

A behavioral study of refraction, corneal curvature, and accommodation in raptor eyes

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Abstract: Since there is much speculation in the literature regarding the accommodative abilities of raptors, we undertook a behavioral study of accommodation in the five families of raptors. The resting refractive state and amplitude of accommodation were measured using infrared video photorefractometry in a variety of wild-caught and captive-bred raptors. The resting corneal curvature and the extent of changes in corneal curvature during accommodation (corneal accommodation) were measured using video keratometry. External ocular and head dimensions were measured with calipers to look for correlates with accommodative amplitude. In general, all eyes examined were of high optical quality and relatively free of aberrations. No significant refractive errors were recorded in any of the birds examined (< 1.0 diopters (D)). In general, significant amplitudes of accommodation were measured in the hawks (up to 25.0 D), but little accommodation was seen in the owls. Corneal accommodation ranging from 2.8 to 6.2 D in magnitude was recorded in a number of the hawks. These differences in the accommodative behaviors of the owls and hawks are discussed with respect to the limitations of the behavioral techniques used, differences in the degree of cooperation of the different species, and real differences in the accommodative abilities of the owls and hawks in relation to their accommodative needs, such as when feeding.

Résumé : Il se fait beaucoup de spéculation dans la littérature au sujet de la capacité d'accommodation des rapaces; pour tenter d'élucider le problème, nous avons procédé à une étude comportementale de l'accommodation chez les rapaces de cinq familles différentes. La réfraction au repos et l'amplitude de l'accommodation ont été mesurées par vidéophotoréfraction à l'infrarouge chez une variété de rapaces capturés en nature ou élevés en captivité. La courbure de la cornée au repos et l'amplitude des changements de la courbure au cours de l'accommodation (accommodation de la cornée) ont été mesurées par vidéokératométrie. Les dimensions externes de l'oeil et la taille de la tête ont été mesurées au moyen d'un compas à calibrer, ce qui a permis d'établir des corrélations avec l'amplitude de l'accommodation. En général, tous les yeux examinés avaient une grande qualité optique et comportaient peu d'aberrations. Aucune erreur significative de réfraction n'a été enregistrée chez les oiseaux examinés ($< 1,0$ D). De façon générale, des amplitudes significatives d'accommodation ont été mesurées chez les rapaces de jour (jusqu'à 25,0 D), mais les hiboux semblent faire peu d'accommodation. L'accommodation de la cornée, 2,8 à 6,2 D d'amplitude, a été notée chez plusieurs rapaces de jour. Ces différences de comportements d'accommodation entre les rapaces de jour et les hiboux sont examinées à la lumière des contraintes imposées par les techniques utilisées, des différences dans l'«obligance» des différences espèces à se prêter aux expériences, et des différences réelles dans la capacité d'accommodation des hiboux et des rapaces de jour en relation avec leurs besoins d'accommodation, par exemple au cours de l'alimentation.

[Traduit par la Rédaction]

Introduction

Recent studies have provided mechanistic descriptions of independent corneal and lenticular accommodation in a few bird species (Glasser et al. 1994, 1995; Murphy et al. 1995a; Glasser and Howland 1995; Pardue and Sivak 1996). While such studies provide insight into the anatomical and physiological bases of accommodation in individual species, they yield no information on the accommodative behaviors. Substantial differences in habitat and feeding and other visual

behaviors among birds have resulted in widely differing accommodative mechanisms being employed (Sivak 1980). Recently, techniques have been developed that facilitate the measurement of accommodative behavior in conscious, uncooperative subjects (Murphy and Howland 1983; Schaeffel et al. 1986, 1987). Such techniques have been used in several studies of accommodation in owls (Murphy and Howland 1983; Howland et al. 1991; Wagner and Schaeffel 1991; Schaeffel and Wagner 1992), but in spite of the many early anatomical and physiological studies on accommodation in raptors, no information exists on the behavioral accommodative abilities of raptors other than owls.

Raptors' eyes have been a frequent subject of anatomical and physiological investigations of accommodation because of their size and pronounced accommodative musculature. In spite of this, many questions about the accommodative abilities of raptors remain. For example, corneal accommodation has been reported to be both present and absent, and the anterior ciliary muscle has been reported to mediate either corneal accommodation only or lenticular accommodation

Received February 21, 1997. Accepted June 25, 1997.

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only. The eyes of raptors have been studied by Crampton (1813), Brücke (1846), Müller (1857), and Beer (1893) with little consensus (for review see Glasser and Howland 1996).

More recently, Lord (1956) compared the ocular anatomy of three falconiform and three passeriform birds and suggested that the development of the ciliary muscles corresponded well to the accommodative ability of each species. The anatomy of the golden eagle eye suggests that the well-developed iris plays a role in lenticular accommodation and that the anterior ciliary muscle is well suited for corneal accommodation (Murphy and Dubielzig 1993). In an anatomical study of the ciliary muscles of four bird species, it was concluded that the kestrel (the only raptor included) probably has little lenticular accommodation and a better developed corneal accommodative mechanism (Pardue and Sivak 1996). The accommodative range of this species has, however, been reported to exceed 12 diopters (D) (Murphy et al. 1995b).

