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## SCIENTIFIC REPORT

# The relationship between accommodative amplitude and the ratio of central lens thickness to its equatorial diameter in vertebrate eyes

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**Aim:** To determine the relationship between accommodative amplitude and central lens thickness/equatorial lens diameter (CLT/ELD) ratio in vertebrates.

**Methods:** Midsagittal sections of lenses from fixed, post mortem eyes from 125 different vertebrate species were photographed. Their CLT/ELD ratios were correlated with independently published measurements of their accommodative amplitudes. Using the non-linear finite element method (FEM), the efficiency of zonular traction (the absolute change in central radius of curvature per unit force [ $|\Delta CR|/F$ ]) for model lenses with CLT/ELD ratios from 0.45 to 0.9 was determined.

**Results:** Vertebrates with CLT/ELD ratios  $\leq 0.6$  have high accommodative amplitudes. Zonular traction was found to be most efficient for those model lenses having CLT/ELD ratios  $\leq 0.6$ .

**Conclusions:** Vertebrates with lenses that have CLT/ELD ratios  $\leq 0.6$  – i.e. "long oval" shapes – have the greatest accommodative amplitudes; e.g. primates, diving birds and diurnal birds of prey. Vertebrates that have oval or spherical shaped lenses, like owls and most mammals, have low accommodative amplitudes. Zonular traction was found to be most efficient when applied to model lenses with CLT/ELD ratios  $\leq 0.6$ . The implications of these findings on the mechanism of accommodation are discussed.

The mechanism of vertebrate accommodation has fascinated scientists for hundreds of years. Multiple evolutionary mechanisms have developed to enable different species to accommodate: amphibians and snakes move their lenses forward; cyclostomes and teleosts move theirs backwards and in mammals the curvature of the lens changes.<sup>1</sup> This latter means, particularly in man, is the most efficient accommodative mechanism of all.<sup>2–7</sup>

Diving birds and primates, most notably humans, exemplify the efficiency and speed of accommodation induced by deformation of the lens. Diving birds and primates, such as the Rhesus monkey, accommodate up to a remarkable 40 to 60 diopters.<sup>8</sup> On the other hand, most other vertebrates with anatomically similar eyes and normal functioning ciliary muscles have minimal accommodative amplitude.<sup>2–7, 9–11</sup>

It has been consistently observed that in those vertebrates that rely on a change in equatorial diameter for accommodation, the presence of a spherical lens usually indicates low accommodative amplitude,<sup>2–7</sup> while recently, it has been proposed that quantification of the ellipticity of vertebrate lenses may be used to differentiate vertebrates with high amplitudes of accommodation.<sup>12</sup> The present study examines this hypothesis.

Using the non-linear finite element method (FEM), the efficiency of zonular traction was tested by determining how the absolute change in central radius of curvature per unit force ( $|\Delta CR|/F$ ) varies with the ratio of central lens thickness to equatorial lens diameter (CLT/ELD). In addition, the CLT/ELD ratios of post mortem vertebrate eyes were compared to their accommodative amplitudes as published in the literature.

## METHODS

### FEM model lens

A non-linear FEM, axisymmetrical generic two-dimensional model lens was constructed using ABAQUS (Version 6.5, ABAQUS, Inc., Pawtucket, RI, 2005). Standard and hybrid

