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Comment on "Nocturnality in Dinosaurs Inferred from Scleral Ring and Orbit Morphology"

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Comment on "Nocturnality in Dinosaurs Inferred from Scleral Ring and Orbit Morphology"

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Schmitz and Motani (Reports, 6 May 2011, p. 705) claimed to definitively reconstruct activity patterns of Mesozoic archosaurs using the anatomy of the orbit and scleral ring. However, we find serious flaws in the data, methods, and interpretations of this study. Accordingly, it is not yet possible to reconstruct the activity patterns of most fossil archosaurs with a high degree of confidence.

Schmitz and Motani (*1–3*) described a method for using orbit and scleral ring morphology to discriminate living species by activity pattern, which they subsequently used to classify 31 species of Mesozoic archosaurs (*1*) as photopic (diurnal), scotopic (nocturnal), or mesopic (cathemeral/crepuscular). If correct, this analysis would represent a major advance in amniote paleobiology. However, we have major concerns that call these conclusions into question.

First, the statistical approach employed by Schmitz and Motani (*1*) does not provide a basis for such definitive interpretations. Their work (*1–3*) uses discriminant function analysis (DFA), which tests whether groups that are defined a priori differ significantly from one another based on a set of predictor variables (*4*). In DFA, group membership for known species is assigned before analysis, and the model predicts group membership of unassigned species based on a set of independent variables [here, orbit length and internal and external scleral ring diameters (*1–3*)]. DFA is useful because the group identity of a fossil species can be inferred based on how closely it plots to a group centroid, which is calculated from the known species.

Given these points, we find key problems with how Schmitz and Motani interpret their DFA results. Although their whole-model results exhibited significant *P* values, substantial overlap exists between their three groups even among extant taxa. In particular, mesopic taxa nearly completely overlap the other two groups, a fact evident in Schmitz and Motani's figure S1 (*1*). These results are consistent with previous research showing that orbit and scleral ring morphologies of diurnal and nocturnal birds and lizards overlap to a degree that precludes confident reconstruction of activity pattern in fossil taxa (*5*, *6*). Furthermore, although DFA tests for differences among all groups, it does not test for differences between any two particular groups (*4*). Classification statistics reveal the ability of the variables to correctly predict species activity patterns by describing the proportion of species that the model correctly assigns to their a priori groups and the percentage chance that each animal will belong to each group. Currently, the only software available to conduct a phylogenetically corrected DFA is the R script created by Schmitz and Motani (*1–3*), which does not provide classification statistics. Therefore, we used their data and the same prior probabilities to conduct a linear DFA and found that ~21% of taxa were considered "misclassified" by the model (table S1). Because Schmitz and Motani reported a very weak phylogenetic effect (Pagel's lambda = 0.08) (*1*), similar results can be expected in both analyses (*7*). Importantly, our model showed that 80% of the 30 species with a mesopic a priori assignment were incorrectly classified. For example, the great blue heron is mesopic, but our model predicts it is only 30.5% likely to be considered mesopic using the Schmitz and Motani data (*3*). These results suggest that the underlying anatomical features are unreliable predictors of activity pattern in extant species. We question whether a method that does not confidently discriminate between living species of known activity pattern should be used to infer the activity patterns of extinct taxa.

Our second concern is that the DFA prior probabilities rely on flawed data and assumptions. Schmitz and Motani used observed proportions of activity patterns among extant amniotes (*1*) but obtained most of their data from the Animal Diversity Web, a nonrefereed resource. Data that we gathered from primary literature and more authoritative sources [e.g., (*8*)] reveal that 26% of the mammals classified as "photopic" in Schmitz and Motani's table S4 (*1*) are either cathemeral or nocturnal. Regardless, no theoretical or empirical justifications are provided for the assertion that Mesozoic amniote activity patterns should conform to those of extant amniotes. Indeed, the Mesozoic archosaurs sampled lived across some 160 million years and did not constitute a single, coeval fauna. These fossils were chosen because they preserve relevant osteological structures and were neither sampled randomly through time nor selected to capture the range of known Mesozoic ecomorphologies. Therefore, they cannot be construed to represent a typical Mesozoic world and should not be apportioned based on modern taxa.

Our third concern is that nearly half of the fossil archosaurs analyzed do not overlap with extant taxa on discriminant axis 2 in Schmitz and Motani's figure S1 (*1*). Interpretations beyond the bounds of the originally sampled data are statistically dubious (*9*). Most fossils overlapping with extant animals are either relatively small-sized fliers or closely related to birds. The outlier fossils are not closely related to each other, and although most are medium- to large-sized species, only a few are outside the size range of the extant sample. These taxa occupy a morphospace that may have no living analog, suggesting that definitive activity pattern assignments may not be possible.

