

Corneal power and underwater accommodation in great cormorants (*Phalacrocorax carbo sinensis*)

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Summary

In great cormorants (*Phalacrocorax carbo sinensis*), corneal refractive powers, determined by photokeratometry, ranged between 52.1 diopters (52.1D) and 63.2D. Photorefractive reflexes, determined by infrared video photorefractometry, indicated that in voluntary dives the cormorants accommodate within 40–80 ms of submergence and with myopic focusing relative to the photorefractor attained when prey was approximately one bill length from the plane of the eye. Underwater, the pupils were not constricted and retained diameters similar

to those in air. These results support previously reported capacities of lenticular changes in amphibious birds yet do not fully correspond with earlier reports in terms of the coupling of iris constriction with accommodation, and time course.

Key words: keratometry, IR photorefractometry, lens, cornea, accommodation, refractive power, amphibious vision, great cormorant, *Phalacrocorax carbo sinensis*.

Introduction

The quality of an image formed on a vertebrate's retina is largely determined by the cornea and the lens. In air, the cornea is the principal refracting agent of light rays and is responsible for approximately two-thirds of the refractive power of the eye, which, in humans, amounts to approximately 40 diopters (40D). This is because the cornea is bordered on its inner surface by the aqueous humor, with a refractive index of 1.33, and on its outer surface by air, with a refractive index of 1.0. The cornea of birds plays an important role in accommodation (Schaeffel and Howland, 1987; Glasser et al., 1994). In the chicken *Gallus gallus*, changes in corneal curvature account for up to 9D of the total 15–17D of accommodation (Schaeffel and Howland, 1987). The focusing power of the cornea in air is a function of its curvature, and corneal accommodation is brought about by curvature changes: the more curved it is, the greater its power (Howland et al., 1997).

The refractive power of the cornea underwater is virtually lost, as the media bathing its inner and outer surfaces (the aqueous humor and water, respectively) are of similar refractive indices. In a submerged eye, the lens becomes the sole agent for accommodative adjustments and must provide for the refractive power lost by the cornea if image quality is to be retained (Fernald, 1990; Land, 1990; but see Pettigrew et al., 2000). The lenses of fish (Fernald, 1990), amphibians (Mathis et al., 1988), penguins (Sivak, 1980) and seals (Sivak et al., 1989) tend to be spherical with an internal gradient of refractive indices. This allows for the continuous refraction of light within the lens itself and not merely at its surfaces

(Fernald, 1990; Sivak et al., 1989). These lenses exhibit a high level of correction for spherical aberrations (Fernald, 1990; Land, 1990; Sivak and Millodot, 1977).

In all vertebrate classes, there are species that perform visually guided motor tasks in both air and water. Eyes that are better adapted for terrestrial vision and are emmetropic (i.e. in focus) in air tend to be hyperopic (i.e. far sighted) underwater, while eyes better adapted for aquatic vision and are emmetropic in water will tend to be myopic (i.e. near sighted) in air. If retinal image is to remain sharp in both media, the eye must cope with large changes in external refractive indices (Martin, 1998; Sivak and Millodot, 1977; Howland et al., 1997; Howland and Sivak, 1984; Land, 1990; Fleishman et al., 1988; Glasser and Howland, 1996).

The corneas of penguins (Sphenisciformes) and albatrosses (Procelariiformes) are relatively flattened and have refractive powers lower than those of avian species of comparable eye size (Tables 3, 4). Such corneas suffer relatively little loss of power when submerged. Penguins, with corneal refractive powers of 11–30D (Sivak and Millodot, 1977; Howland and Sivak, 1984) are emmetropic in air and slightly hyperopic in water, which is well within the compensatory power of the lens (Sivak, 1976; Sivak et al., 1987; Howland and Sivak, 1984; Table 3). Seals have flattened corneas and, in common with penguins, make use of spherical lenses (Sivak et al., 1989).

Several other bird species that are pursuit-divers have strongly curved corneas. Such corneas have a high refractive power in air, and, indeed, pronounced capacities for lenticular

accommodation are observed in these species, indicating their capacity to compensate for corneal loss of power during dives. Accommodation in these species involves considerable changes in lens curvature and is associated with highly developed muscular mechanisms. In his pioneering studies, Hess (1909, 1913; cited in Glasser and Howland, 1996) demonstrated that, in cormorants (*Phalacrocorax* sp.), the lens, when stimulated electrically, undergoes pronounced changes in shape. The changes result in the lens being literally squeezed into, and partially through, the rigid iris by the ciliary muscle. The front surface of the now strongly curved lens produces a region of high refractive power ($>60D$). Subsequent studies have verified the extent of lenticular accommodation (e.g. Sivak et al., 1977; Levy and Sivak, 1980; Table 3), although there is still no agreement as to the precise muscular mechanisms involved.

