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Effects of Phylogeny on Structural Correlations of Vertebrate Eyes

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Effects of Phylogeny on Structural Correlations of Vertebrate Eyes

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Abstract:

Common ancestry prevents scientists from using traditional statistical tests in dimensional comparisons that span entire clades. Data in these cases are non-independent, so a variety of special statistical methods have been developed specifically for phylogenetic comparative analyses. A phylogenetic least squares method was used to re-examine four published datasets detailing structural correlates of eyes while factoring in the different ways the phylogeny was expected to affect the covariance in trait values. All analyses were carried out in a strict phylogenetic context, using published time-calibrated phylogenies and the statistical platform R. Specifically, Pagel's lambda was used to determine how much of an influence phylogeny had on each pair of traits. In all tested soft and hard tissue correlations, the phylogeny of the species slightly altered the trend lines of the measurements, compared to lines that did not take phylogenetic relationship into consideration. These results do not contradict previous results, but further work needs to be done to determine the implications that significant phylogenetic signal has on subsequent analyses. Future studies should account for phylogenetic relationships which have been shown to influence the relationship between traits.

Introduction:

Observations from species related by a phylogenetic tree are often statistically non-independent due to common ancestry (Felsenstein, 1985). For evolutionary scientists looking to compare interspecific traits between multiple species they need to factor in that closely related species have traits that are more similar to each other compared to species that are more distantly related (Blomberg *et al*., 2003). This relationship prevents the usage of common statistical comparison tests such as linear regressions and correlations. Scientists have relied on such comparisons to draw conclusions about relationships between species and their morphological traits (Cheverud *et al.*, 1985; Garland, 1993; Revel and Collar, 2009) by using tests tailored to compare traits across clades without being limited by independence assumptions that the data cannot meet (McDonald, 2009).

The time at which a species deviates is directly related to physiological and morphological characteristics. Closely related, relatively new species are expected to look and act like each other while species that have deviated farther back in the evolutionary history are expected to look and act very differently (Felsenstein, 1985; Blomberg *et al*., 2003).

Phylogenetic comparative methods have been improving to meet the demand by scientists as more and more is understood about evolutionary relationships, focusing on testing character and behavioral correlations such as body size, limb proportions, phenotypes, and activity patterns (Felsenstein, 1985; Kohlsdorf *et al*., 2001; Bloomberg *et al*., 2003; Motani and Schmitz, 2011). Felsenstein (1985) developed the method of phylogenetic independent contrasts as a way to combine a hierarchical evolutionary history and phylogeny to regression and correlations statistics with the integration of phylogenetic trees. This has

further been improved upon by modifying it to accommodate different types of variables and for accommodating different models of evolution such as the Ornstein–Uhlenbeck process.

The comparative method is a central tool for investigating the adaptive significance of organismal traits (Butler, 2004), soft to hard tissue ratios (Schultz, 1940), physiological criteria (Garland *et al*., 1993), and animal behavior in extinct species (Hall, 2008; Schmitz, 2009; Hall, 2009; Schmitz & Motani, 2011). While these methods have reduced the issue of phylogenetic relationships between data and statistical analyses, it has created a whole new problem for evolutionary biologists. In order to perform these methods, there needs to be an accurate phylogeny, which has not always been readily available at the time. Not only have well supported evolutionary trees not been readily available, with the new techniques such as gene analysis, phylogenies remain unsettled, as scientists dispute where species should be placed (Dumbacher *et al.*, 2003).

Prior to these tree releases, scientists all dealt with the lack of information in different ways. In some situations, scientists would circumvent the lack of a semi-unanimous tree by using another method that doesn't require a phylogeny. Another way to obtain the necessary phylogeny would be to fuse together piecemeal, several smaller phylogenies (Hall, 2008). The problem with combining phylogenies is that often the smaller trees come from different sources and from different times which can reduce the accuracy of the final constructed tree.

In the past, scientists have used alternate tests to analyze correlations between continuous traits, as there has been some debate about which tests were the best to use and the amount of weight that phylogeny should have versus the ecology (Webb *et al*., 2002). Various tests have included ANCOVAs, where the non-independent data was ignored, OLS

unweighted linear regression analysis (Schmitz, 2009), or a reduced major axis regression analysis (Muchlinski and Perry, 2011).

In this study, datasets from four papers (Schultz, 1940; Hall, 2008; Schmitz, 2009; Hall, 2009) detailing correlations between soft and hard tissue in vertebrate skulls will be reexamined using a method that accounts for the phylogenetic covariance between all of the study species. This analysis will use recently published phylogenetic trees that were unavailable at the time of the original study to determine if phylogeny affects the correlation between different pairs of traits.

Materials and Methods:

Measurements of eyeball diameter, eyeball axial length, and external diameter of scleral ring in 84 species (n = 84) were taken from a paper about estimating visual performances in birds (Schmitz, 2009). More measurements of orbit depth, orbit diameter, internal scleral ring diameter and outer scleral ring diameter (EXT), scleral maximum length, corneal diameter, and axial length were compiled from a paper on eye morphology in 53 bird species (n = 53) and how that relates to their activity times (Hall, 2008).

Eye measurements of squamates were gathered in approximately the same manner, from a paper on the eye morphology and its relationship to activity times (Hall, 2009). From this dataset, I used orbit depth, orbit diameter, inner and outer (EXT) scleral ring diameters, axial length and scleral maximum length (n = 43).