We have observed accommodative behaviors in several species of raptors and have measured the amplitudes of accommodation and corneal accommodation using infrared photorefractometry and video keratometry. While these techniques facilitate behavioral measurements of accommodation rather than that induced through pharmacological or electrophysiological means, they depend on the cooperation of the subject. When no accommodation is seen, this could be due to a lack of cooperation by the individual or to an actual inability to accommodate. Similarly, the amplitude of accommodation measured in individuals may not reflect the maximal amplitude available to each species because of differences in the degree of cooperation and willingness to accommodate. This said, the frequency and extent of the accommodation that was elicited from the birds and their remarkable cooperation suggest that we observed natural accommodative ability. Disparities exist between behaviorally and physiologically (drugs or electrical stimulation) induced accommodation in birds (Schaeffel and Howland 1987; Glasser et al. 1994; Glasser and Howland 1995). It is just as likely that physiological stimulation produces more accommodation than is naturally available to the animal, as was suggested by pharmacologically stimulated accommodation in monkeys (Crawford et al. 1990), as it is that the behaviorally measured amplitude is less than the maximal accommodative response. Whichever the case, we have been able, under behavioral conditions, to measure substantial amplitudes of accommodation and the presence of corneal accommodation in a number of raptors. A preliminary report of these findings has appeared elsewhere (Pardue et al. 1996).

The raptors of North America are flesh-eating birds belonging to five families: (1) the American vultures (family Cathartidae), which are scavengers with weak talons that are ill-suited for grasping prey; (2) kites, hawks, and eagles (family Accipitridae), large diurnal birds with strong talons, which include two smaller groups, the accipiters (long-tailed woodland hawks) and the buteos (broad-tailed soaring hawks); (3) falcons (family Falconidae), diurnal and crepuscular birds, which are swift and agile flyers with long, pointed wings bent at the wrist; and (4) two families of owls, the barn owls (Tytonidae) and the typical owls (Strigidae) (National Geographic Society 1987).

Materials and methods

Wild-caught birds captured for rehabilitation or relocation from Toronto International Airport and captive birds, comprising one species of vulture, five species of hawks, one species of falcon, and six species of owls, were used in this study ($n = 30$). Each bird was videotaped on one occasion for 30–45 min, the time being divided equally between keratometry and photorefractometry. The birds were hand-held under light restraint by experienced bird handlers. All measurements were made in a darkened room to facilitate pupil dilation.

Infrared photorefractometry

An infrared photoretinoscope (Schaeffel et al. 1987) with all LEDs operating continuously (Schaeffel et al. 1994) was used to measure resting refraction and observe the dynamics of accommodation at a working distance of 0.5 m (Murphy et al. 1995b). The camera was connected to a VCR and a video monitor visible to the experimenters. Infrared illumination produces a bright fundus reflection, the properties of which can be used to determine the plane of focus of the eye (Figs. 1b, 1c, and 1d). A bright crescent appears at the top of the pupil in an eye that is focused hyperopically with respect to the camera (i.e., behind the camera). Conversely, a bright crescent appears at the bottom of the pupil in an eye focused myopically with respect to the camera (i.e., in front of the camera). A pupil of uniform brightness appears in an eye focused conjugate with the plane of the camera (Fig. 1c). Thus, an emmetropic eye (i.e., focused at optical infinity) will be focused beyond the 0.5-m working distance of the camera and will have an apparent hyperopia of 2.0 D (the reciprocal of the working distance). Resting refraction was measured by holding an infrared interference filter (Kodak Wratten gelatin filter No. 89B) in front of the eye to block vision and accommodation while the resting photorefractive reflex was neutralized by holding ophthalmic lenses of varying power in front of the eye. Thus, an emmetropic eye with the camera at 0.5 m would produce 2.0 D of apparent hyperopia and a +2.00 D lens would neutralize the resting photorefractive reflex (Figs. 1b and 1c). The sensitivity of this technique is roughly 0.5 D.

Accommodation was observed on the video monitor through changes in the photorefractive crescents in the pupils while the birds attended to a variety of visual stimuli presented to them over a period of roughly 15 min. In an emmetropic eye the photorefractive crescent flips from the top of the pupil to the bottom of the pupil when the eye accommodates from beyond the camera plane to in front of the camera plane. The amplitude of accommodation was measured by holding negative ophthalmic lenses in front of an otherwise unoccluded eye while watching for the appearance of a myopic crescent or "clearing" of the apparent hyperopic crescent. If the bird accommodated to an extent greater than the power of the lens held in front of the eye, a myopic crescent was observed through the lens, which was then replaced with a negative lens of greater power. If the hyperopic crescent created by the negative lens was "cleared" by accommodation without a myopic crescent being observed, the bird accommodated to an amplitude equivalent to the lens power plus the reciprocal of the working distance.

Video keratometry

To measure the corneal power and the changes in corneal curvature during accommodation (corneal accommodation), we used a video keratometer (Schaeffel and Howland 1987; Glasser et al. 1994), which consists of a ring of eight visible LEDs positioned concentrically around the lens of the video camera. The video camera is focused on the cornea at a distance of 30 cm and the LEDs reflected from the cornea are visible in the video image (Figs. 1f, 1h, and 1i). The image is recorded on videotape and subsequent computer-aided analysis allows repeated measurements of corneal curvature and

Fig. 1. (a) A Eurasian eagle owl with an apparent resting hyperopia, as shown by the bright crescent at the top of the pupil (b). (c) A +2.5 D lens held in front of the eye almost completely neutralizes the hyperopic crescent, resulting in a more uniformly illuminated pupil, while a +3.0 D lens causes the reflex to pass the neutral point and become brighter in the lower part of the pupil (d). The brighter crescent seen in the upper part of the pupil in spite of the neutralized (c) or myopic (d) photorefractive reflex is attributed to the annular pad of the lens. This was often seen in the widely dilated pupils of owl eyes when the eye was viewed slightly off-axis. The keratometry technique was used in a snowy owl (e), showing the video image with the eight keratometer light spots reflected off the cornea (f). (g) Keratometric measurement of corneal accommodation in a red-tailed hawk. (h) In the unaccommodated eye, the diameter of the pupil as well as the unpigmented portion of the iris are relatively unstricted. The diameter of keratometer LEDs is at a maximum. (i) During accommodation the pupil diameter decreases, the diameter of the unpigmented portion of the iris constricts, and the diameter of the ring of keratometer LEDs decreases as the corneal curvature increases.