Schmitz and Motani (*1–3*) argue that they can interpret activity pattern from the orbit and scleral ring because these variables are functionally informative for vision. To interpret the visual capabilities of an eye, two measurements are minimally required: corneal diameter, correlated with how much light can enter the eye, and axial length, correlated with focal length (*10*). We agree that the inner diameter of the scleral ring surrounds the cornea and is a good proxy for corneal diameter (*1–3*, *5*, *6*, *11*). Similarly, because mammalian eyes are essentially spherical, their transverse diameter is nearly the same as axial length (*12–14*). Accordingly, orbit diameter, an osteological correlate of transverse eye diameter, can be used to approximate axial eye diameter in mammals, although the correlation deteriorates with increasing body size (*12*, *13*, *15*). However, many living diapsid eyes are nonspherical, with a transverse eye diameter that is substantially greater than axial length (*14*). For many diapsids, orbit diameter is thus a poor proxy for axial eye diameter (*5*, *6*). None of the fossil archosaurs included preserved osteological features that permit reliable inference of eye axial diameter.

In sum, the model presented by Schmitz and Motani is much less powerful than they suggest. Definitive interpretation of fossil activity patterns based on these osteological characteristics may not be possible except in cases of morphological extremes. Substantial improvements are likely to come only from concentrated efforts to analyze eye shapes and identify new osteological correlates in extant animals.

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Supporting Online Material

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Table S1

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This PDF file includes:

Table S1

Supplementary Table 1. Classification results from a non-phylogenetic discriminant function analysis (DFA) based on the data presented in Schmitz and Motani 2011. Note that only 6 of 30 mesopic species are correctly classified. Our non-phylogenetic results should be similar to the phylogenetic DFA conducted by Schmitz and Motani because their Pagel's lambda value was 0.08, indicating that phylogeny had a very weak effect in the model.

Species	A priori Class.	Misclass.?	Photopic prob.	Mesopic prob.	Scotopic prob.	DFA Axis 1	DFA Axis 2
Accipiter_gentilis	Photopic	no	0.461	0.398	0.140	0.562	1.088
Accipiter_striatus	Photopic	no	0.546	0.183	0.272	0.604	0.114
Ameiva_ameiva	Photopic	no	0.677	0.029	0.293	0.175	-1.477
Anas_strepera	Photopic	no	0.542	0.326	0.132	0.402	0.891
Anolis_carolinensis	Photopic	no	0.994	0.003	0.003	-2.496	-1.576
Anolis_sagrei	Photopic	no	0.932	0.007	0.061	-0.956	-2.096
Aphelocorna_californica	Photopic	no	0.581	0.190	0.229	0.498	0.192
Asturina_nitida	Photopic	no	0.476	0.319	0.205	0.667	0.736
Basiliscus_basiliscus	Photopic	no	0.828	0.114	0.058	-0.404	0.229
Basiliscus_vittatus	Photopic	no	0.881	0.056	0.063	-0.533	-0.403
Bubulcus_ibis	Photopic	no	0.446	0.187	0.366	0.860	0.085
Buteo_buteo	Photopic	no	0.490	0.379	0.131	0.484	1.056
Buteo_jamaicensis	Photopic	no	0.450	0.366	0.184	0.679	0.916
Buteo_swainsoni	Photopic	no	0.556	0.331	0.113	0.320	0.961
Callipepla_californica	Photopic	no	0.710	0.175	0.115	0.063	0.343
Callipepla_gambeli	Photopic	no	0.694	0.219	0.087	-0.003	0.651
Calypte_anna	Photopic	no	0.548	0.037	0.416	0.494	-1.369
Carpodacus_purpureus	Photopic	no	0.809	0.143	0.049	-0.422	0.489
Catharthes_aura	Photopic	no	0.618	0.234	0.148	0.310	0.524
Catharus_guttatus	Photopic	no	0.617	0.144	0.240	0.431	-0.073
Catharus_ustulatus	Photopic	no	0.658	0.123	0.219	0.324	-0.185
Chaetura_pelagica	Photopic	no	0.825	0.055	0.119	-0.220	-0.661
Chamaeleo_calyptratus	Photopic	no	0.989	0.011	0.000	-3.042	0.331
Chamaeleo_vulgaris	Photopic	no	0.987	0.012	0.000	-3.351	0.762
Chlamydosaurus_kingii	Photopic	no	0.946	0.047	0.007	-1.569	0.375
Chrysolophus_pictus	Photopic	no	0.568	0.318	0.114	0.305	0.913
Cnemidophorus_tigris	Photopic	no	0.926	0.011	0.063	-0.858	-1.730
Coccothraustes_vespertinus	Photopic	yes	0.431	0.106	0.463	0.879	-0.462
Coccyzus_americanus	Photopic	no	0.501	0.087	0.412	0.702	-0.631
Cordylus_giganteus	Photopic	no	0.942	0.029	0.029	-1.023	-0.646
Corvus_brachyrhynchos	Photopic	no	0.522	0.420	0.057	0.110	1.464
Corvus_corax	Photopic	yes	0.452	0.511	0.036	0.037	1.870
Crotaphytes_bicinctores	Photopic	no	0.973	0.015	0.011	-1.567	-0.765
Ctenosaura_clarki	Photopic	no	0.917	0.028	0.055	-0.744	-0.925
Ctenosaura_hemilopha	Photopic	no	0.897	0.097	0.006	-1.483	1.050
Ctenosaura_pectinata	Photopic	no	0.927	0.062	0.011	-1.284	0.383
Dipsosaurus_dorsalis	Photopic	no	0.957	0.022	0.021	-1.232	-0.726
Dryocopus_pileatus	Photopic	no	0.603	0.102	0.296	0.474	-0.436
Elanus_leucurus	Photopic	yes	0.445	0.464	0.091	0.423	1.411
Falco_rusticolus	Photopic	no	0.465	0.416	0.119	0.495	1.191
Falco_sparverius	Photopic	no	0.590	0.168	0.242	0.492	0.068
Falco_tinnunculus	Photopic	no	0.785	0.132	0.083	-0.188	0.210
Furcifer_cephalolepis	Photopic	no	0.985	0.015	0.000	-3.077	0.682