In the bird and reptile data (Hall, 2008; Hall, 2009), the external diameter of the scleral ring, which is an important measurement used often in eye analysis correlations, had to be solved for with the given data. To solve for the outer external scleral ring diameter, the root of the squared scleral ring maximum length subtracted from the squared axial scleral ring length, was doubled, and then added to the scleral ring inner diameter (Equation 1). This calculation was done for the reptile and bird scleral rings in order to study the correlations the external scleral ring diameter has with things such as the axial length of the eyeball.

$$Ext = 2 \times \sqrt{\text{Scleral ring max length}^2 - \text{Axial scleral ring length}^2} + \text{Scleral ring inner diameter} \quad (1)$$

A dataset containing the orbit volume and eyeball diameter of female and male, 18 and 13 different species, respectively was used in this study on eye and body mass

correlations in primates (Schultz, 1940). This paper did not publish any skull dimensions and the body mass was not needed for this specific analysis.

We used phylogenies by Jetz et al. (2012, birds), Bergmann and Irschick (2011, squamates), and Arnold et al. (2010, primates). The Jetz et al. phylogeny is based off the Ericson backbone and contains 6670 OTU's (Ericson, 2012). In the analysis, one bird tree was randomly chosen out of 1000 trees. A more robust analysis would be to run the analysis for each of the 1000 trees before reporting on the findings and repeating the analysis using the Hackett backbone trees (Hackett *et al.*, 2008). Time constraints and the deadline to complete this project prevented this from being done.

Phylogenetic influence was determined by performing phylogenetic generalized least square analysis while optimizing Pagel's lambda (Grafen, 1989; Pagel, 1999). If trait residuals were largely dependent on phylogeny, then the lambda would be close to 1. Conversely, if there was little phylogenetic influence, the lambda value would be closer to 0. All analyses were performed in R (Paradis *et al*., 2004; Harmon *et al*., 2008; Orme, 2011; Pinheiro *et al.,* 2014)

Data that were not identified to the species level, data with suspected typographical errors, or were missing values were removed from the final datasets. The data were separated out by clades, and in the case of the primate's dataset, gender. Primates do not have ossified structures in their eyes. The comparisons studied are as follows:

Table 1. List of trait comparisons by group.

	Trait Comparisons:
Birds	Eyeball Diameter and External Scleral Ring
	Eyeball Length and External Scleral Ring
	Eyeball Diameter and Eyeball Length
	Orbit Diameter and Axial Length
	Orbit Length and Axial Length
	External Sclerotic Ring Diameter and Axial Length
	Internal Sclerotic Ring Diameter and Corneal Diameter
Reptiles	Eyeball Diameter and Eyeball Length
	Eyeball Diameter and External Scleral Ring
	Eyeball Length and External Scleral Ring Diameter
Primates	Orbit Volume and Eye Diameter ♀
	Orbit Volume and Eye Diameter ♂

Results:

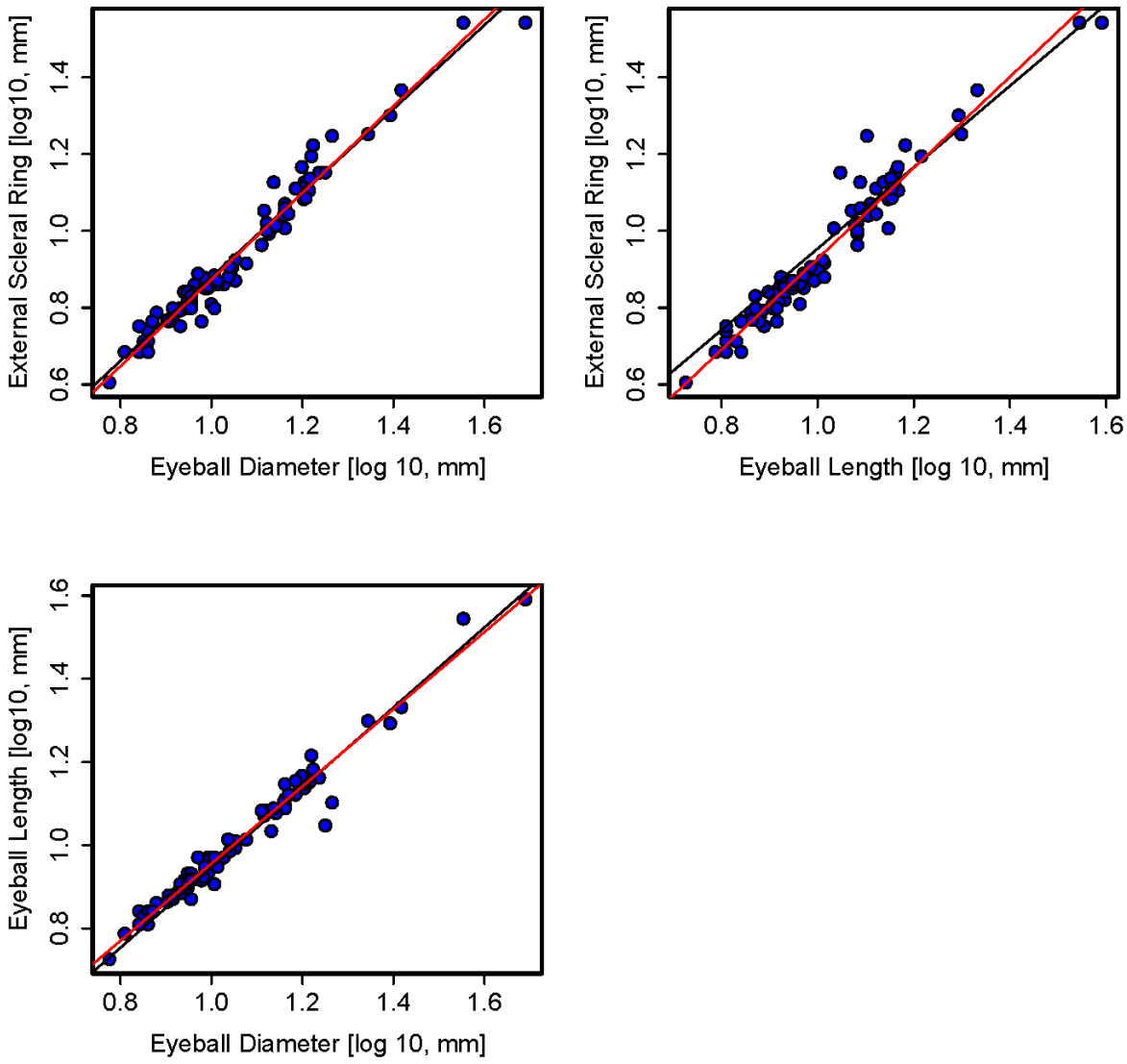

Figure 1. Scatterplots showing the bird dimension comparisons of the eyeball diameter and external scleral ring ($\lambda = 0.483$), eyeball length and external scleral ring ($\lambda = 0.794$), and eyeball diameter and eyeball length ($\lambda = 0.693$), with a red trend line that accounts for phylogenetic relationships between points and a black trend line that ignores phylogeny (Schmitz, 2009).

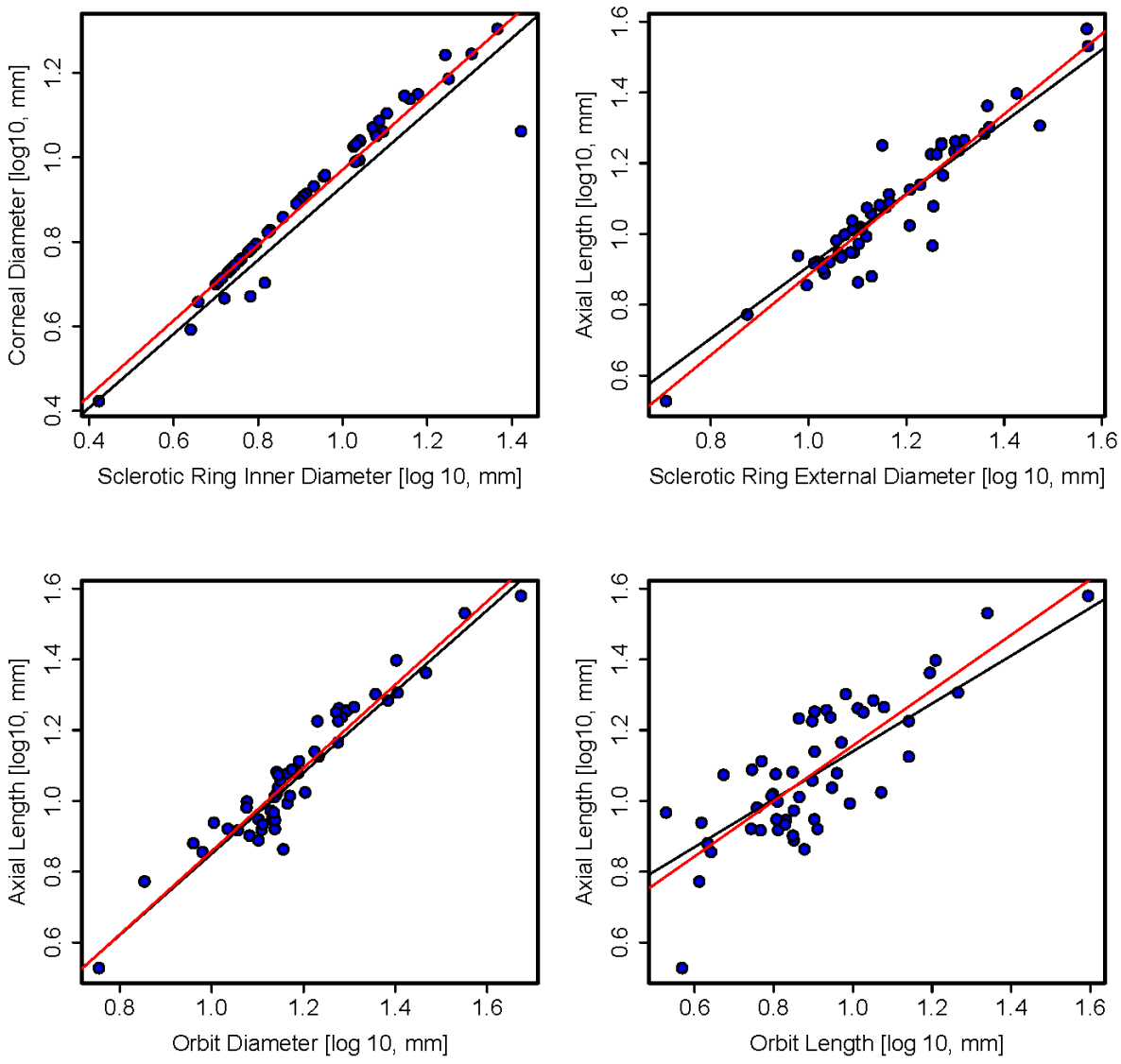

Figure 2. Scatterplots showing the bird morphology comparisons of the internal sclerotic ring diameter and corneal diameter ($\lambda = 1.069$), external sclerotic ring diameter and axial length ($\lambda = 0.882$), orbit diameter and axial length ($\lambda = 0.900$), and orbit length and axial length ($\lambda = 0.914$), with a red trend line that accounts for phylogenetic relationships between points and a black trend line that ignores phylogeny (Hall, 2008).

