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Crocodiles don't focus underwater

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Summary. Crocodilians are amphibious reptiles which hunt prey both on land and in water. Previous refractive and anatomical studies have suggested that their eyes can focus objects in air and that their ability to refocus the eye underwater may be limited. Examination of the plane of focus of six species of crocodilians both in air and underwater has revealed that they are generally well focused in air for distant targets and severely defocused underwater. These results suggest that sensory systems other than vision must play an important role in prey capture underwater.

Introduction

Amphibious animals often have specialized adaptations for maintaining their focus in both air and water (Howland and Sivak 1984; Sivak 1980; Underwood 1970). Surprisingly, little attention has been devoted to eyes of crocodilians. Beer (1898) showed that the American alligator, *Alligator mississipiensis*, has a very limited range of accommodation. Based on this observation, Walls (1967) claimed that crocodilians lack the ability to focus underwater; however, this assertion has never been directly tested. We wished to answer the question: can crocodilians focus both in air and underwater?

Materials and methods

We used both conventional retinoscopy and video photorefraction on six species of crocodilians to measure their ability to focus in air and water. Both retinoscopy and photorefraction involve shining a light into an eye and examining the returning reflection. In retinoscopy the motion of the eyeshine in the subject's pupil is noted as the retinoscopic beam is swept across the subject's eye (Michaels 1985). In orthogonal photorefraction, a point source of light is shone into the eye and the extent of the spot of light returned to the camera is measured (Howland and Howland 1974; Murphy and Howland 1983). Both measures give an objective estimate of the degree of defocus of the eye in diopters (reciprocal meters) relative to the retinoscopic peephole or camera aperature. (A human eye underwater is approximately 50 diopters out of focus.)

Specimens of four species were measured while swimming freely in large aquaria at the National Zoological Park in Washington, DC. Of particular interest were the results for the gharial, *Gavialis gangeticus*, which is primarily fish-eating and is one of the most completely aquatic of the crocodilians. Two of the species (*Crocodylus acutus* and *Caiman sclerops*) were measured, while hand-held, in a laboratory at the Smithsonian Tropical Research Institute in Panama. Additional measurements were made of one of these species (*C. sclerops*) in the wild in the Chagres River in Panama.

Abbreviation: D diopter

Results and discussion

Our results are given in Table 1. All crocodilians showed a good ability to focus in air as indicated by the refractions of their eyes, which are all within a few diopters of emmetropia (the condition in which an eye is normally focused at infinity when the muscles of accommodation are relaxed) regardless of whether they were in the wild, in an aquarium, or simply hand-held. Underwater, however, they were all severely hyperopic (farsighted), much as are humans when they submerge their eyes.

It should be noted that our ability to measure the refractive state underwater was limited in retinoscopy by the maximum available positive lens, and in photorefraction, by vignetting of the reflex. Thus the crocodilians may be far more hyperopic underwater than the lower limits given in Table 1.

In most cases when the animals were held underwater, the nictitating membrane was drawn over the eye. In order to be certain that their perception was not materially affected by the nictitating membrane, we also refracted an animal in air who, when its eye was irritated, drew the nictitating membrane across the cornea. Although the quality

Table 1. Refractions of crocodilians

Species	Eye	Medium	Meridional Power (in diopters)		Method
			Horiz	Vert	
Crocodylus acutus	*	Air	1.5	2.0	Retinoscopy
	same	Water	>10.5	>10.5	Hand-held
Crocodylus acutus	*	Air	2.0	2.0	Retinoscopy
	same	Water	>10.5	>10.5	Hand-held
Caiman sclerops	*	Air	4.5	4.5	Retinoscopy
	same	Water	>10.5	>10.5	Hand-held
	*	Air	2	2	Retinoscopy and photorefraction in wild
Crocodylus johnstoni	R	Air	0.6	0.4	Video photorefraction
	R	Water	>20	>20	free swimming in aquarium
Crocodylus rhombifer	R	Air	2.2	0.0	Video photorefraction
	L	Air	4.0	0.5	free swimming
	L	Water	>20	>20	in aquarium
Paleosuchus palpebrosus	R	Air	1.5	0.7	Video photorefraction
	R	Water	>20	>20	free swimming in aquarium
Gavialis gangeticus	L	Air	− 0.1	0.0	Video photorefraction
	L	Water	>20	>20	free swimming in aquarium

* Not recorded

of the retinal reflex was diminished, the refraction was not quantitatively altered.

We measured the corneal curvatures of specimens of three of the species from Table 1. We employed photokeratometry to measure the corneal curvatures (Fig. 1C) and found the following corneal powers: *C. rhombifer*: 55.5 D, *C. johnstoni*: 58 D, and *P. palpebrosus*: 40 D. Without accommodation, all of these eyes would increase their refraction by these amounts underwater when the cornea-air interface is eliminated.

Although we used continuous video photorefraction, we observed no cases of accommodation in either air or water, even when we followed the reflex continuously as the animal emerged from the water. In all cases, the pupil size appeared to diminish when the animal submerged its eyes. The major diameters of the gharial's pupils were reduced by a factor of 2, and those of Johnston's crocodile by a factor of 2.6, when the animals were underwater. The reduction in pupil size may serve to increase the depth of field and to some extent compensate for the inability of the animal to focus underwater.

There are two possible ways to make an eye refractively amphibious. It must either have an extreme accommodative range, such as is seen in turtles and diving ducks, and/or there must be a flattening of the cornea so that the refractive role of the air-corneal interface is reduced, such as in penguins (Howland and Sivak 1984; Sivak 1980; Underwood 1970). It is clear from our results that the crocodilians possess neither of these adaptations.

With the possible exception of the gharial, all of the species we tested hunt both on land and in water. Several workers have noted the apparent lack of importance of visual cues for underwater feeding by crocodilians (Neill 1971). Schaller and Crawshaw (1982) found that feeding efficiency was nearly the same in clear and turbid water in free-living *Caiman sclerops*. Recently it has been demonstrated (Fleishman and Rand, in press) that this species can capture fish in total darkness. Thus, the ability to hunt underwater with the absence of visual cues, the highly curved corneas, and the lack of any accommodative ability suggest that the crocodilian eye is adapted almost exclusively for vision in air.

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