Two important aspects have been left open in studies of lenticular capacities in pursuit-diving birds. First, a prevailing assumption to date is that, when diving, pursuit divers such as cormorants and mergansers (*Mergus* spp.) keep the retinal image sharply focused. However, this assumption has not been verified experimentally to date, while examples from other vertebrate groups indicate that pursuit and capture of fish is not necessarily coupled with high visual acuity. Thus, while otters (*Amblonyx cinerea cinerea*; Schusterman and Barrett, 1973; Balliet and Schusterman, 1971) and sea lions (*Zalophus californianus*; Schusterman and Balliet, 1970) retain similar grating acuity in air and in water, crocodiles (including *Gavialis*, which feed exclusively on fish) do not accommodate underwater (Fleishman et al., 1988), implying that crocodiles can manage with blurred images.

The second aspect relates to methods of experimentation on which conclusions on accommodation have been drawn. In most experiments, drugs or electrical stimulation were employed to elicit accommodation, or conditions of submergence were achieved by forcibly holding the birds' head underwater (e.g. Goodge, 1960; Sivak et al., 1977; Levy and Sivak, 1980; Table 3). To the best of our knowledge, states of accommodation during voluntary dives of birds have been recorded, to date, in

penguins only (Howland and Sivak, 1984; Sivak et al., 1987) and not in bird species that are said to have curved corneas and may employ pronounced lenticular accommodation.

In the present study, we aimed to determine, in great cormorant, *P. carbo sinensis*, (1) the refractive power of the cornea in air, and thus the extent of compensatory power required by the lens upon submergence, and (2) the capacity to accommodate and the refractive range when freely diving.

Materials and methods

Seven great cormorants (*Phalacrocorax carbo sinensis* L.; Cramp and Simmons, 1977) were tested for underwater accommodation (infrared photorefractometry), and five of these seven birds were tested for corneal curvature (photokeratometry). The birds were hand-reared and kept in a large outdoor aviary in the Hula Valley, Israel. They were fed on live and frozen fish and dived regularly for food in a large pool. The birds' age, sex and mass at the time of testing are provided in Table 1.

Photokeratometry

The photokeratometer used to determine corneal curvature was that described by Howland and Sayles (1985; also Howland et al., 1997). It consisted of a 35 mm Nikon SLR camera, with an f/1.2, 55 mm Nikkor lens mounted on a 31 mm extension tube, and operated at full aperture to minimize depth of field. Eight light sources (the tips of fiberoptic light guides, 1.5 mm diameter) were embedded in an aluminum ring, 75 mm in diameter, at the radii of a 67.5 mm circle around the optic axis, and the ring was mounted on the camera's objective lens. The proximal tips of the light guides were held in a bundle directly in front of an electronic flash.

For calibration, we used a set of 10 steel ball bearings of various diameters. Each ball was measured to the nearest 0.05 mm using vernier calipers, and its photograph (Kodachrome/Ektachrome 100/200 ASA) was taken with the photokeratometer mounted on a tripod. The focus of the camera lens was set at infinity, yet, because of the extension

Table 1. Corneal radii and corresponding refractive power

Bird*	Age (years)	Mass (kg)	Mean right eye corneal radius (mm)	Mean right eye corneal power (D)	Mean left eye corneal radius (mm)	Mean left eye corneal power (D)
F1	1	1.39	5.51	60.6	5.40	61.8
F2	1	1.63	5.87	56.9	5.92	56.4
F3	4	1.66	5.85	57.1	5.89	56.7
M1	4	2.40	6.31	52.9	6.67	50.1
M2	3	2.10	6.47	51.6	6.15	54.3
M3	5	1.95	—	—	—	—
M4	4	2.26	—	—	—	—

Corneal radius is provided as the mean of four measurements at 0°, 40°, 90° and 135° for the two slides used. M3 and M4 were tested for infrared photorefractometry only.

*F denotes female, M denotes male.

tubes, the actual focus was at 150 mm. In taking the photographs, the camera-to-ball distance was adjusted for the sharpest image. For each ball, the distances between opposite reflections of the eight keratometric reflection points were determined with a measuring microscope accurate to 1.0 μm . This resulted in four measurements along the 0°, 45°, 90° and 135° meridians. The mean of the four measurements was calculated and we then regressed the ball bearing diameters against the mean reflection distances measured on the film plane. We used this regression equation to estimate the corneal radii (corresponding to half of the diameters of the calibration ball bearings). To determine the dioptric power, F , of a cornea (measured in diopters), the following equation was used: $F=337.5/R$, where R is the corneal radius (measured in mm). This equation expresses the power of the human cornea as a function of the radius of its first surface (Borish, 1995) and is frequently applied in animal work.