Fig. 2. (a) A bald eagle, showing an apparent hyperopia (b) that is completely neutralized by a +2.0 D lens held in front of the eye (c). (d) Accommodation to a near stimulus held in front of the eye, producing a myopic crescent at the bottom of the pupil. (e) Accommodation through a -4.0 D lens resulting in an almost emmetropic reflex (a slight bright crescent can be seen at the top of the pupil) accounting for roughly 6.0 D of accommodation. (f) A red-tailed hawk, showing a resting hyperopia (g), which is neutralized with a +2.5 D lens (h). A myopic crescent is seen during accommodation on a near stimulus (i), and accommodation through a -7.0 D lens results in a neutralized reflex to produce 9.0 D of accommodation (j).

Fig. 3. (a) A barn owl, showing symmetrical resting hyperopic reflexes in both eyes (b). A +2.0 D lens held over the left eye neutralizes the resting reflex in that eye alone (c), and myopic crescents are seen in both eyes during accommodation to produce an accommodative response greater than 2.0 D (d). The extent of the accommodation could not be determined more accurately in this bird because it failed to accommodate when negative lenses were held in front of the eyes. (e) A 1-month-old Eurasian eagle owl, showing a resting hyperopia (f) that was neutralized with +2.0 D lenses (not shown). (g) This bird showed a good accommodative response and strong pupillary constriction to a near stimulus resulting in more than 2 D of accommodation.

changes in corneal curvature that may occur during accommodation (Glasser et al. 1994). After each bird was measured, a set of three calibration ball bearings was held in front of the video keratometer and these images were also recorded to verify the keratometer calibration. The accuracy of this technique is roughly 0.5 D (Schaeffel and Howland 1987). Corneal power is a measure of the unaccommodated (resting) corneal curvature. This represents the average of at least eight measurements of independent video frames from both eyes of each bird while in the unaccommodated state. To measure corneal accommodation, the eye is determined to be focused on a near object on the basis of a contraction of the iris and constriction of the pupil. It was impossible to simultaneously measure the extent of accommodation during keratometric measurements. Corneal accommodation represents the difference between the mean resting corneal power (as defined above) and the mean accommodated corneal power (the average of several independent measurements of corneal curvature during accommodation). A maximum value of corneal accommodation is also presented. This is the difference between the mean resting corneal power and the single highest corneal power measured.

Head dimensions (head length, measured from the back of the head to the point on the beak where the facial skin and feathers end, and head width behind the eyes) and ocular dimensions (corneal diameter, interocular distance, and pupil diameter) were measured on each bird by means of calipers. The age of the birds was recorded when possible, while in the wild-caught birds, feather and (or) iris coloring was used to distinguish juveniles from adults. All experimental procedures were conducted in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Results

In general, all eyes examined were of high optical quality with no significant ametropic resting refractions (Table 1). There were no indications of significant optical aberrations or astigmatism independent of documented ocular injuries. This was assessed through the clarity and uniformity of the infrared fundus reflex (Figs. 1b, 1c, and 1d). Fundus reflectivity is generally considerably brighter than that of human eyes, especially in birds that are active under crepuscular or

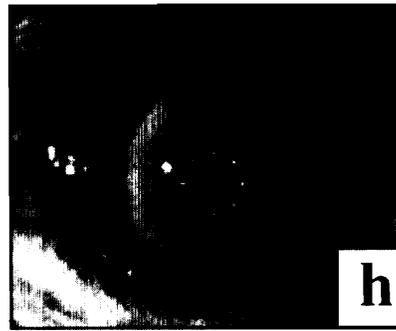
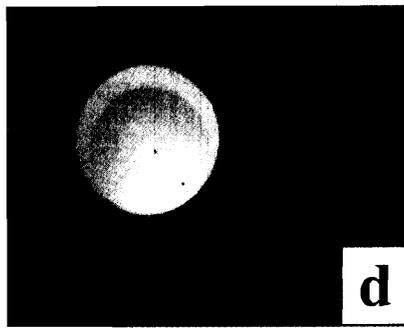
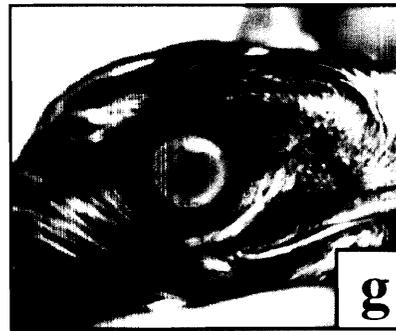
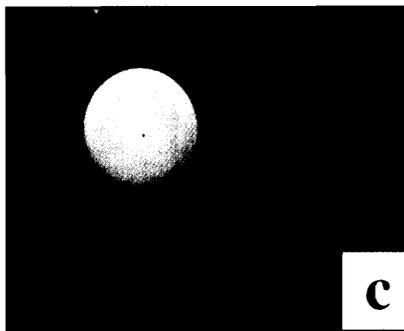
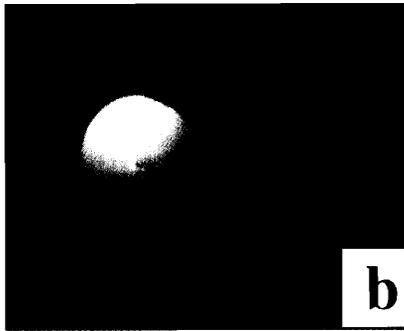
nocturnal conditions (i.e., owls). This is due to the presence of the highly reflective tapetum lucidum (Walls 1967) and the lower f number (focal length/pupil diameter) of nocturnal eyes. Fundus reflectivity in the diurnal raptors such as the red-tailed hawks and turkey vultures was unremarkable.