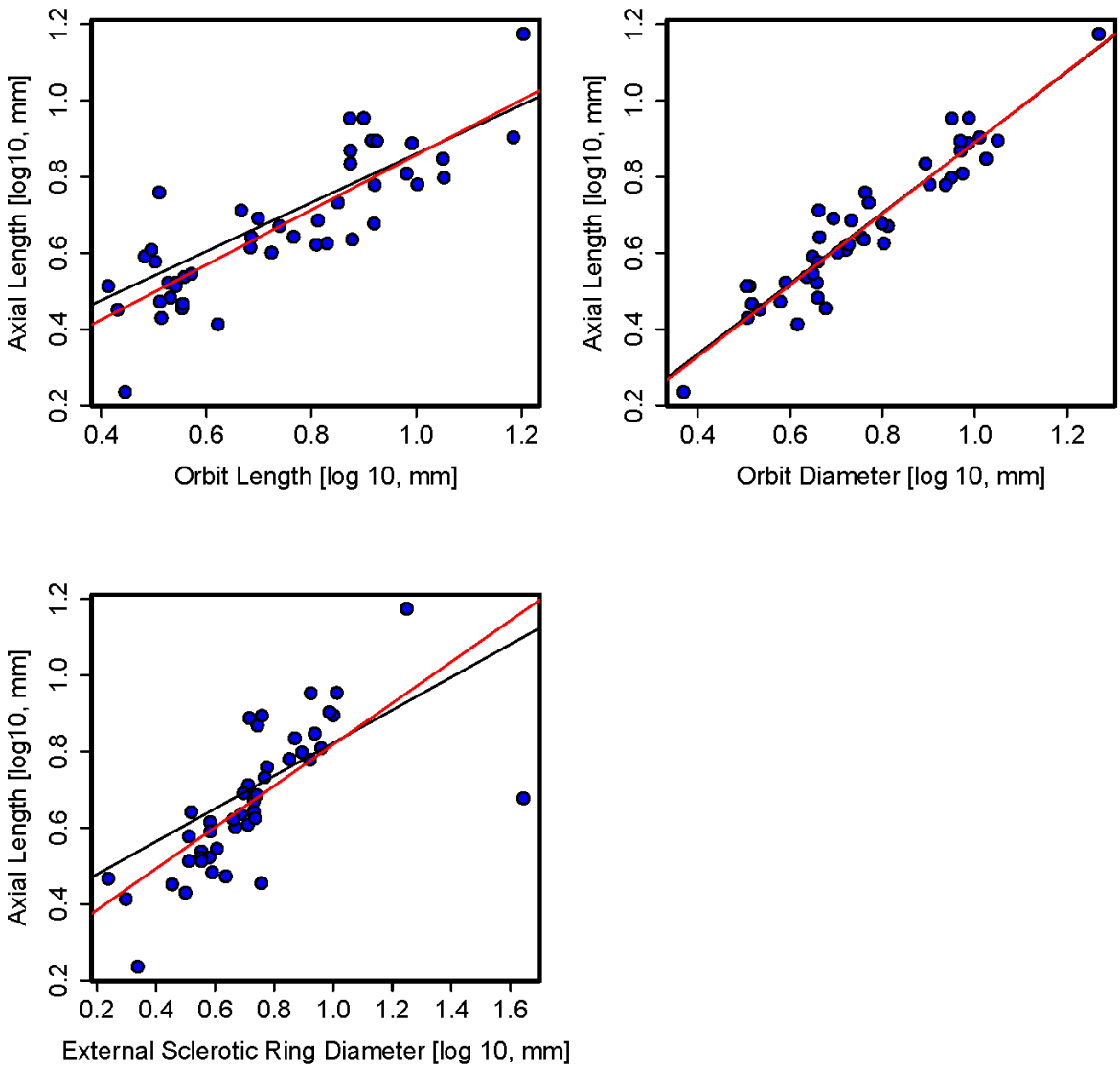

Figure 3. Scatterplots showing the squamate morphology comparisons of the orbit length and axial length ($\lambda = 0.583$), orbit diameter and axial length ($\lambda = 0.107$), and external sclerotic ring diameter and axial length ($\lambda = 0.613$), with a red trend line that accounts for phylogenetic relationships between points and a black trend line that ignores phylogeny (Hall, 2009).