The bird to be tested was held by one investigator, while another investigator photographed each of the bird's eyes with the hand-held photokeratoscope. The room was lit by two 60 W incandescent bulbs, positioned 2.5 m above the bird. In taking the photographs, the camera-to-bird distance was adjusted for the sharpest image. Each eye of each of the five cormorants was photographed 12 times. Pronounced eye movements and rapid flicking of the nictitating membrane resulted in a proportion of the slides being unsuitable for analysis. For each eye of each bird, the two slides that provided the sharpest and best-centered images of the photokeratometric light reflections were used for extracting the values of the distances between opposite reflections along the four meridians.

Infrared photorefractions

Photoretinoscopy was performed on the cormorants to measure their natural accommodation with the use of an infrared (IR) video photoretoscope (Fig. 1). The principles underlying the retinoscope are detailed elsewhere (Schaeffel et al., 1987). In brief, the IR retinoscope is based on a light source adjacent, and eccentric, to a video-camera lens' axis that projects light rays parallel to the camera's axis and records the reflection from the fundus. IR is used to minimize disturbance to the animals. The reflected light appears as a crescent in the pupil, and the position of the reflex indicates the sign of the defocus relative to the camera. In hyperopia, the reflex appears at the top of the pupil, while in myopia the reflex appears at the bottom of the pupil. The amount of defocus (D) may be obtained from the size of the reflex: $D=E/(2 \times A \times DF \times R)$, where E is the eccentricity of the light source, A is the distance of the camera to the eye, DF is the dark fraction in the pupil and R is the pupil radius (all dimensions in meters). To improve the precision of the measurements, light sources at five different eccentricities are employed in a row, consecutively providing five different crescents. Due to the high

mobility of the birds' head and eyes, no attempt was made to verify the amount of defocus by the use of correction lenses. Filming was conducted when the bird was 1.2–1.4 m from the camera lens, and the horizontal distance of the eye to the glass wall was approximately 5 cm. This provides an optical distance (distance in air + distance in water/1.33) of approximately 1.0 m.

Seven cormorants were tested over two consecutive days (Table 1). A single bird was allowed into the test room from its home cage and was encouraged to climb a short sloping gangway, leading to a test aquarium. The room was lit by four 100 W lamps and by indirect daylight from the open door. The aquarium (80 cm \times 40 cm \times 50 cm; length \times width \times height) was kept three-quarters full of water, and the bird could perch comfortably on its narrow side. One investigator then held a small fish (*Tilapia* sp. or carp *Cyprinus carpio*) at the side farthest from the bird and moved it to attract the bird's attention. He then dipped the fish and kept it underwater. The bird would submerge its head, search for the fish and capture it. Often, the fish was held against the outside of the aquarium glass wall, and, if the bird attempted to capture it from within, it was rewarded with a fish. The cormorants were acquainted with this procedure and were continuously rewarded for climbing the gangway and searching for fish in the experimental aquarium. During the week preceding the tests, they were fed daily in this manner.

As the cormorant climbed the gangway, the second investigator, positioned so as to view the aquarium's long axis and to be level with the water surface, filmed the bird. Filming was with the video camera held by hand, with the filming axis perpendicular to the plane of approach of the bird. Filming was continuous and conducted for as long as the bird searched for fish. The termination of a test session was when the bird left the aquarium and attempted to get back to the home cage.

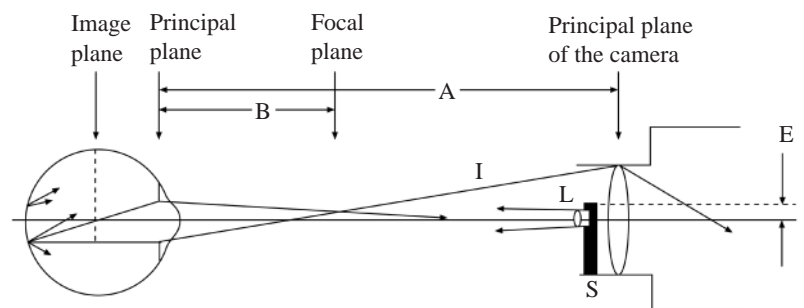


Fig. 1. Scheme of the optics of the infrared (IR) photoretoscope used in this study (based on Schaeffel et al., 1987). L, light source; S, black metal shield covering the lower half of the camera's lens; E, eccentricity (the distance of the light source from the upper margin of the black shield); I, the highest ray above the optical axis; A, the distance from the eye to the camera. Here, in a myopic eye (focal plane at B), a real image of the light source is created at the image plane, in front of the retina, and a blurred spot appears on the retina. Reflected light entering the pupil from the back will refocus in the focal plane of the eye (B) in front of the camera and subsequently diverge. Due to the shield, only rays emerging from the bottom part of the pupil will be detected by the unvignetted part of the aperture.