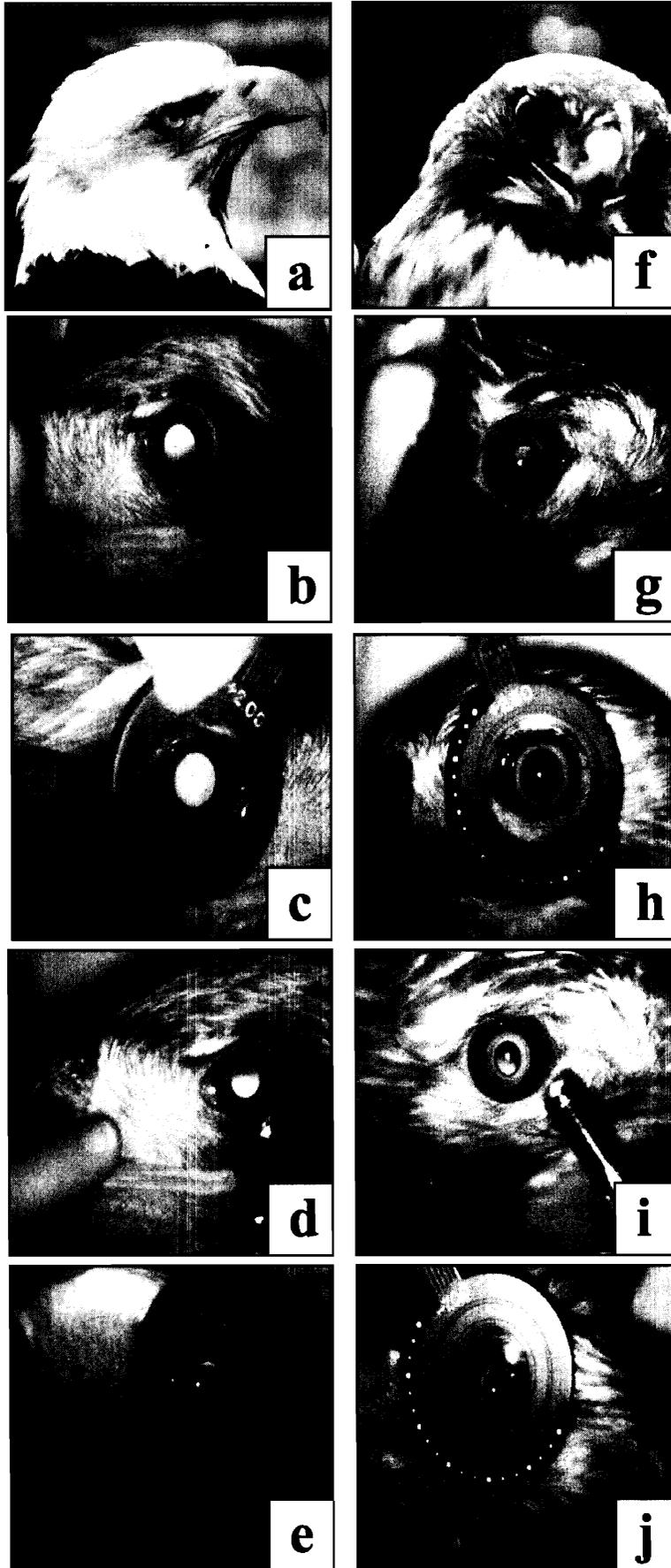
In most cases, because of their natural curiosity, the birds would actively accommodate when looking around and while looking at a variety of visual stimuli held in front of them (food items, shiny objects, pens, etc.) (Figs. 2d and 2i). When visual stimuli failed to elicit accommodation, an occasional touch to the facial feathers or a tap on the beak would often elicit accommodation. Many of the hawks, particularly the red-tailed hawks and the golden and bald eagles, changed their accommodative state continually. The wild-caught birds remained very still, while showing insatiable curiosity and continually changed the focus of their eyes. Less cooperation and accommodation were seen in captive birds that had been handled more frequently. In some cases, no accommodation could be elicited under any circumstances, particularly in the owls, although juveniles tended to accommodate more than adults. Only a small amount of accommodation was seen in the juvenile owls (i.e., roughly 2.0 D) (Fig. 3g).

There was a striking difference in accommodative behaviors between the hawks and owls in their ability to accommodate independently in the two eyes. This was consistently observed in the hawks and vultures but was never seen in any of the owls (Figs. 4a-4f). In many instances, hawks and vultures were observed to view and accommodate on objects presented to one eye while the focus of the other eye remained unchanged (Figs. 4b, 4c, and 4f). A visual stimulus presented at the beak between the two eyes of the hawks inevitably produced a coupled and symmetrical accommodative response.

Table 1 is a summary of the species studied, resting refractive states, corneal powers, accommodative amplitudes, and amplitudes of corneal accommodation.