Gallinula_chloropus	Photopic	no	0.723	0.221	0.057	-0.209	0.821
Gallus_gallus	Photopic	no	0.604	0.289	0.107	0.221	0.840
Gambelia_wislizenii	Photopic	no	0.962	0.017	0.021	-1.276	-0.955
Garrulus_glandarius	Photopic	no	0.750	0.193	0.057	-0.254	0.696
Gerrhosaurus_major	Photopic	no	0.738	0.019	0.243	-0.037	-1.775
Glaucidium_gnoma	Photopic	no	0.500	0.032	0.468	0.577	-1.488
Iguana_iguana	Photopic	no	0.902	0.081	0.017	-1.046	0.442
Ixoreus_naevius	Photopic	no	0.521	0.103	0.377	0.669	-0.473
Lacerta_sp	Photopic	no	0.972	0.016	0.012	-1.549	-0.720
Lanius_ludovicianus	Photopic	no	0.636	0.167	0.197	0.354	0.121
Larus_occidentalis	Photopic	yes	0.429	0.469	0.101	0.495	1.387
Laterallus_jamaicensis	Photopic	no	0.835	0.094	0.070	-0.359	-0.012
Liolaemus_belli	Photopic	no	0.976	0.015	0.009	-1.672	-0.683
Liolaemus_bibronni	Photopic	no	0.991	0.007	0.002	-2.389	-0.777
Liolaemus_buergeri	Photopic	no	0.971	0.011	0.018	-1.430	-1.232
Lophophorus_impeyanus	Photopic	no	0.618	0.313	0.069	0.031	1.084
Mabuya_mabuya	Photopic	no	0.930	0.005	0.065	-1.000	-2.434
Meleagris_gallopavo	Photopic	yes	0.334	0.237	0.429	1.148	0.318
Meleagris_ocellata	Photopic	no	0.466	0.301	0.233	0.725	0.643
Melospiza_melodia	Photopic	no	0.720	0.097	0.183	0.150	-0.339
Microhierax_caerulescens	Photopic	no	0.532	0.122	0.346	0.651	-0.304
Microlophus_peruvianus	Photopic	no	0.990	0.007	0.003	-2.267	-0.842
Milvus_milvus	Photopic	no	0.485	0.447	0.068	0.240	1.471
Numenius_americanus	Photopic	no	0.602	0.229	0.168	0.377	0.464
Ophisaurus_ventralis	Photopic	no	0.929	0.004	0.066	-1.013	-2.545
Passerella_iliaca	Photopic	yes	0.320	0.027	0.653	0.962	-1.603
Pavo_pavo	Photopic	no	0.436	0.259	0.305	0.854	0.433
Perisoreus_canadensis	Photopic	no	0.598	0.252	0.150	0.349	0.589
Petrochelidon_pyrrhonata	Photopic	no	0.792	0.087	0.120	-0.109	-0.279
Petrosaurus_thalassinus	Photopic	no	0.966	0.026	0.008	-1.612	-0.203
Phasianus_colchicus	Photopic	no	0.548	0.434	0.018	-0.419	1.968
Phelsuma_astriata	Photopic	no	0.818	0.013	0.169	-0.328	-1.989
Phelsuma_cepediana	Photopic	no	0.559	0.009	0.432	0.249	-2.513
Phelsuma_madagascarensis	Photopic	yes	0.450	0.038	0.513	0.710	-1.360
Phelsuma_sundbergi	Photopic	yes	0.347	0.024	0.630	0.874	-1.724
Phrynocephalus_mystaceus	Photopic	no	0.984	0.012	0.003	-2.132	-0.445
Phrynosoma_cornutum	Photopic	no	0.986	0.011	0.003	-2.188	-0.461
Phrynosoma_mcallii	Photopic	no	0.978	0.017	0.005	-1.913	-0.357
Phrynosoma_solare	Photopic	no	0.988	0.011	0.000	-3.225	0.548
Phymaturus_palluma	Photopic	no	0.970	0.018	0.013	-1.493	-0.689
Physignathus_cocincinus	Photopic	no	0.968	0.021	0.011	-1.527	-0.510
Physignathus_lesueurii	Photopic	no	0.835	0.090	0.075	-0.343	-0.076
Pica_nuttalli	Photopic	no	0.690	0.249	0.060	-0.133	0.912
Pipilo_maculatus	Photopic	no	0.623	0.179	0.197	0.381	0.184
Poecile_gambeli	Photopic	no	0.665	0.082	0.252	0.306	-0.575
Pogona_barbarata	Photopic	no	0.983	0.015	0.002	-2.295	-0.078
Pogona_vitticeps	Photopic	no	0.978	0.018	0.005	-1.941	-0.245
Porphyrio_porphyrio	Photopic	no	0.657	0.314	0.028	-0.388	1.439
Regulus_calendula	Photopic	no	0.753	0.105	0.143	0.028	-0.187
Sator_angustus	Photopic	no	0.988	0.009	0.003	-2.244	-0.667