Video films (Sony 8mm) were digitized, and selected sequences were captured using Adobe Premier 6. From these sequences, the states of accommodation were determined.

Results

Photokeratometry

For each eye of each of the five cormorants, 2–3 photographs (with sharp light reflections and that were well centred) were used (Fig. 2). Corneal radii, obtained from the photographs, ranged from 5.4 mm to 6.6 mm. These radii correspond to corneal powers of approximately 62 D and 50 D, respectively (Table 1). No astigmatism was detected, and the refractive power of the females' corneas was higher than that of the males'. Although it cannot be statistically verified, this phenomenon is most probably related to body size rather than gender.

Photorefraction

All cormorants readily climbed onto the side of the test aquarium and took fish from the hand, both in air and underwater. They searched for fish underwater and attempted to capture them, even when the fish were presented beyond the aquarium's glass wall. Approximately 300 sequences of accommodation footage were acquired for the five cormorants tested for both air and water.

Photorefraction in air

In most recorded sequences, the eyes appeared to be in a state of hyperopia, while emmetropia and myopia were observed less frequently. An example of a state of myopia, with a bird holding a fish halfway down its bill immediately prior to swallowing, is depicted in Fig. 3B. Mean pupil diameter in air during myopia and hyperopia did not differ

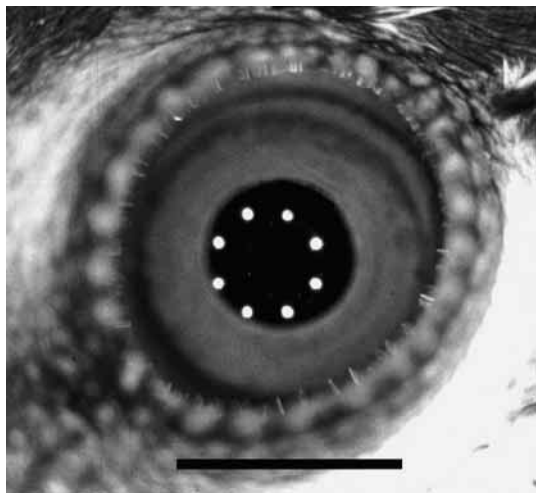


Fig. 2. Photokeratometry. The light points are the reflection off a cormorant's cornea of the eight light sources in the photokeratometer ring. The distance between opposite points of reflection is a measure of the corneal radius of curvature. Scale bar, 6 mm.

(9.9 ± 0.9 mm and 9.7 ± 1.1 mm, respectively). Mean refractive states ranged from -0.44 D to $+0.45$ D (Table 2).

Photorefraction in water

The eyes appeared to be focused hyperopically relative to the camera, while emmetropia and myopia were observed less frequently. Mean pupil diameter did not differ between myopia