Corneal powers ranged from 111.4 D in an American





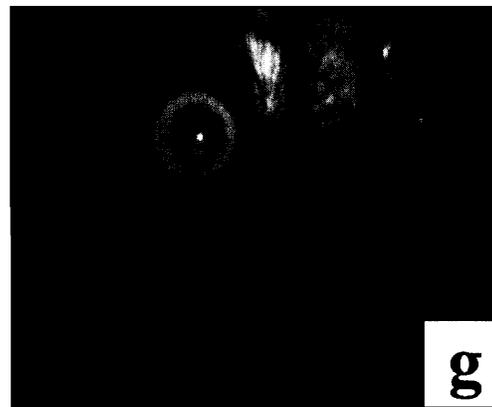
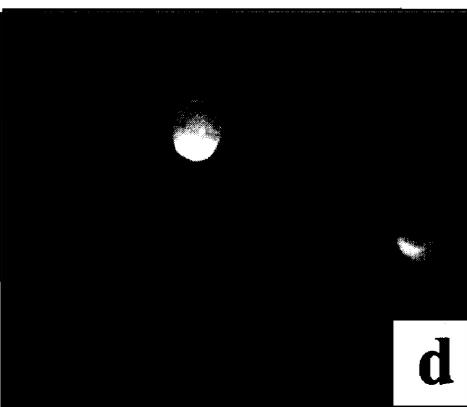
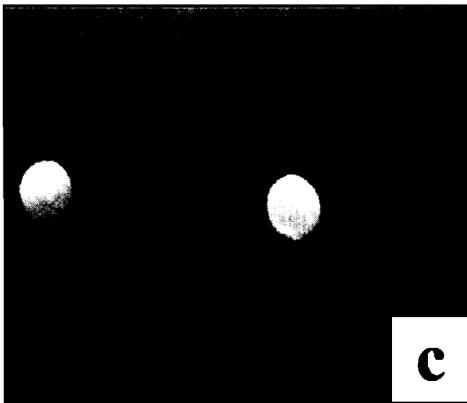
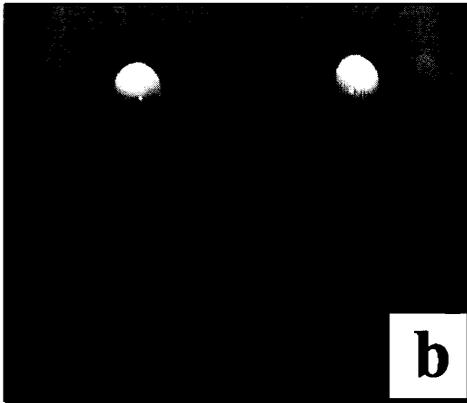
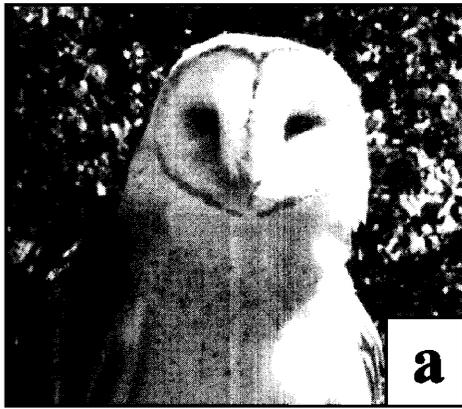


Fig. 4. A red-tailed hawk, showing resting hyperopia in both eyes (*a*), accommodation in the right eye only (*b*), accommodation in the left eye only (*c*), symmetrical accommodation in both eyes (*d*), and mild accommodation in the right eye, making it emmetropic with the camera (i.e., 2 D), while a far stronger accommodative response is seen in the left eye, making it myopic relative to the camera (*e*). (*f*) A turkey vulture accommodating in the right eye only while the left eye remains hyperopic relative to the camera. Note the considerably greater extent of the binocular visual field of the red-tailed hawk compared with that of the turkey vulture, owing to the more frontally placed eyes. This accommodative behavior was elicited either by holding a near stimulus to only one eye at a time or by holding the stimulus directly in front of the bird.