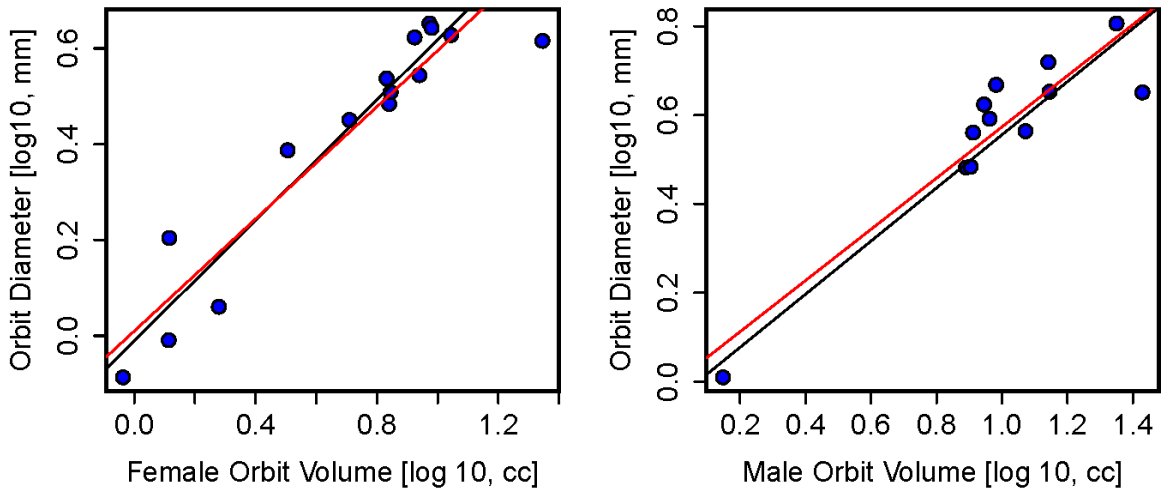

Figure 4. Scatterplots showing the primate morphology comparisons of the orbit volume and eye diameter in females ($\lambda = 1.050$) and males ($\lambda = 0.979$), with a red trend line that accounts for phylogenetic relationships between points and a black trend line that ignores phylogeny (Schultz, 1940).

Table 2. Correlation Statistics

	Comparison	λ	Log Restricted Likelihood	x- Intercept	Slope	Residual SE
Birds - Hall	Orbit Diameter and Axial Length	0.900	84.900	-0.296	1.147	0.059
	Orbit Length and Axial Length	0.914	55.023	0.464	0.676	0.108
	External Sclerotic Ring Diameter and Axial Length	0.882	70.145	-0.111	1.020	0.078
	Internal Sclerotic Ring Diameter and Corneal Diameter	1.069	93.074	0.057	0.875	0.060
Birds - Schmitz	Eyeball Diameter and Eyeball Length	0.693	176.188	-0.017	0.963	0.035
	Eyeball Diameter and External Scleral Ring	0.483	152.290	-0.214	1.094	0.042
	Eyeball Length and External Scleral Ring	0.794	143.142	-0.106	1.060	0.056
Reptiles - Hall	Orbit Diameter and Axial Length	0.107	58.051	-0.036	0.926	0.061
	Orbit Length and Axial Length	0.583	38.014	0.220	0.641	0.111
	External Sclerotic Ring Diameter and Axial Length	0.613	30.176	0.392	0.431	0.135
Primates - Schultz	Orbit Volume and Eye Diameter ♀	1.050	7.843	0.045	0.503	0.148
	Orbit Volume and Eye Diameter ♂	0.979	6.097	0.443	0.146	0.100

The orbit volume and eye diameter in female primates (n = 18, $\lambda > 1$, **Figure 4**), and the internal scleral ring diameter and corneal diameter in birds (n = 53, $\lambda > 1$, **Figure 2**), are both only dependent on phylogeny (**Table 2**). The comparisons between the orbit diameter and axial length (n = 53, $\lambda = 0.900$, **Figure 2**), orbit length and axial length in birds (n = 53, $\lambda = 0.914$, **Figure 2)**, and orbit volume and eye diameter in primates (n = 13, $\lambda = 0.979$, **Figure 4**) all were highly dependent on phylogeny. Interestingly, the orbit diameter and axial length of squamates was almost independent of any phylogeny (n = 43, $\lambda = 0.107$, **Figure 3**).

Discussion:

The analysis of vertebrate eye correlations follows the same pattern of previous studies (Hall, 2008; Schmitz, 2009) even when phylogenetic covariance is accounted for. However, including the phylogeny into the calculations does have an effect on the trend line in comparison to a trend line that doesn't account for species relatedness. This shows promise for more accurate estimates of soft-tissue eye structures on the basis of skeletal dimensions and consequently improved correlates linked to types of behavior.

The lowest optimal lambda value was found for the correlation of orbit length and axial eyeball length in squamates. The bird datasets and primate data in general tended to have more phylogenetic signal. For all of the correlations tested from the smaller of the two bird datasets, there were three optimized lambda values greater than 0.882. This shows that these correlations are strongly influenced by phylogeny. In the larger bird dataset (Schmitz, 2009), the optimized lambda values were lower, but this could be a result from the different measurements that were done.

These have implications for the studies that have used eye correlates to hypothesize the behavior and activity in extant fossils (Hall, 2008; Schmitz, 2009; Hall, 2009; Schmitz and Motani, 2011). Depending on what bony correlates are used, the phylogeny might play an influential role in the morphological characteristics. The exact, quantified, amount of statistical significance phylogeny has on eye correlates still needs to be determined. However, the results of finding phylogenetic signal in the correlations between the soft- and hard-tissues emphasizes the importance of incorporating phylogeny in methods that infer diel activity patterns in fossil vertebrates (Hall, 2008; Schmitz, 2009; Hall, 2009; Schmitz and Motani, 2011; Motani and Schmitz; 2011).