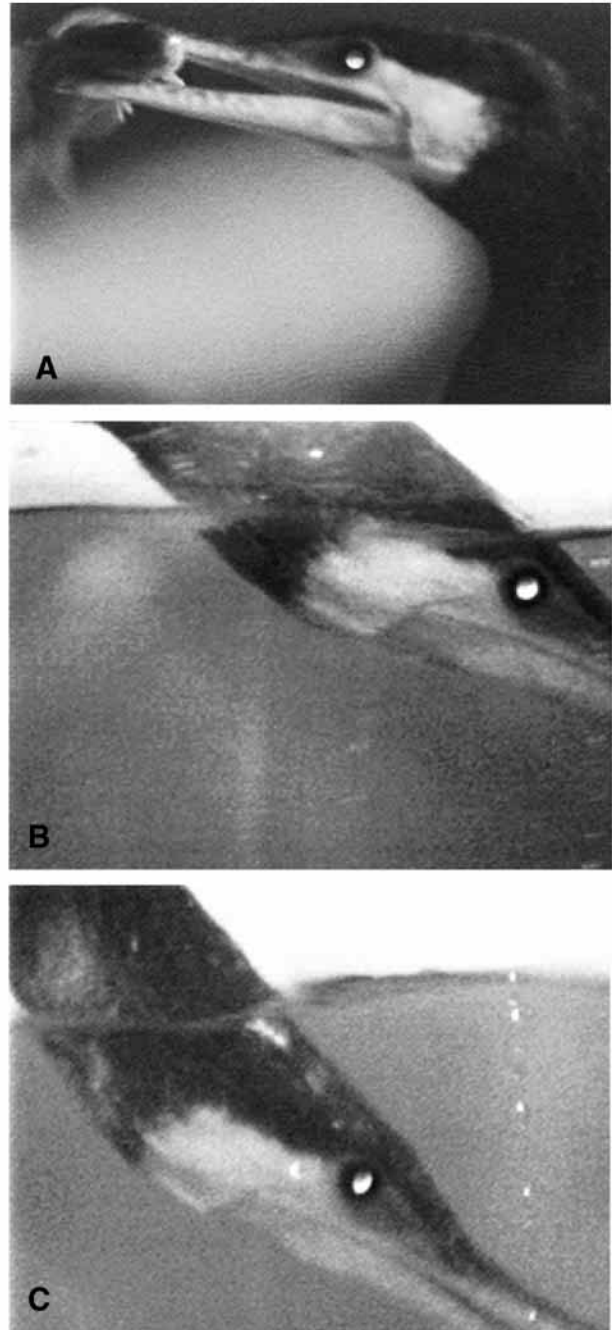


Fig. 3. (A) A cormorant holding a fish in its bill. The reflected infrared light crescent at the bottom of the pupil indicates a state of myopia. (B,C) States of myopia (light crescent at the bottom of the pupil) observed underwater during capture attempts by two individuals.

Table 2. States of accommodation and pupil size in cormorants in air and in water

	Air		Water	
	Hyperopia (10)	Myopia (10)	Hyperopia (6)	Myopia (14)
Refractive state (D)				
Mean	+0.45	-0.44	+0.50	-0.56
Range	+1.00 to +0.11	-0.89 to -0.14	+0.89 to +0.25	-1.79 to -0.26
s.d.	0.33	0.07	+0.22	0.41
Pupil diameter (mm)				
Mean	9.70	9.90	8.86	8.71
Range	8-11	9-12	8-10	-
s.d.	1.06	0.88	0.69	2.34

Numbers in parentheses indicate the total number of video frames analyzed for the seven birds (1-3 frames per bird).

and hyperopia (8.7 ± 2.3 mm and 8.9 ± 0.7 mm, respectively). Mean refractive states ranged from -0.56 D to $+0.50$ D (Table 2). Most sequences of a state of myopia occurred when the target (fish) was close to the plane of the eye, one to two bill lengths (approximately 6-12 cm) away (Fig. 3B,C).

Discussion

We have found that the corneas in great cormorants are curved and may provide up to 62 D of refractive power in air. We have further demonstrated that, while freely submerging their head and searching for underwater prey, the cormorants were well accommodated and could reach approximately -2 D in a state of myopia, relative to the camera at an optical distance of 1.00 m, for example, when focusing on a fish close to the plane of the eye. Accommodation achieved by the great cormorants thus exceeded 64 D, with transitions between states of accommodation being frequent and rapid. The double crested cormorant *Phalacrocorax auritus* was also found to be emmetropic in air and in water (Sivak et al., 1977). Because double crested cormorants are similar in size or smaller than great cormorants, it is expected that they would exhibit a corneal refractive power greater than 60 D, yet the mean corneal refractive power obtained was approximately 34 D only (table 2 in Sivak et al., 1977).

The demanding nature of amphibious vision in mammals (e.g. Ballard et al., 1989) and birds (e.g. Glasser and Howland, 1996) has attracted attention for nearly a century (Glasser and Howland, 1996). Hess (1909, 1913) first elucidated the capacity of the highly pliable lens of a diving bird (cormorant) to undergo dramatic changes in shape through the exceptionally well-developed iris and ciliary muscles. Hess (*loc. cit.*) concluded that these changes compensated for the approximately 60 D of corneal loss of power caused by submergence. Subsequent studies indicated that, in penguins, the corneas tend to be flattened and a penguin's lens must consequently accommodate for 10-30 D lost during eye submergence (Howland and Sivak, 1984).