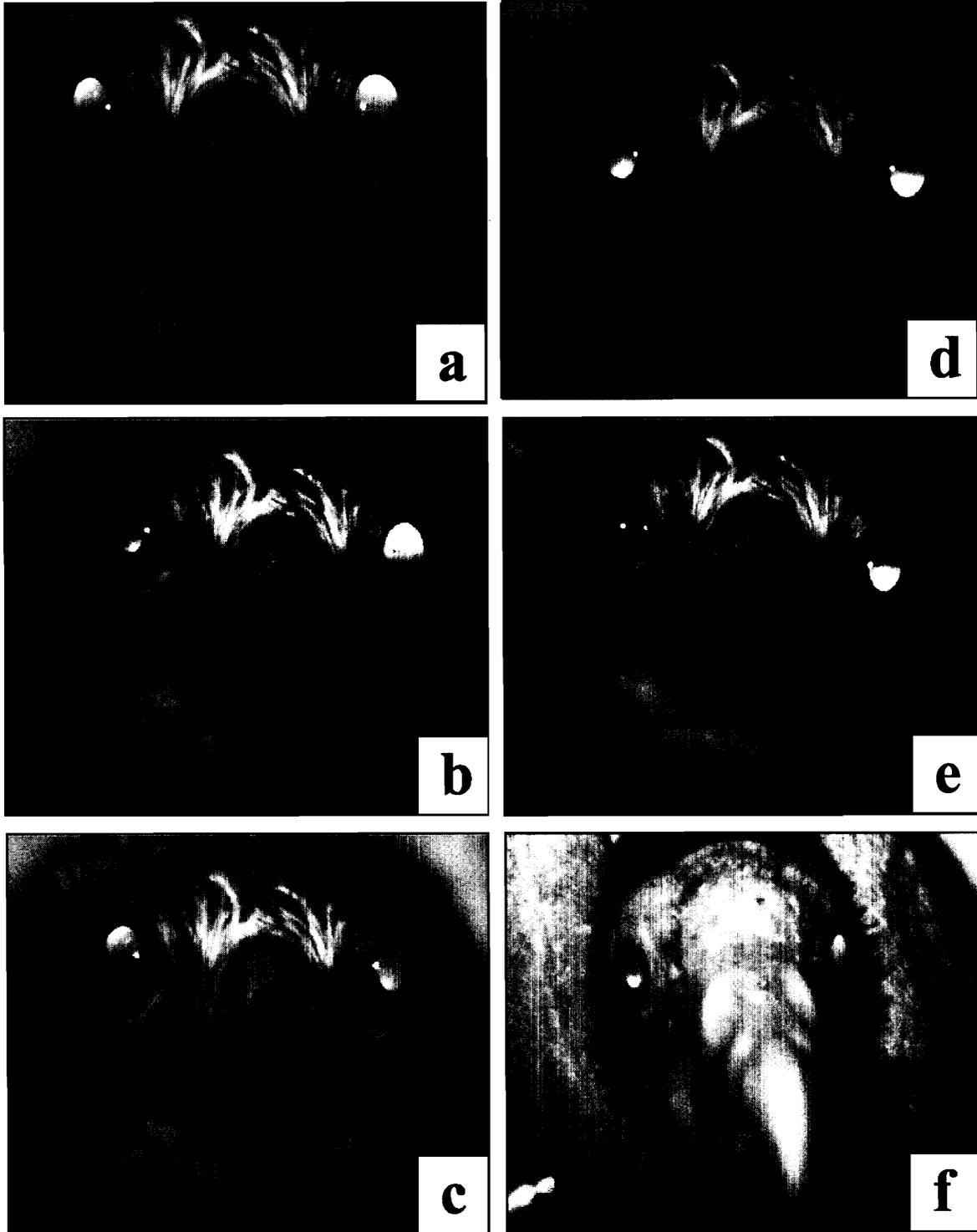


Table 1. Resting refraction, corneal power, total range of accommodation, and extent of corneal accommodation measured in the 30 raptors studied.

	No. of birds	Resting refraction	Corneal power	Range of accommodation	Corneal accommodation
Turkey vulture, <i>Cathartes aura</i>	2	-0.3	78.4 61.3 ^a	8.5 (max. 9.0)	4.0 (max. 8.0), 2.8 (max. 3.3) ^a
Bald eagle, <i>Haliaeetus leucocephalus</i>	3	-0.1±0.1	66.5±5.45	6.8±1.9 (max. 9.0)	4.1±2.3 (max. 7.7)
African fish eagle, <i>Haliaeetus vocifer</i>	1	-0.5	73.3	9.0	6.2
Golden eagle, <i>Aquila chrysaetos</i>	9	0.0±0.4	66.6±6.6	6.7±2.1 (max. 10.0)	3.4±1.4 (max. 4.9)
American kestrel, <i>Falco sparverius</i>	1	0.0	111.4	16.0 (max. 17.0)	—
Sharp-shinned hawk, <i>Accipiter striatus</i>	1	-0.3	80.8	4.0	—
Red-tailed hawk (<1 year), <i>Buteo jamaicensis</i>	4	0.2±0.3	65.2±3.9	10.3±2.0 (max. 14.0)	2.9±2.4 (max. 5.8)
Red-tailed hawk (>1 year), <i>Buteo jamaicensis</i>	5	0.1±0.2	44.0±2.6	25.8±1.9 (max. 28.0)	3.3±2.7 (max. 9.0)
Great horned owl, <i>Bubo virginianus</i>	1	-0.5	37.7	0.0	0.0
Snowy owl, <i>Nyctea scandiaca</i>	2	0.0	29.6	2.0 ^b	0.0
Saw-whet owl, <i>Aegolius acadicus</i>	1	-1.0 ^c	53.5	0.0	0.0
Eurasian eagle owl, <i>Bubo bubo</i>	3	-0.1±0.6	43.9±9.6	>2.0 ^d	0.0
Short-eared owl, <i>Asio flammeus</i>	1	0.5	63.3	0.0	0.0
Barn owl, <i>Tyto alba</i>	2	0.8	76.1	2.0 ^b	0.0

Note: Each value is the mean from both eyes of each bird. Where two or more birds of the same species were studied, the mean and standard deviation are given. The units are diopters.

^aCorneal powers and corneal accommodation for the two turkey vultures (of unknown sex and age) are given.

^bAccommodation was seen in only one owl in these species.

^cHyperopia was probably due to documented ocular injury.

^dAccommodation was seen in two of three Eurasian eagle owls, both 1 month old.

kestrel to 29.6 D in the snowy owls. The high standard deviations for the Eurasian eagle owls and golden eagles are due to variation in the age and size of individuals. The juvenile golden eagles had a mean corneal power of 74.7 D and the two adults had corneal powers averaging 62.5 D. The corneal powers of the individual Eurasian eagle owls were 55.9 D for the youngest bird (~1 month), 40.4 D at 1–2 months old, and 35.4 D for the adult bird (>1 year). The age difference is also evident among the red-tailed hawks, which were readily divided into two groups, one composed of juveniles and the other of birds more than 1 year old, based on tail-feather coloring and the degree of pigmentation in the iris. All the juvenile red-tailed hawks had significantly steeper corneas (greater corneal power) and significantly lower amplitudes of accommodation (Table 1). Sex, and hence size, may also account for individual differences in corneal power. Of the two turkey vultures studied, a wild-caught bird of unknown age had a mean corneal power of 78.4 D and a second bird at least 14 years old had flatter corneas with a mean power of 61.3 D. Among all birds studied, corneal power showed good agreement between the two eyes (<2.0 D), with a maximum difference of 5.0 D in one bald eagle. Good agreement between our data and those of Murphy and Howland (1983) was obtained for the saw-whet owl and the snowy owls. Differences between the two studies most likely reflect individual age or sex differences.