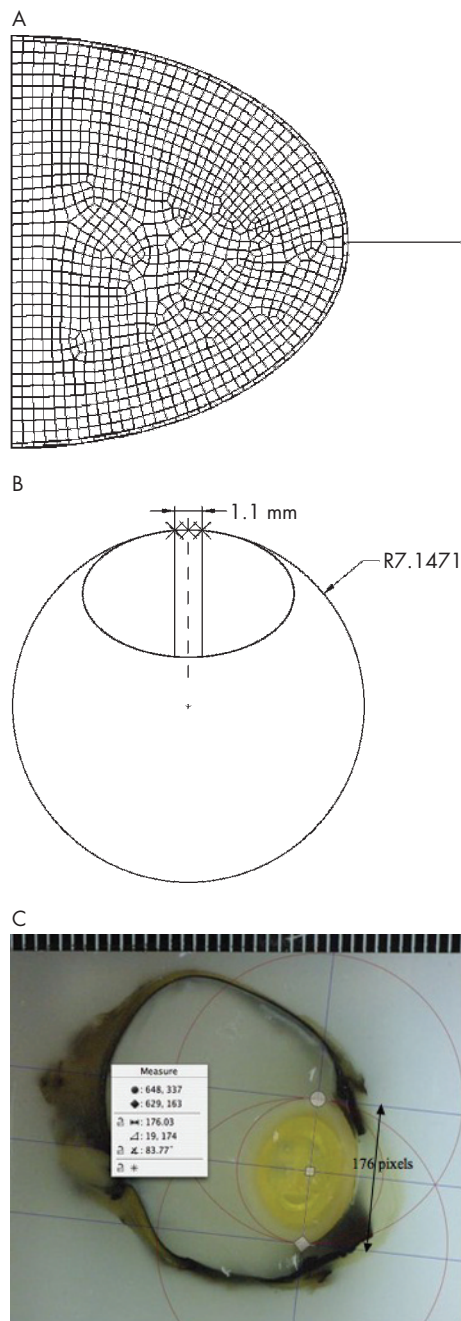
quadrilateral elements were used for the capsule and lens, respectively. The number of lenticular elements was varied, until 1345 lenticular and 76 capsular elements were found to consistently result in a converged solution (fig 1A). In general, a three-dimensional model is more realistic; however, since the lens is axisymmetric, and proper constitutive relationships and a hybrid formulation were used, a two-dimensional model is sufficient.<sup>13</sup>

For simplicity, the baseline profile of the model lens was a symmetrical ellipse. The baseline CLT/ELD ratio was varied from 0.45 to 0.9 by holding the equatorial diameter constant at 3.0 mm and changing the CLT. The lens capsule was assigned an elastic modulus of 1.5 MPa, a uniform thickness of 20  $\mu\text{m}$ , and a Poisson's ratio of 0.47.<sup>13</sup> The lens tissue was considered incompressible, with a Poisson's ratio equal to 0.5 and an elastic modulus of 150 Pa.<sup>13</sup> Contact elements with a stiffness of 0.1 N/mm and a frictional coefficient of 0.005 were placed between the capsule and stroma.<sup>13</sup> The zonules were modelled with an elastic modulus of 1.5 MPa.<sup>13</sup> Incremental displacements of the zonules were applied and the forces were obtained from the analyses. The central radius of curvatures were obtained by determining the radii of the spheres that best fitted the central lenticular surfaces of each model lens within a 1.1 mm aperture before and after the application of zonular traction (fig 1B).<sup>13</sup> The  $|\Delta CR|/F$ , required to obtain a 0.06 mm (2%) increase in the ELD was quantified.

### Vertebrate lenses

Paraffin blocks of the midsagittal sections of 125 vertebrate eyes from vertebrates that were at least 1 month of age were obtained from the Zoological Society of San Diego and photographed on a copy stand using a digital camera with a macro lens. A millimeter ruler was included in all photographs for calibration. The photographs were downloaded onto a computer and triplicate measurements, in pixels (Pixel Stick, version 1.1, [www.pixelatedsoftware.com](http://www.pixelatedsoftware.com)), of central thickness

and equatorial diameter of each lens were made (fig 1C). The person making the measurements (RAS) did not know the species at the time of the measurements, but did know the working hypothesis. The means and standard deviations of the CLT and ELD of the lenses, and their ratios, were calculated.