In pursuit-diving bird species (but not penguins) tested to

date, the corneas seem to be curved and there exists a capacity for marked change in lens shape through the action of highly developed intraocular muscles. Thus, in the hooded merganser (*Mergus cucullatus*), red headed duck (*Aythya americana*), double crested cormorant and black guillemot (*Cepphus grylle*), the ranges of accommodation span 40-80 D (Table 3), while in non-divers [e.g. pigeon (*Columba livia*) and chicken (*Gallus gallus*)], the total range of accommodation is approximately 10-20 D. A high range of accommodation is also found in the dipper (*Cinclus mexicanus*), a passerine that captures insects underwater (Goodge, 1960). The capacity of these species to accommodate underwater has been supported, to date, by anatomical and histological characteristics of the intraocular muscles and by changes in the lens shape elicited by stimulation of intraocular muscles.

The ciliary muscle in birds comprises three muscle fiber groups: the anterior muscle group (Crampton), the posterior muscle group (Brücke) and the internal muscle group (Müller). The Crampton muscle group is responsible for enhancing the steepness of the central cornea and thus increasing the corneal power, the Brücke group reduces the lens radius of curvature, while the Müller group affects both cornea and lens. Comparing four avian species, Pardue and Sivak (1997) found that, in the hooded merganser, the majority of the ciliary muscle fibers are in the posterior and internal fiber groups, suggesting predominance of lenticular accommodation. By contrast, in the pigeon, kestrel (*Falco sparverius*) and chicken, the majority of muscle fibers are in the anterior muscle group, suggesting emphasis on corneal accommodation. Hooded mergansers also exhibit an especially large number of muscle fibers in the peripheral iris, the region that is supposed to be responsible for lens squeezing (Glasser et al., 1995). These authors conclude that mergansers have the largest structures associated with lenticular accommodation of the species studied.

Accommodation in the hooded merganser is achieved by the pressure of the malleable lens against the rigid iris plate, thus resulting in the bulging of the lens through the pupil (Levy and Sivak, 1980). The iris sphincter muscles presumably aid the

Table 3. *Optical parameters and performance of avian species**

Common name <i>Species name</i>	Source	Cornea	Accommodation	Pupil constriction [†]
Black guillemot <i>Cephus grylle</i>	Sivak et al., 1978	Radius: NA Power: NA Effective index: 1.370	RS: Air=0 D, Water=+5.0 D. Methods: retinoscope, forced submergence. N=6 birds.	NA
Common goldeneye <i>Bucephala clangula</i>	Sivak et al., 1985	Radius: NA Power: 74.5 [‡] Effective index: NA	Range: 66.8 D, peaks in approx. 0.4 s. Methods: electric elicitation of iris. N=1 bird.	4→3.4
Great cormorant <i>Phalacrocorax carbo sinensis</i>	Present study	Radius: 6.7–5.4 Power: 50.1–61.8 Effective index: NA	RS: Air=+0.45 D; Water=-1.79 D. Range: 64 D. Methods: voluntary dives. N=7 birds.	Not apparent
Double crested cormorant <i>Phalacrocorax auritus</i>	Sivak et al., 1977	Mean radius: 9.3 Mean power: 34.8 [‡] Effective index: 1.37	RS: Air=0 D; Water=+3.0 D to +36.0 D. Methods: retinoscopy, forced submergence. Anaesthetized underwater. N=3 birds.	NA
	Sivak et al., 1978	Radius: NA Power: NA Effective index: 1.371	RS: Air=0 D, Water=+3.0 D. Methods: forced submergence. N=2 birds.	NA
Dipper <i>Cinclus mexicanus</i>	Goodge, 1960	Radius: NA Power: NA Effective index: NA	RS: Air=-2.0 D to +1.5 D; Water=+40 D to +44 D; induced: 46–48 D. Methods: forced submergence. N=2 eyes.	NA
Hooded merganser <i>Mergus cucullatus</i>	Levy and Sivak, 1980	Radius: NA Power: NA Effective index: NA	RS: Air=0 D; induced=50 D. Methods: nicotine sulfate, excised eyes. N=4 eyes.	3→1 In tens of seconds
	Sivak et al., 1978	Radius: NA Power: NA Effective index: NA	RS: Air=+1.25 D; Water=+7.0 D.	
	Sivak et al., 1985	Radius: NA Power: 78.5 [‡] Effective index: NA	Range 78.3 D; peaks in approx. 0.5 s. Methods: electric stimulation of iris. N=4 eyes.	3.8→3.1 4.6→3.9 3.9→3.2
Mallard <i>Anas platyrhynchos</i>	Levy and Sivak, 1980	Radius: NA Power: NA Effective index: 1.373	RS: Air=+1.0 D; induced -5 D. N=8 eyes.	
	Sivak et al., 1978	Radius: NA Power: NA Effective index: 1.373	RS: Air=0 D; Water=45.0 D. N=2 birds.	Unpublished data
	Sivak et al., 1985	Radius: NA Power: 76.5 [‡] Effective index: 1.375	Range 2.7 D. Methods: electric elicitation of iris. N=2 birds.	4.7→3
Red headed duck <i>Aythya americana</i>	Levy and Sivak, 1980	Radius: NA Power: NA Effective index: NA	RS: Air=0 D; induced 50 D. Methods: nicotine sulfate on excised eyes. N=4 eyes.	5→1 In minutes
	Sivak et al., 1985	Radius: NA Power: 83 [‡] Effective index: NA	Range 16 D; peaks in 0.15 s. Methods: electric elicitation of iris. N=1 bird.	2.9→2.3
Wood duck <i>Aix sponsa</i>	Sivak et al., 1985	Radius: NA Power: 74.5 [‡] Effective index: NA	Range 6.5 D; peaks in 0.3 s. Methods: electric elicitation of iris. N=1 bird.	4→2.7
Gray headed albatross <i>Diomedea chrysostoma</i>	Martin, 1998	Radius: 14.5 Power: 23 Effective index: NA	NA	NA