Maximal accommodative amplitude (28.0 D) was recorded in a red-tailed hawk (Table 1) and, in general, birds of this species accommodated the most (mean of 17.0 D; $n = 9$). The American kestrel had 16.0 D of accommodation and the African fish eagle had 9.0 D. In the three golden and three bald eagles, maximal amplitudes of 9.0 and 10.0 D, respectively, were measured, with an average of 6.0 D in each

species. Only 4.0 D of accommodation was seen in the sharp-shinned hawk. Considerably lower amplitudes of accommodation were seen in the owls. Good accommodation was observed, but not measured because of a lack of cooperation, in a barn owl (Fig 3). Murphy and Howland (1983) reported more than 10 D in this species, but Wagner and Schaeffel (1991) measured only 6.0 D. When we were able to elicit accommodation from the owls, it was most often in the younger birds (Fig. 3).

Corneal accommodation was measured in all of the larger hawks. Owing to the high-powered corneas of the American kestrel and the sharp-shinned hawk, no changes in corneal curvature could be measured. No corneal accommodation was measured in any of the owls, since little accommodation was seen. The widely varying contribution of corneal accommodation to total accommodation for the hawks may be due to three factors: (1) different species may employ corneal accommodation to different extents; (2) disproportionate amounts of corneal or total accommodation may have been measured; or (3) we may have overestimated resting corneal power by using the mean of several measurements rather than choosing the lowest value recorded.

Table 2 is a summary of head and eye dimensions measured using calipers. No significant relationships between accommodative amplitude and any of the biometric data were found, unlike the significant inverse correlation between accommodative amplitude and body size shown by Murphy and Howland (1983).

Discussion

The literature on avian accommodation contains considerable discussion regarding the relationship between accommoda-

Table 2. Head and eye dimensions, measured using calipers. Head length was measured from the back of the head to the front of the head, where the beak is clear of facial feathers. Head width was measured at the posterior orbit.

	No. of birds	Head length ^a	Head width ^b	Corneal diam.	Pupil diam. ^c	Intraocular distance
Turkey vulture	2	79.5	39	10.75	7.00	36.0
Bald eagle	3	70.7±1.2	60.0±3.5	18.0±1.7	10.33±0.6	56.0±1.0
African fish eagle	1	50	54	17	7	51
Golden eagle	3	70.0±5.0	60.3±4.9	18.0±1.0	10.0±0.0	53.3±7.5
American kestrel	1	29	29	11	3	27
Sharp-shinned hawk	1	32	28	9	5	22
Red-tailed hawk (<1 year)	4	63.4±9.8	52.4±0.6	19.2±0.5	8.4±1.7	49.2±1.1
Red-tailed hawk (>1 year)	5	57.0±1.8	53.3±2.1	17.0±0.8	7.3±0.5	46.8±2.5
Great horned owl	1	85	84	22	13	57
Snowy owl	2	80	75	24	15	55
Saw-whet owl	1	50	37	14	10	27
Eurasian eagle owl	3	51.7±2.9	73.0±9.9	23.7±5.5	13.3±5.1	51.3±4.5
Short-eared owl	1	43	46	18	13.5	35
Barn owl	2	47.3	52.0	15.7	— ^d	42.7

Note: When more than two birds of the same species were studied, the mean and standard deviation are given. The units are millimetres.

^aMeasured from the back of the head to the front, where the beak is clear of facial feathers.

^bMeasured at the posterior orbit.

^cMeasured in a dimly lit room.

^dPupil diameters were not measured in the barn owls, but were observed to be very close to the corneal diameters.

tive amplitude and visual needs among raptors. Given the diversity of environments inhabited by raptors, the lighting conditions in which they hunt, the prey items upon which they feed, and their ocular anatomy (Lord 1956), considerable diversity in accommodative abilities and mechanisms might be expected.

Hess (1912) proposed that the accommodative needs of various raptors were determined by their feeding habits. He argued that the nocturnal raptors, which are capable of capturing prey using auditory cues alone, require very little or no accommodation. The barn owl has been shown to be capable of capturing its prey in the dark (Payne 1971). While this species has been shown to have an unusually large accommodative amplitude compared with other owls (Murphy and Howland 1983), owls from the same family (Tytonidae) have also been shown to have a limited range of accommodation (Howland et al. 1991). Thus, the relationship between accommodative needs and feeding behaviors may be more complex than was originally suggested by Hess (1912).

Lord (1956) has discussed the relationship of the visual behaviors of hawks to their accommodative needs. He speculates that hawks may use the relatively more hyperopic central fovea monocularly to scan the ground for prey while in flight and the relatively myopic temporal fovea binocularly while diving in pursuit of prey. In addition, he notes that "live captured hawks could seldom be induced to observe a near object with one eye" (Lord 1956).