**Figure 1** A. An FEM converged mesh of a model lens, CLT/ELD = 0.6, with 1345 hybrid quadrilateral stromal and 76 standard quadrilateral capsular elements. B. Determining the CR from the best-fitted sphere to the central 1.1 mm aperture of the anterior surface of the model lens. C. Measuring the equatorial lenticular diameter with the pixel-measuring software.

The vertebrates were assigned high or low accommodative amplitudes according to literature reports based on their accommodation (high if >5 diopters) or classification and visual needs based on eating requirements.<sup>2-11</sup> Accommodation induced by a change in corneal curvature, forward or backward movement of the lens, or which involved a system of force mediated by a structure other than the ciliary muscle were not included. Statistical analysis was performed using two binomial distributions: one for the vertebrates with high accommodative amplitudes and one for the vertebrates with low accommodative amplitudes.

## RESULTS

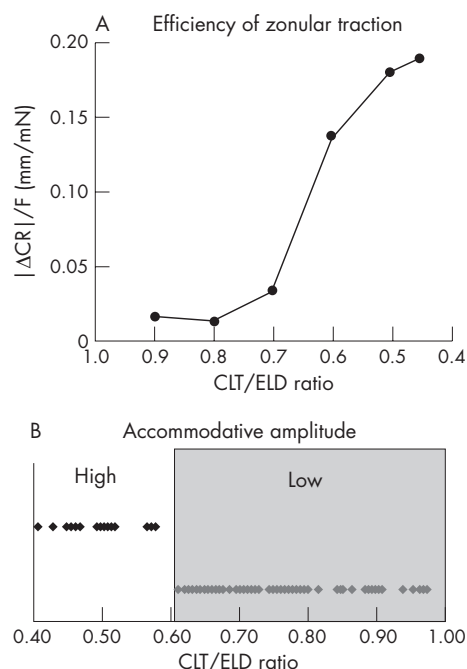
### FEM model lens

The FEM predicted that when zonular traction was applied to model lenses with CLT/ELD ratios  $\leq 0.6$ , the  $|\Delta CR|/F$  was  $\geq 0.13$  mm/mN, and when the CLT/ELD ratio was  $\geq 0.7$ , the  $|\Delta CR|/F$  was  $\leq 0.04$  mm/mN (fig 2A).

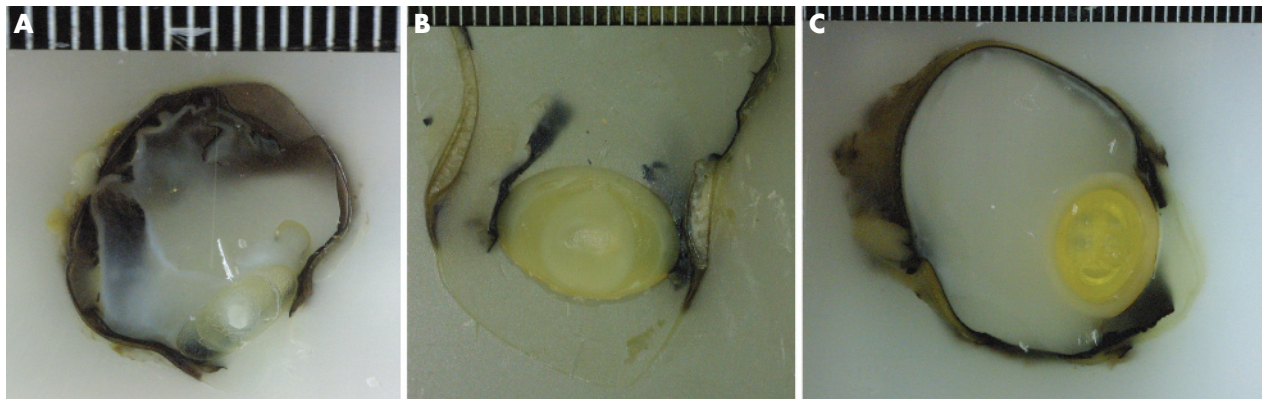
### Vertebrate lens accommodation

Post mortem vertebrate lenses with CLT/ELD ratios  $\leq 0.6$  had high amplitudes of accommodation and lenses with ratios  $>0.6$  had low accommodative amplitudes (figs 2B and 3; tables 1 and 2).

