraction of seawater of 1.336, the vergence of light entering the crystalline lens of a little penguin with the eye in air is 33.71 D. However, with the eye in seawater the vergence entering the crystalline lens is only 0.78 D. Therefore, if the little penguin is to be emmetropic in air and when diving, the eye must accommodate by 32.93 D. A similar calculation for the gentoo penguin finds entering vergences of 23.73 D in air and 2.84 D in seawater, with an accommodative requirement of 20.89 D. Thus the smaller the penguin the greater the accommodative effort required when transitioning from air to water, given their steeper corneas and assuming emmetropia in both environments. We did observe 11 D to 15 D of accommodation in little penguins; however, this is insufficient to achieve emmetropia in both conditions. Investigation of the underwater refractive status and the mechanism of accommodation in the smaller penguins, for instance to determine if the lens moves anteriorly within the eye while accommodating, may be rewarding given that, unless they have other means of accommodating, they must possess a range of lenticular accommodation only exceeded in Aves by diving birds (Sivak, Hildebrand, & Lebert, 1985).

4.6. Spherical aberration and corneal asphericity

The average human cornea is steeper in the centre than in the periphery to reduce positive spherical aberration. The residual positive spherical aberration is, in teenage humans, compensated for by the negative spherical aberration of the lens (Holladay, 2006). The penguin cornea also tends be steeper in the centre and flatter in the periphery.

4.7. Refractive indices

The refractive indices of corneas in various vertebrates were summarised by Sivak (1976), who noted that all were between 1.35 and 1.38 except the pigeon, which he quoted at 1.337, using data from Gundlach et al. (1945). Martin and Young (1984) used a value of 1.376 for the Humboldt penguin cornea, based on these data, 1.334 for the aqueous and vitreous and 1.336 for seawater. This study's result of 1.371 for the gentoo and 1.369 for little penguin cornea is consistent with Sivak (1976) and our reading of the paper by Gundlach et al. (1945) is that it was the combined refractive index of the cornea and vitreous that they estimated to be 1.334 and that the cornea was not measured separately.

The lenticular refractive indices that we measured (1.37 to 1.4155) are very close to the range of 1.400 to 1.45 found by Gundlach et al. (1945) and Chard and Gundlach (1938). Unfortunately, because of the limitations of our instrumentation and expertise this study was unable to determine the presence or absence of a gradient of refractive index in the lens, which is common in marine animals; rather, we were only able to determine the index of refraction at the surface of the lens (Matthiessen, 1882, Schaeffel et al., 1988). Perhaps other refractometers, such as the older ones mentioned by Matthiessen (1882), may be more useful in this regard. The vitreous has a refractive index (1.3364) very similar to that of water and similar to that used by Martin and Young (1984), as expected due to its predominantly aqueous nature.

In summary, our measurements of refractive indices demonstrate that previously assumed values based on other animals can be applied to penguins also, noting the limitations of our study in regard to the crystalline lens.

5. Conclusions

To achieve useful vison in both air and water, most penguins have relatively flat corneas. However, with decreasing body size the eye also becomes smaller and the corneal curvature increases. Assuming all penguins are emmetropic both underwater and above, smaller penguins must possess a greater amplitude of accommodation than their larger relatives; more research in this area would be rewarding as would closer examination of the structure and variation in refractive index across the lens. The little penguin eye also appears to have a lesser light gathering ability than other penguins, but it does not forage as deeply and thus may not require as low a visual threshold as the others.

CRediT authorship contribution statement

Peter W. Hadden: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft. **Misha Vorobyev:** Investigation, Resources, Validation. **Stephanie B. Cassidy:** Investigation. **Akilesh Gokul:** Formal analysis, Investigation. **Samantha K. Simkin:** Investigation, Writing – review & editing. **Henry Tran:** Investigation. **Charles N.J. McGhee:** Funding acquisition, Resources, Supervision. **Jie Zhang:** Formal analysis, Project administration, Resources, Software, Supervision, Visualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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The following are the Supplementary data to this article:

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Supplementary Data 1.

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Supplementary Data 2.

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Data availability

The raw data that support the findings of this study, including anterior segment OCT, keratoscopy images, ultrasonography, pupil videos and corneal topography are available in the online open access repository https://doi.org/10.17608/k6.auckland.c.5844161.v1 (Digital Science, London, UK).

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