Future work needs to be done on bird eye correlates that take the same measurements from similar sets of species to determine why there are such different optimized lambda values for the two datasets of birds. While the pairs of measurements are different, there could also be an effect from the different species in each dataset or the amount of species within each dataset.

Another improvement to this study would be to incorporate more species, on two different levels. On the individual level, there were a fair number of instances where the measurements came from only one or two individuals from which an "average" was derived from. By having a larger sample size by species, it would improve the data by dampening the effect of individual outliers with eye differences. On a species level, more species in the analysis would also improve the results. The approach relies on having a wide variety of species in a phylogeny, so adding more species would only make the results more accurate. The small sample size may have a bias towards one particular clade due to unequal representation. Large amounts of species had to be removed from the initial datasets due to missing measurement values and uncorrectable typos in order to maintain the integrity of the data and log-log plots.

I would like to conclude my thesis by noting the importance of natural history museums. Museums that cater to the academic community have been the go to locations for data gathering because of their large collections of specimens. Sadly, such facilities have become rarer and rarer because of a decrease in available funding. This study is heavily based on data that is only gatherable in facilities that house measurable bone collections and soft tissue collections. One of the unavoidable problems with the data was small samples sizes measured in one or two individuals of a single species. In the future, larger data sets

with an adequate sample size for all species utilizing the same method could be done to solidify the understanding about different correlations of the vertebrate skull and scleral ring among vertebrates.

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I would like to thank Dr. Schmitz for his supervision of this project by offering significant guidance, help, and feedback throughout the entire semester. All of the R coding and analysis wouldn't have been possible without his help with the initial code, along with the continuous troubleshooting that needed to be done to get it to work for my specific data. I'd also like to express my gratitude to the entire Schmitz lab for their assistance in the R coding sessions. I would also like to thank Dr. McFarlane for his grading as my second reader.

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Appendix:

Table i. Skeletal and tissue measurements of the birds (Hall, 2008).

Taxon	Orbit Length (mm)	Orbit Diameter (mm)	Axial Length (mm)	Internal Sclerotic Ring Diameter (mm)	External Sclerotic Ring Diameter (mm)	Corneal Diameter (mm)
Athene noctua	10.28	18.92	18.27	12.46	19.96	11.52
Athene brama	7.30	18.90	17.11	10.99	19.86	10.92
Glaucidium brasilianum	8.57	19.73	18.05	11.95	18.70	11.44
Glaucidium perlatum	7.89	16.99	16.80	10.97	17.81	10.97
Glaucidium jardinii	6.38	14.55	11.92	7.91	14.39	7.91
Bubo africanus	15.64	29.28	23.03	20.19	23.20	17.58
Bubo bubo	21.86	35.58	33.95	23.23	37.30	20.15
Strix aluco	16.17	25.25	24.96	17.8	26.65	15.35
Otus scops	8.00	16.76	13.78	10.94	16.92	9.86
Megascops asio	9.59	22.75	20.04	14.42	23.42	13.76
Otus rutilus	8.77	19.22	17.24	12.72	20.29	12.72
Otus longicornis	8.00	19.59	17.89	11.78	18.69	11.78
Tyto alba	10.62	18.67	17.80	12.01	14.15	11.24
Podargus strigoides	18.43	25.40	20.23	15.06	29.72	14.11
Aegotheles insignis	3.37	13.66	9.27	8.06	17.92	8.09
Nyctibius griseus	11.26	24.21	19.24	17.48	22.88	17.48
Caprimulgus europaeus	7.04	13.85	12.06	10.71	13.97	9.77
Caprimulgus macrurus	5.88	15.50	12.95	10.61	14.60	10.61
Caprimulgus madagascariensis	7.90	14.11	11.42	9.02	13.42	9.02
Uropsalis segmentata	4.71	13.96	11.85	10.75	13.16	10.75
Eurostopodus macrotis	11.98	20.42	18.41	13.99	20.80	13.99
Hydropsalis climacocerca	5.72	11.91	9.58	7.77	11.40	7.77
Nyctidromus albicollis	5.56	14.96	12.25	10.68	14.63	10.68
Podager nacunda	9.35	18.84	14.64	12.2	18.83	12.2
Nyctiphrynus ocellatus	6.23	14.80	10.33	8.54	12.86	8.54
Falco sparverius	9.11	15.42	11.98	8.2	18.00	8.2
Ictinia plumbea	13.84	18.87	16.81	9.08	18.28	9.08
Collocalia fuciphaga	4.14	10.11	8.68	6.05	9.51	4.69
Collocalia esculenta	4.09	7.14	5.92	4.37	7.49	3.91
Collocalia brevirostris	4.38	9.55	7.17	4.55	9.91	4.55
Apus apus	6.45	11.93	9.96	6.54	11.85	5.05