Given the lack of overlap in CLT/ELD ratios between those with high accommodative amplitudes ( $n = 22$ ) and those with low accommodative amplitudes ( $n = 103$ ), it can be said with 95% confidence (calculated from two exact binomial 97.5% confidence intervals, one for the high accommodators and one for the low accommodators) that any point of separation between the CLT/ELD ratios of 0.58 and 0.61 (e.g. a CLT/ELD ratio = 0.60) is simultaneously above the 84.6<sup>th</sup> percentile of



**Figure 2** A. A graph of zonular efficiency,  $|\Delta CR|/F$  (mm/mN), versus the baseline CLT/ELD ratio of the model lens for a 2% increase in equatorial lens diameter. B. Plot of the qualitative accommodative amplitudes of the vertebrates ( $n = 125$ ) versus their CLT/ELD ratios.



**Figure 3** Digital photographs of the paraffin blocks of the midsagittal sections of A. A diurnal bird of prey, North American kestrel (falcon), CTL/ELD = 0.43. B. A nocturnal bird of prey, Pacific horned owl, CTL/ELD = 0.74. C. A mammal, black buck (antelope), CTL/ELD = 0.78.

the target population of the high accommodative amplitude group and below the 3.5<sup>th</sup> percentile of the target population of the low accommodative amplitude group.

## DISCUSSION

Many vertebrates with minimal lenticular accommodation possess ciliary musculature with associated neural-ciliary muscle function, zonules, lens capsules and lenticular material properties that do not significantly differ from vertebrates with large amplitudes of accommodation.<sup>2-7 9-11</sup> Remaining possible explanations for the large differences in accommodative amplitudes between vertebrates with high and low amplitudes are geometric factors: the size and shape of their lenses and the relative size of the eye. In the rodent eye, for example, the lens occupies most of the interior of the eyeball, leaving little room for accommodation. Clearly such eyes have low or no accommodation. However, even when the lens does not occupy the bulk of the eyeball there will be variations in accommodative amplitude that are based on the geometry of the lens itself. This study has considered the effect of lens shape on accommodation.

The FEM analysis demonstrated that for a fixed increase in ELD, model lenses with the CTL/ELD ratios  $\leq 0.60$  responded at least three times more efficiently to zonular traction than lenses with CTL/ELD ratios  $\geq 0.7$  (fig 2A). These results may not apply to all vertebrates because the FEM model lens was generic, symmetrical and assumed that the nucleus and cortex of the accommodating lens have the same material properties. However, midsagittal sections of vertebrate eyes revealed that vertebrates with CTL/ELD ratios  $\leq 0.6$  have high amplitudes of accommodation, while those eyes with CTL/ELD ratios  $> 0.60$  have low accommodative amplitudes. Only 125 vertebrate eyes were studied. Although there was a strong statistical association between shape and accommodative amplitude, some experimental error may have been arisen from fixation artifacts and deviation from perfect midsagittal sectioning. In addition, the ages of lenses varied and hence every lens can be treated representative of the species at that given age.

The qualitative accommodative amplitudes of vertebrates can be predicted from the CTL/ELD ratios of their lenses. Interestingly, it has been observed that the suture patterns of some vertebrate lenses relate to accommodative amplitude.<sup>14</sup> This could be expected since the lens suture pattern directly

relates to dimensions of the lens and therefore to the CTL/ELD ratio. However, it is unlikely that either the pattern of lens sutures or the innate structure of the sutures has a direct mechanical influence on accommodative amplitude. The lens sutures have a preferential orientation. Therefore, if the lens sutures had a direct effect on the mechanical response of the lens to zonular traction, the viscoelastic shear properties of the lens should be affected by lens orientation. No such relation has been found. Furthermore, it has been demonstrated that the shear modulus of the lens tissue is low and that the lens tissue is more viscous than elastic.<sup>15</sup> Consequently, it is improbable that the relatively small area occupied by the lens sutures induces sufficient anisotropy in the lens to significantly affect its overall mechanical response to zonular traction.