*Data exclude those of penguins.

[†]Pupil constriction (mm) is during accommodation. RS, refractive state; NA, data not available.

[‡]Corneal power (measured in diopters) was calculated as $F=337.5/R$, where R (measured in mm) is corneal radius. Effective corneal refractive index was measured in meters.

formation of a rigid ring or plate against which the lens is pushed to create lenticonus (Sivak and Vrablic, 1982). Studies in the cormorant, double crested cormorant, dipper and red headed duck (Hess, 1909, 1913; Goodge, 1960; Sivak et al., 1977, 1985; Pardue and Sivak, 1997) lend support to the existence of an iris accommodative mechanism capable of producing dramatic lens changes in these species. Such phenomena were not observed in non-diving species.

Curved corneas coupled with strong muscular mechanisms have been demonstrated in otters as well as in several species of pursuit-diving birds. Sea otters (*Enhydra lutris*; Murphy et al., 1990), with a corneal refractive power of 59 D, are nearly emmetropic in both air and water. Based on their findings that the iris musculature, meridional ciliary muscle and corneal scleral plexus are highly developed in this species, Murphy et

al. (*loc. cit.*) concluded that sea otters rely on a powerful accommodation mechanism for underwater vision. Similar conclusions were drawn for the Canadian river otter (*Lutra canadensis*; Ballard et al., 1989), although in this species the states of accommodation while diving were not recorded.

Several studies point to a marked constriction of the pupil while accommodating. Thus, Levy and Sivak (1980) reported a fivefold decrease in pupil diameter in the red headed duck and a threefold decrease in the hooded merganser during accommodation stimulated with nicotine sulfate (Table 3). Reduction of pupil aperture increases image quality and may also be part of the formation of a rigid plate by the iris, against which the lens is pressed. However, in the present study, we observed only a slight constriction of the pupil (Fig. 3; Table 2), suggesting that the coupling of pupillary changes and

Table 4. *Optical parameters and performance of penguins*

Common name <i>Species name</i>	Source	Cornea	Accommodation
Blackfoot <i>Spheniscus demersus</i>	Sivak, 1976	$N=2$ birds, 1 eye each. Mean radii: 14.8, 16.3 Power: 22.8, 20.7*	RS: air: emmetropic water: mean = +18.5 D. $N=4$ birds, both eyes each.
Gentoo <i>Pygoscelis papua</i>	Sivak and Millodot, 1977.	$N=2$ birds, 1 eye each. Radii: 22.6, 22.1 Power: 14.9, 15.3	RS: air: -0.5 D to -1.75 D water: +9 D to +13.0 D. Method: water-filled goggles.
	Howland and Sivak, 1984	$N=NA$ Radii: NA Power: NA	RS: air: mean = -0.4 D (9 eyes) water: mean = +0.2 D. $N=3$ eyes.
Humboldt <i>Spheniscus humboldti</i>	Sivak et al., 1987	$N=4$ birds. Radii: 10.10–10.76 Power: 33, 31.3*	RS: air: emmetropic water: emmetropic. $N=7$ birds, both eyes each.
	Martin and Young, 1984	$N=NA$ Radii: 11.33 Power: 29.9*	RS: air: myopic water: emmetropic.
King <i>Aptenodytes patagonica</i>	Sivak and Millodot, 1977.	$N=2$ birds, 1 eye each. Radii: 29.3, 30.3 Power: 11.5, 11.1	Refractive error: air: mean = -1.25 D water: mean = +10.0 D. Method: water-filled goggles.
	Howland and Sivak, 1984	$N=NA$ Radii: NA Power: NA	RS: air: emmetropic water: emmetropic. Photorefractive limits: water 0.35 D. $N=4$ eyes.
Magellanic <i>Spheniscus magellanicus</i>	Howland and Sivak, 1984	$N=2$ eyes Mean radii: 11.5 Mean power: 29.3	Photorefractive limits: air: mean = -0.1 D ($N=5$ eyes) water: mean = +0.17 D ($N=12$ eyes)
Rockhopper <i>Eudyptes cristatus</i>	Sivak and Millodot, 1977	$N=3$ birds, 1 eye each. Radii: 18.5, 18.9, 19.8 Power: 18.2, 17.8, 17.0	Refractive error: air: mean = -1.0 D, water: mean = +9.0 D. Method: water-filled goggles.
	Howland and Sivak, 1984	$N=6$ eyes Mean radii: 11.1 Mean power: 30.4	Air: emmetropic; water: emmetropic. Photorefractive limits: air: -0.25 D ($N=10$ eyes); water: 0 D ($N=2$ eyes).