We have seen no evidence of a myopic temporal fovea nor have we experienced any difficulty in eliciting monocular accommodation in hawks. Clearly, the measurement of accommodative behavior is an important substitute for speculation based on anatomical findings. We have seen no evidence of significant resting ametropias in any of the birds studied. To our knowledge, only one study has reported sys-

tematic refractive errors in a bird (the kiwi), and this was chiefly attributed to the artifact of retinoscopy in the small nocturnal eye (Sivak and Howland 1987). Among adult humans, it is not uncommon to find ametropias as great as 10% of the focal power of the eye (Saunders 1981). Indeed, in some human populations prevalent refractive errors represent the rule rather than the exception (Lin et al. 1996). Certainly, natural selection must play an important role in preventing the perpetuation of refractive errors in raptors, but the truly remarkable extent to which this is accomplished, judging from our study population, indicates the extent to which raptors must rely on good visual abilities to survive.

Walls (1967) has speculated on the accommodative amplitudes of various birds as "being lowest in the owls, highest in the hawks, with granivorous birds and bug-eaters fitting neatly in between." This ranking is attributed to accommodation, visual acuity, and movement detection, which are all related in birds (Walls 1967). Previous measurements of physiologically induced accommodation in granivorous birds (chickens) (Glasser et al. 1994) were lower than the greatest amplitude we measured in raptors, using behavioral techniques (28 D in a red-tailed hawk). No previous studies have shown such a high naturally occurring accommodative amplitude in a terrestrial bird species, and it may be more than double the largest accommodative amplitude previously recorded among the owls. Substantially greater accommodation has been measured in aquatic birds (50 D in the hooded merganser) (Levy and Sivak 1980) than in any of the raptors we studied here, so we dispute Walls' (1967) contention that raptors have the greatest amplitudes of accommodation among birds.

The presence of corneal accommodation in raptors has been speculated upon (Crampton 1813; Brücke 1846), demon-

strated (Beer 1893), and disputed (Hess 1912) (reviewed in Glasser and Howland 1996). The results of anatomical studies suggest that raptors have corneal accommodation (Beer 1893; Lord 1956; Murphy and Dubielzig 1993; Pardue and Sivak 1996), but there are no behavioral measurements. We have, for the first time, observed and measured changes in corneal curvature during behaviorally elicited accommodation in several species of raptors. The technique employed is limited in that we cannot restrict eye movements, simultaneously measure accommodative state, compensate for corneal asphericity, or ensure that the keratometer LEDs are reflected off the cornea at the same eccentricity in the different species, owing to differences in eye size. In spite of these limitations, however, it is clear that corneal accommodation is part of the natural accommodative response of some species of raptors. In chicks, corneal accommodation represents roughly 40% of the full accommodative response (Glasser et al. 1994), so corneal accommodation can contribute substantially to the accommodative capacity of species that employ it.

It is of interest to compare the accommodative behaviors of owls and hawks. Although considerable accommodation in owls (Murphy and Howland 1983) has been observed using a slightly different dynamic photorefractive technique, very little accommodation was seen in another study in which owls were observed by means of the technique that we employed (Howland et al. 1991). Howland et al. (1991) discuss the possibility that the disposition of the owls may influence the ability to elicit accommodation in the experimental setting. Certainly, in our case the birds were brought indoors from their outdoor pens, but this was true for both the hawks and the owls. It is unlikely that the testing environment or the handling technique was a factor in limiting the accommodative behavior of the owls specifically unless they are more reluctant to accommodate or are more easily alarmed by handling or by the environment. It is also possible that a negative lens held in front of only one eye may be less likely to stimulate accommodation in owls that have previously been shown to have symmetrical and coupled accommodation in the two eyes (Schaeffel and Wagner 1992). In the hawks, which do not have coupled accommodation, a lens over one eye would represent a strong monocular accommodative stimulus.

An additional new result from this study is the distinction between the hawks and owls in their ability to accommodate independently in the two eyes (uniocular or aniso-accommodation). Certainly, in the hawks that have greater ocular mobility, more laterally placed eyes, and more laterally placed foveas than the owls, the propensity for uniocular accommodation would be both expected and functionally adaptive.

Owls may have considerably reduced accommodative ability compared with hawks. When accommodation was observed in the owls it was typically in juvenile birds (Fig. 3g). The young altricial birds would have a greater need for accommodation in order, for example, to focus the beak of a parent as food is presented. In general, the feeding habits of owls, which tend to catch small rodents and swallow them whole, differ from those of the hawks, which tend to catch larger prey such as rabbits and pigeons and tear at the flesh while holding the carcass in the talons. Tearing at

a carcass presents a greater accommodative demand than the act of swooping down to grasp a prey item in the talons, a behavior that is similar for hawks and owls and can be accomplished by owls in complete darkness (Payne 1971). Eating with the beak, as is evident in granivorous birds pecking at seeds or in aquatic birds that capture prey using their beaks, rather than capturing prey with the talons may be the strongest determinant of accommodative ability. This hypothesis is supported by the observation that vultures, which are scavengers with weak talons ill-suited for catching or holding prey but with hooked bills ideal for tearing at flesh, have as much accommodation as the fish eagle and the older group of red-tailed hawks. Thus, the reasonably good accommodative ability of vultures cannot be required for prey capture, but is more likely to be determined by the visual demands imposed when tearing at a carcass in a similar manner to hawks and eagles.

Acknowledgments

Thanks are extended to the Halton Region Conservation Authority, Ontario, Canada; the Mountsberg Raptor Rehabilitation Center, Ontario, Canada (Michelle Bartlett and Martin Wernaart), the African Lion Safari, Ontario, Canada (Carol Precious and Jill Marvin), Robin Jones, and Andrew Norwinski. This work was funded in part by Natural Sciences and Engineering Research Council of Canada grants to J.G.S. and A.G. All procedures used in this study comply with "Principles of Animal Care," Publication No. 86-23, revised 1985, of the National Institutes of Health, and also with the current laws of Canada. The authors thank the anonymous reviewers for their comments.

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