The finding that vertebrate lenses with CTL/ELD ratios  $\leq 0.6$  – i.e. a “long oval” shape<sup>12</sup> – have high amplitudes of accommodation may have implications for understanding the mechanism of accommodation. According to Helmholtz’s theory of accommodation, the post mortem lens is expected to be in its most accommodated state given that the tension imposed by the ciliary muscle via the zonule is no longer functional. If this is the case, then post mortem lenses with the highest accommodative amplitudes could be expected to be more spherical than lenses from eyes with less or no accommodation. The opposite has been found. Post mortem lenses with a “long oval” shape have the largest accommodative amplitudes.

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Competing interests: RAS has a financial interest in the surgical reversal of presbyopia

Table 1 CLT/ELD ratios of vertebrate lenses.\*

Common Name	Scientific Name	Age	CLT/ELD Ratio	Common Name	Scientific Name	Age	CLT/ELD Ratio	Common Name	Scientific Name	Age	CLT/ELD Ratio
<b>Diving Birds, Waders, Group Feeders</b>											
Goliath Heron	<i>Ardea goliath</i>	10yr 7mo	0.40	Spotted Whistling Duck	<i>Dendrocygna guttata</i>	15yr 5mo	0.78	Central Chinese Goral	<i>Nemorhaedus goral arnouxius</i>	2yr 11mo	0.74
African Darter	<i>Anhinga melanogaster mufa</i>	13yr 8mo	0.45	Black-capped Lory	<i>Lorius lory erythrothorax</i>	15yr 1mo	0.78	Addax	<i>Addax nasomaculatus</i>	7yr 1mo	0.74
Harlequin Duck	<i>Histrionicus histrionicus</i>	2yr 3mo	0.49	Southern Purple-crested Turtaco	<i>Ploceus baglataecht reichenowi</i>	1yr 9mo	0.78	Lowland Wisent	<i>Bison bonasus bonasus</i>	19yr 7mo	0.75
Pink-backed Pelican	<i>Pelecanus rufescens</i>	20yr 1mo	0.49	Western Golden-masked Tanager	<i>Tauraco porphyreolophus</i>	9yr 3mo	0.79	Eastern Yellow-backed Duiker	<i>Cephalophus silvicultor silvicultor</i>	3yr 9mo	0.75
Black Heron	<i>Egretta ardesiaca</i>	6yr 1mo	0.51	Reitulated Giraffe	<i>Tangara larvata franciae</i>	2yr 8mo	0.96	Creten Wild Goat	<i>Capra aegagrus cretica</i>	7yr 6mo	0.75
Black-headed Heron	<i>Ardea melanocephala</i>	18yr 0mo	0.56	Scimitar Horned Oryx	<i>Giraffa camelopardalis reticulata</i>	2yr 3mo	0.61	Gemsbok	<i>Oryx gazella gazella</i>	1yr 11mo	0.76
Dalmatian Pelican	<i>Pelecanus crispus</i>	27yr 4mo	0.57	East African Sitatunga	<i>Oryx dammah</i>	10yr 4mo	0.61	Domestic Cattle	<i>Bos primigenius f. taurus</i>	7yr 3mo	0.76
Cranes, Ibises, Ruffs, Shelducks				Masai Giraffe	<i>Tragelaphus speki speki</i>	2yr 7mo	0.62	North Indian Muntiac	<i>Muntiac munitiac vaginalis</i>	17yr 8mo	0.76
West African Crane	<i>Balaearica pavonina pavonina</i>	15yr 1mo	0.45	Domestic Bactrian Camel	<i>Giraffa camelopardalis hippelskirchi</i>	0yr 1mo	0.62	South African Be-eared Fox	<i>Odocoyle megalotis megalotis</i>	7yr 8mo	0.76
Waldtrapp Ibis	<i>Geranotus eremita</i>	18yr 3mos	0.45	Southern White Rhinoceros	<i>Cervus fimoensis russa</i>	6yr 2mo	0.62	Chinese Bharal	<i>Pseudois nayaur szechuanensis</i>	1yr 1mo	0.77
Ruff	<i>Philomachus pugnax</i>	1yr 0mo	0.47	West Caucasian Tur	<i>Capra ibex caucasica</i>	1yr 1mo	0.62	Javan Banteng	<i>Bos javanicus javanicus</i>	15yr 9mo	0.77