*Radii only are provided.

Corneal power (measured in diopters) was calculated as $F=337.5/R$, where R (measured in mm) is corneal radius.

RS, refractive state; NA, data not available.

underwater accommodation should be further investigated. The initial large pupil diameter seen here was most probably related to the dim illumination in the room, because, under bright light, pupil diameters are less than 2 mm (G. Katzir and H. C. Howland, personal observation).

Certain important areas of amphibious vision are, however, in need of further investigation. One area pertains to the actual refractive power lost upon submergence in pursuit-diving birds. Most studies imply that approximately 60D of corneal refractive power is lost upon submergence, yet data on corneal curvature and refractive power in air are usually lacking (Tables 3, 4; but see Sivak et al., 1977, 1985). While the results in the present study indicate that, indeed, the corneal refractive power of the great cormorant may exceed 60D, both intra- and interspecific differences are expected as a function of eye size.

Another area is related to the manner of eliciting accommodation. Two approaches have been used to determine states of accommodation: (1) by recording naturally occurring changes in accommodation from a distance and (2) by stimulating intraocular muscles. The former method, using photorefractometry and retinoscopy, was mostly employed in studies of penguins (e.g. Howland and Sivak, 1984; Sivak and Millodot, 1977; Sivak et al., 1987; Table 4), while the latter was used predominately for other pursuit-diving species (Table 3). Thus, studies that demonstrated changes in the lens during accommodation were performed by electrical or chemical stimulation of the eyes of anaesthetized or dead birds (Hess, 1909, 1913; Goodge, 1960; Sivak et al., 1985; Levy and Sivak, 1980). Simulation of submergence was obtained by forceful holding of birds' heads underwater (Goodge, 1960; Sivak et al., 1977, 1978). Such methods may have yielded results somewhat different from naturally occurring phenomena. For example, the results in the present study indicate that, in the great cormorant, transitions from hyperopia in air to myopia underwater, i.e. over 60 D, may occur within 40–80 ms (1–2 frames), while such changes obtained by electrical or chemical stimulation were an order of magnitude longer (Sivak et al., 1985). Moreover, while states of emmetropia or myopia underwater were retained for only tens of milliseconds in the present study, those achieved through electrical stimulation (Sivak et al., 1985) were in the order of hundreds of milliseconds.

Finally, visual performance underwater must be considered. Amphibious animals that actively pursue fish underwater are assumed to retain a sharp image on the retina. However, neither the eyes of crocodiles (Fleishman et al., 1988) nor those of the amphibious snakes studied by Schaeffel and Mathis (1991) were well accommodated underwater, and, while clawless otters (*A. cinerea cinerea*) are emmetropic in both air and water, their acuity in either media is not high (Schusterman and Barrett, 1973). Thus, during underwater pursuits, animals may 'make do' with blurred images or make use of non-visual information. Moreover, visual acuity, the capacity of the visual system to extract detailed information, is determined not only by the eye's optics but also by the underlying neural structures (retina and brain), neural processing and the environment.

Compared with air, the underwater light environment has much more deleterious effects on acuity, due to turbidity, pronounced attenuation and chromatic absorption of light (Loew and McFarland, 1990). To date, there are relatively few behavioral studies on visual acuity, the performance of visually guided tasks (Schusterman and Barrett, 1973) and the effects of the underwater light environment in amphibious animals and none, to the best of our knowledge, in pursuit-diving birds.

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