Cypsiurus parvus	4.29	9.12	7.59	5.25	13.46	4.64
Streptoprocne rutila	5.53	10.84	8.34	5.08	10.39	5.08
Streptoprocne phelpsi	5.84	11.40	8.26	5.18	10.26	5.18
Thalurania glaucopis	3.70	5.68	3.37	2.65	5.11	2.65
Chaetura brachyura	11.79	15.98	10.57	4.78	16.09	4.78
Deroptyus accipitrinus	13.84	17.10	13.34	7.22	16.12	7.22
Poicephalus senegalus	8.85	13.96	10.90	6.65	12.29	6.65
Pyrrhura perlata	7.05	12.09	7.98	5.55	10.69	5.55
Polytelis alexandrae	7.09	12.64	7.74	5.44	10.78	5.44
Aratinga weddellii	6.74	12.92	8.59	6.08	11.67	6.08
Chalcopsitta atra	7.32	13.70	10.26	6.23	12.30	6.23
Turtur afer	6.47	12.84	8.28	5.01	10.59	5.01
Gallicolumba luzonica	7.54	14.32	7.30	6.22	12.62	6.22
Leptotila verreauxi	9.82	14.62	9.84	5.98	13.11	5.98
Geotrygon montana	6.41	12.65	8.87	5.69	12.19	5.69
Treron vernans	8.14	13.73	8.33	5.76	11.05	5.76
Chalcophaps indica	7.99	13.53	8.87	6.23	12.37	6.23
Stigmatopelia chinensis	6.77	13.74	8.83	5.35	11.51	5.35
Pterocles coronatus	6.28	13.85	10.46	6.73	12.77	6.73
Patagioenas plumbea	7.09	13.44	9.39	6.24	12.67	6.24
Struthio camelus	39.30	47.19	38.00	26.41	37.06	11.53

Table ii. Skeletal and tissue measurements of birds (Schmitz, 2009).

Taxon	Eyeball Diameter (mm)	Eyeball Length (mm)	External Sclerotic Ring Length (mm)
Accipiter striatus	15.32	14.27	12.90
Aegolius acadicus	16.74	15.22	16.72
Ammodramus caudacutus	7.42	6.94	5.81
Ammodramus maritimus	10.16	8.06	6.29
Amphispiza belli	8.23	7.42	6.29
Anas bahamensis	14.52	12.90	11.77
Anas discors	13.06	11.77	11.29
Anas platyrhynchos	15.32	13.23	12.90
Aphelocoma californica	14.78	13.23	11.08
Baeolophus bicolor	8.87	8.06	6.45
Bombycilla cedrorum	9.84	9.35	7.10
Branta sandvicensis	16.59	16.43	15.65
Bubo virginianus	35.79	35.04	34.86
Calidris mauri	8.55	7.74	5.65
Caprimulgus carolinensis	18.43	12.66	17.68

Carduelis psaltria	5.97	5.32	4.03
Carpodacus purpureus	8.06	7.58	5.81
Catharus guttatus	11.29	10.24	8.39
Catharus ustulatus	11.05	10.00	7.90
Catoptrophorus semipalmatus	14.44	12.74	10.97
Chamaea fasciata	8.87	8.55	6.61
Charadrius vociferus	14.52	12.42	11.45
Chondestes grammacus	9.35	9.35	7.74
Coccyzus americanus	13.23	12.10	10.48
Colaptes auratus	13.71	12.26	13.39
Contopus virens	8.71	8.23	6.94
Cygnus olor	22.10	19.90	17.87
Dendroica caerulescens	7.58	7.26	6.13
Dendroica coronata	8.01	7.31	5.86
Dendroica fusca	7.26	6.94	4.84
Dromaius novaehollandiae	49.00	39.00	34.86
Dryocopus pileatus	15.81	14.68	14.68
Dumetella carolinensis	11.13	10.00	8.06
Eudocimus albus	16.45	14.19	13.71
Himantopus mexicanus	15.89	14.52	12.98
Icterus bullockii	9.68	9.19	7.26
Icterus spurius	8.87	7.90	6.94
Junco hyemalis	8.87	8.06	6.29
Lanius ludovicianus	13.87	11.94	10.32
Larus atricilla	16.40	14.70	12.74
Loxia curvirostra	8.55	7.66	6.21
Loxia leucoptera	7.26	6.45	5.48
Melanitta fusca	16.02	13.71	13.39
Melanitta perspicillata	16.13	14.35	12.90
Melospiza melodia	9.03	8.31	6.53
Nucifraga columbiana	15.97	14.03	12.10
Nycticorax nycticorax	24.72	19.64	20.00
Passer domesticus	8.39	7.66	6.21
Passerella iliaca	9.60	8.39	7.58
Phalacrocorax auritus	17.80	11.15	14.19
Phalacrocorax penicillatus	26.16	21.47	23.27
Phalaropus fulicarius	9.52	8.23	5.81
Pica nuttalli	16.13	14.27	12.18
Picoides arcticus	10.97	9.68	8.06
Picoides pubescens	9.03	7.42	6.77
Pipilo chlorurus	9.68	8.87	7.10
Pipilo crissalis	11.29	9.84	7.42
Pipilo maculatus	10.89	10.32	7.58

Piranga ludoviciana	10.16	9.35	7.66
Polioptila caerulea	6.45	6.13	4.84
Porphyrio martinica	13.39	12.10	9.84
Quiscalus quiscula	12.90	12.10	9.19
Rallus longirostris	13.55	10.81	10.16
Regulus calendula	7.26	6.45	4.84
Regulus satrapa	6.94	6.94	4.84
Sayornis saya	10.00	9.19	6.45
Seiurus aurocapilla	9.03	8.55	6.94
Sialia currucoides	10.65	9.35	7.26
Sitta canadensis	7.26	6.45	5.16
Sitta carolinensis	8.55	8.06	6.29
Somateria mollissima	17.26	14.53	14.19
Sphyrapicus ruber	10.32	8.87	7.26
Sphyrapicus varius	10.32	8.87	7.42
Spizella passerina	6.94	6.45	5.65
Sturnella neglecta	13.23	12.10	10.00
Synthliboramphus antiquus	14.52	12.26	11.45
Tyrannus tyrannus	11.94	10.32	8.23
Uria aalge	14.52	14.03	10.16
Vermivora celata	7.10	6.77	5.16
Vireo gilvus	8.23	7.58	5.97
Vireo olivaceus	9.19	8.39	7.26
Zonotrichia atricapilla	9.84	8.55	7.18
Zonotrichia leucophrys	9.03	8.23	6.29

Table iii. Skeletal and tissue measurements of squamates (Hall, 2009).