Common Shelduck	<i>Tadorna tadorna</i>	0yr 1 mo	0.51	Southern African Cheetah	<i>Acinonyx jubatus jubatus</i>	13yr 7mo	0.63	Zambesi lechwe	<i>Kobus leche leche</i>	2yr 4mo	0.77
Northern Hadada Ibis	<i>Bostrychia hagedash nilotica</i>	20yr 4mo	0.52	Domestic Bactrian Camel	<i>Camelus ferus f. bactrianus</i>	24yr 5mo	0.63	Dendrologus Tree Kangaroo	<i>Dendrologus goodfellowi kangaroo</i>	16yr 0mo	0.78
Diurnal Birds of Prey				Transvaal Lion	<i>Panthera leo krugeri</i>	0yr 5mo	0.63	Queensland Koala	<i>Phascogale cinereus adustus</i>	9yr 10mo	0.78
North American Kestrel	<i>Falco sparverius sparverius</i>	10yr 3mo	0.43	Southern White Rhinoceros	<i>Ceratotherium simum simum</i>	8yr 10mo	0.64	Sichuan Takin	<i>Budorcas taxicolor tibetana</i>	20yr 3mo	0.78
Northern Aplomado Falcon	<i>Falco femoralis septentrionalis</i>	16yr 8mo	0.46	Indochinese Sika	<i>Cervus nippon pseudaxis</i>	15yr 1mo	0.64	Black Buck	<i>Antelope cervicapra renalis</i>	7yr 2mo	0.78
Western Rüppell's Vulture	<i>Gyps rueppellii rueppellii</i>	19yr 6mo	0.46	Nilgiri Tahr	<i>Hemitragus hylocrius</i>	6yr 10mo	0.64	Kenya Impala	<i>Aepyceros melampus</i>	7yr 9 mos	0.79
Northern Bald Eagle	<i>Haliaeetus l. washingtonensis</i>	28yr 11mo	0.47	Yael Rhebok	<i>Pelea capreolus</i>	7yr 4mo	0.64	Nilgai	<i>Boselaphus tragocamelus</i>	14yr 3mo	0.79
African Pygmy Falcon	<i>Polyhierax semitorquatus</i>	2yr 8mo	0.50	Eastern Kiang Somali Wild Ass	<i>Equus kiang holdereri</i>	21yr 2mo	0.64	South African Sable Antelope	<i>Hippotragus niger niger</i>	19yr 6mo	0.79
Andean Condor	<i>Vultur gryphus</i>	35yr 5mos	0.52	Blesbok	<i>Damaliscus dorcas phillipsi</i>	0yr 3mo	0.65	Armenian Mouflon	<i>Ovis orientalis gmelini</i>	5yr 8mo	0.80
Secretary Bird	<i>Sagittarius serpentarius</i>	0yr 1mo	0.57	Altai Wapiti	<i>Cervus elaphus sibiricus</i>	14yr 6mo	0.65	Himalayan Tahr	<i>Hemitragus jemihicus</i>	8yr 7mo	0.81
Flightless and Nearly Flightless Birds				East African Sitatunga	<i>Tragelaphus speki speki</i>	8yr 4mo	0.65	California Raccoon	<i>Procyon lotor psora</i>	6yr 5mo	0.84
Kagu	<i>Rhynchotus jubatus</i>	12yr 6mo	0.50	Jimela Topi	<i>Damaliscus lunatus jimela</i>	10yr 8mo	0.65	Burgers' Tree Kangaroo	<i>Dendrologus goodfellowi buergersi</i>	10yr 0mo	0.85
Ostrich	<i>Struthio camelus massaicus</i>	7yr 8mo	0.58	Transcaspan Urial	<i>Ovis vignei arkal</i>	2yr 6mo	0.66	Southern Gerenuk	<i>Litocranius walleri walleri</i>	11yr 9mo	0.85
Primates				Uganda Giraffe	<i>Giraffa camelopardalis rothschildi</i>	12yr 10mo	0.66	California Sea Lion	<i>Zalophus californianus californianus</i>	36yr 6mo	0.85
Gelada Baboon	<i>Theropithecus gelada</i>	19yr 9mo	0.57	Sudan Barbary Sheep	<i>Bubo virginianus pacificus</i>	28yr 5 mo	0.74	Bornean Bearded Pig	<i>Sus barbatus barbatus</i>	13yr 10mo	0.86
Nocturnal Birds of Prey				Pacific Horned Owl	<i>Bubo virginianus pacificus</i>	28yr 5 mo	0.74	Alpine Ibex	<i>Capra ibex ibex</i>	2yr 1mo	0.86
Pacific Horned Owl	<i>Bubo virginianus pacificus</i>	28yr 5 mo	0.74					Bontebok	<i>Damaliscus dorcas dorcas</i>	14yr 3mo	0.88

Table 1 Continued

Common Name	Scientific Name	Age	CLT/ELD Ratio	Common Name	Scientific Name	Age	CLT/ELD Ratio	Common Name	Scientific Name	Age	CLT/ELD Ratio
<b>Diving Birds, Waders, Group Feeders</b>											
<b>Non-diving Birds (continued)</b>											
Non-diving Birds				Eastern Giant Eland	<i>Taurotragus derbianus</i>	2yr 5mo	0.66	Southern Steenbok	<i>Raphicenus campestris campestris</i>	2yr 7mo	0.88
Mountain Bamboo Partridge	<i>Bambusicola fytchii fytchii</i>	8yr 4 mo	0.63	East African Bongo	<i>Tragelaphus eurycerus isaaci</i>	3yr 9mo	0.67	African Hedgehog	<i>Atelerix albiventris</i>	3yr 9mo	0.89
Mandarin Duck	<i>Aix galericulata</i>	15yr 1mo	0.63	White-lipped Deer	<i>Cervus albirostris</i>	14yr 5 mo	0.67	Siberian Musk Deer	<i>Moschus moschiferus moschiferus</i>	1yr 1mo	0.89
Wrinkled Hornbill	<i>Aceros corrugatus</i>	8yr 4mo	0.65	Malayan Sambar	<i>Cervus unicornis malaccensis</i>	10yr 0mo	0.67	Canadian Otter	<i>Lontra canadensis canadensis</i>	14yr 1mo	0.90
Javan Green Peafowl	<i>Pavo muticus muticus</i>	10yr 5mo	0.66	Siberian Reindeer	<i>Rangifer tarandus sibiricus</i>	9yr 1mo	0.67	Bornean Prevost's Squirrel	<i>Callosciurus borneoensis</i>	13yr 9mo	0.90
Ross's Goose	<i>Anser rossii</i>	2yr 9mo	0.67	Przewalski's Wild Horse	<i>Equus przewalskii</i>	5yr 1mo	0.68	Burmese Thamin	<i>Cervus eldi thamin</i>	4yr 11 mo	0.97
Red-Billed Malkoha	<i>Phaenicopterus javanicus</i>	0yr 2mos	0.67	Fringe-eared Oryx	<i>Oryx gazella callotis</i>	1yr 4mo	0.68	Uganda Kob	<i>Kobus kob thomasi</i>	0yr 6mo	0.97
Sulawesi Tarictic Hornbill	<i>Penelopides exarhatus sanfordi</i>	7yr 3mo	0.68	South African Springbok	<i>Antidorcas marsupialis marsupialis</i>	0yr 6mo	0.68	Reptiles			
Curl-crested Araucari	<i>Pteroglossus beauharnaesii</i>	1yr 5mo	0.68	South African Greater Kudu	<i>Tragelaphus strepsiceros strepsiceros</i>	15yr 9mo	0.69	Cuban False Chameleon	<i>Chamaeleon chamaeleonidae</i>	5yr	0.63