Taxon	Orbit Diameter (mm)	Orbit Length (mm)	External Sclerotic Ring Diameter (mm)	Axial Length(mm)
Brookesia superciliaris	4.32	3.62	3.58	3.45
Chamaeleo africanus	9.68	9.81	5.20	7.73
Chamaeleo chamaeleon	9.31	7.49	5.54	7.39
Chamaesaura macrolepis	3.29	3.59	1.73	2.93
Cordylus cordylus	5.40	6.50	5.50	4.85
Cordylus niger	5.33	6.45	4.59	4.19
Platysaurus intermedius	4.57	3.18	3.25	3.78
Coleonyx variegatus	4.13	4.19	1.99	2.59
Gehyra variegata	3.89	3.48	3.57	3.33
Gonatodes vittatus	3.42	2.70	2.85	2.83
Lepidodactylus lugubris	3.25	3.48	3.58	3.26
Lygodactylus picturatus	3.20	2.59	3.25	3.26

Phelsuma madagascariensis	6.35	6.76	5.43	4.22
Gerrhosaurus major	8.64	8.33	8.35	6.01
Amblyrhynchus cristatus	10.57	11.23	8.66	7.04
Callisaurus draconoides	5.67	5.84	5.38	4.39
Ctenosaura similis	9.30	8.41	5.74	7.84
Dipsosaurus dorsalis	7.82	7.49	7.41	6.84
Draco melanopogon	5.79	3.24	5.96	5.74
Gonocephalus grandis	11.2	8.22	10.02	7.86
Leiocephalus carinatus	7.98	10.05	7.10	6.03
Leiolepis belliana	8.90	7.47	8.40	8.98
Sceloporus grammicus	4.61	4.85	3.31	4.38
Sceloporus magister	8.88	11.29	7.84	6.28
Acanthodactylus boskianus	4.55	3.37	3.80	3.33
Acanthodactylus cantoris	5.23	4.83	3.83	4.12
Acanthodactylus pardalis	4.75	3.58	5.71	2.85
Meroles anchietae	4.45	3.04	3.84	3.90
Eremias persica	5.26	3.13	5.14	4.06
Gallotia atlantica	4.46	3.73	4.04	3.51
Gallotia galloti	6.29	8.31	44.05	4.76
Lacerta agilis	5.04	5.30	4.66	3.99
Lacerta viridis	6.48	5.49	5.39	4.69
Takydromus septentrionalis	4.57	3.4	3.90	3.04
Trachylepis perrotetii	5.89	7.09	5.85	5.40
Scincus mitranus	4.59	4.64	5.15	5.15
Tiliqua gigas	10.24	15.3	9.71	8.01
Egernia frerei	9.40	9.58	9.10	6.44
Eugongylus rufescens	5.75	7.55	4.86	4.32
Tupinambis teguixin	9.70	7.94	10.28	9.00
Lepidophyma gaigeae	3.22	3.27	3.16	2.69
Xantusia henshawi	3.79	3.25	4.32	2.97
Xantusia riversiana	4.94	5.00	4.96	4.91
Xantusia vigilis	2.34	2.79	2.18	1.72
Sphenodon punctatus	18.53	15.99	17.74	14.96

Table iv. Skeletal measurements of female primates (Schultz 1940).

Taxon	Orbit Volume (cc)	Eye Diameter (mm)
Lemur catta	3.20	2.44
Galago senegalensis	0.92	0.82
Perodicticus potto	1.90	1.15
Nycticebus menagensis	1.30	1.60

Daubentonia madagascariensis	5.12	2.82
Carlito syrichta	0.18	0.31
Saguinus geoffroyi	1.30	0.98
Aotus zonalis	4.79	3.58
Alouatta palliata	6.92	3.05
Cebus capucinus	6.79	3.45
Macaca fascicularis	7.00	3.23
Macaca nemestrina	11.06	4.25
Macaca mulatta	9.55	4.39
Nasalis larvatus	8.70	3.50
Hylobates moloch	8.39	4.20
Hylobates lar	9.40	4.49
Pongo pygmaeus	22.14	4.13
Homo sapien	21.41	8.23

Table v. Skeletal measurements of male primates (Schultz 1940).

Taxon	Orbit Volume (cc)	Eye Diameter (mm)
Saguinus geoffroyi	1.41	1.02
Alouatta palliata	7.77	3.03
Ateles geoffroyi	8.16	3.64
Chlorocebus aethiops	9.17	3.90
Mandrillus sphinx	22.40	6.40
Macaca fascicularis	8.02	3.05
Macaca nemestrina	13.99	4.50
Macaca mulatta	13.86	5.24
Nasalis larvatus	11.80	3.66
Hylobates moloch	8.82	4.20
Hylobates lar	9.60	4.66
Pongo pygmaeus	26.86	4.48
Homo sapien	26.44	8.59