Collared Imperial-Pigeon	<i>Ducula mullerii</i>	1yr 6mo	0.69	Cape Buffalo	<i>Syncerus caffer caffer</i>	25yr 6mo	0.70	Cuban Iguana	<i>Cyclura nubila nubila</i>	12yr 9mo	0.72
Victoria Crowned Pigeon	<i>Goura victoria</i>	5yr 8mos	0.71	Mhorr Gazelle	<i>Gazella dama mhorr</i>	14yr 1mo	0.70	Prehensile-tailed Iguana	<i>Polychrus marmoratus</i>	2yr 8mo	0.73
Caribbean Flamingo	<i>Phoenicopterus ruber ruber</i>	9yr 9mo	0.72	Lowland Nyala	<i>Tragelaphus angasii</i>	10yr 2 mo	0.70	Johnson's Crocodile	<i>Crocodylus johnstoni</i>	4yr 1 mo	0.80
Reichenow's Helmeted Guineafowl	<i>Numida meleagris reichenowi</i>	0yr 8mo	0.72	Turkmen Markhor	<i>Capra falconeri heptheri</i>	12yr 4 mo	0.70	Pyramid Agama	<i>Laudakia stellio</i>	2yr 4mo	0.81
Fukien Niltava	<i>Niltava davidi</i>	8yr 7mo	0.74	Rocky Mountain Goat	<i>Oreamnos americanus</i>	16yr 8mos	0.71	Malaysian Giant Turtle	<i>Orlitia borneensis</i>	8yr 2mo	0.91
Western Double-eyed Fig Parrot	<i>Cyclopsitta diophthalma diophthalma</i>	9yr 0mo	0.75	Eastern White-bearded Gnu	<i>Connochaetes taurinus albobabatus</i>	16yr 4mo	0.71	Reticulated Python	<i>Python reticulatus</i>	18yr 4mo	0.94
W Green-naped Pheasant Pigeon	<i>Otidiphaps nobilis nobilis</i>	10yr 6mo	0.77	Barasingha	<i>Cervus duvauceli duvauceli</i>	9yr 10mo	0.74	Fiji Island Banded Iguana	<i>Brachylophus fasciatus</i>	15yr 3mo	0.95
				Indian Gaur	<i>Bos gaurus gaurus</i>	15yr 5mos	0.74				

\*Qualitative accommodative amplitudes for each group are given in Table 2.

**Table 2** Vertebrate accommodative amplitudes verses mean CLT/ELD ratios.

Classification	Accommodative Amplitude	Number	Mean CLT/ELD Ratio	Standard Deviation
Diving Birds, Waders, Group Feeders	High	7	0.50	0.06
Cranes, Ibises, Ruffs, Shelducks	High	5	0.48	0.03
Diurnal Birds of Prey	High	7	0.49	0.05
Flightless and Nearly Flightless Birds	High	2	0.54	0.06
Primates	High	1	0.57	N/A
Nocturnal Birds of Prey	Low	1	0.74	N/A
Non-diving Birds	Low	20	0.70	0.04
Mammals	Low	74	0.73	0.09
Reptiles	Low	8	0.81	0.11

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