Sauromalus_ater	Photopic	no	0.946	0.030	0.024	-1.107	-0.542
Sceloporus_occidentalis	Photopic	no	0.985	0.012	0.003	-2.163	-0.460
Sceloporus_undulatus	Photopic	no	0.987	0.009	0.004	-2.093	-0.804
Streptoprocne_zonaris	Photopic	no	0.625	0.168	0.207	0.387	0.112
Teius_teyou	Photopic	no	0.931	0.016	0.053	-0.865	-1.356
Tiliqua_occipitalis	Photopic	no	0.932	0.063	0.004	-1.727	0.834
Tragopan_satyra	Photopic	no	0.500	0.375	0.125	0.453	1.055
Tropidurus_torquatus	Photopic	no	0.974	0.014	0.011	-1.579	-0.824
Tupinambis_merianae	Photopic	no	0.962	0.036	0.002	-2.170	0.686
Turdus_merula	Photopic	no	0.609	0.106	0.285	0.458	-0.389
Turdus_migratorius	Photopic	no	0.586	0.135	0.279	0.516	-0.172
Uromastyx_maliensis	Photopic	no	0.980	0.015	0.005	-1.970	-0.377
Varanus_beccarii	Photopic	no	0.917	0.060	0.023	-0.986	0.068
Wilsonia_pusilla	Photopic	no	0.586	0.051	0.363	0.456	-1.064
Zonotrichia_atricapilla	Photopic	no	0.681	0.120	0.199	0.258	-0.181
Aix_sponsa	Mesopic	yes	0.469	0.317	0.214	0.693	0.719
Anas_acuta	Mesopic	yes	0.578	0.392	0.030	-0.246	1.646
Anas_americana	Mesopic	yes	0.462	0.400	0.138	0.556	1.098
Anas_platyrhynchos	Mesopic	yes	0.455	0.343	0.201	0.699	0.820
Apus_apus	Mesopic	yes	0.809	0.060	0.131	-0.155	-0.633
Aquila_audax	Mesopic	no	0.349	0.535	0.116	0.702	1.515
Aquila_chrysaetos	Mesopic	no	0.275	0.609	0.116	0.873	1.711
Ardea_herodias	Mesopic	yes	0.295	0.306	0.399	1.240	0.603
Athene_cunicularia	Mesopic	yes	0.239	0.059	0.702	1.316	-0.884
Buteo_regalis	Mesopic	yes	0.412	0.335	0.254	0.856	0.740
Caprimulgus_carolinensis	Mesopic	yes	0.265	0.166	0.569	1.346	-0.001
Catoptrophorus_semipalmatus	Mesopic	yes	0.540	0.186	0.274	0.616	0.128
Charadrius_vociferus	Mesopic	yes	0.434	0.209	0.357	0.887	0.196
Chordeiles_acutipennis	Mesopic	yes	0.154	0.066	0.780	1.652	-0.664
Chordeiles_minor	Mesopic	yes	0.241	0.075	0.684	1.340	-0.687
Cygnus_columbianus	Mesopic	no	0.381	0.606	0.012	-0.290	2.527
Dendragapus_obscurus	Mesopic	yes	0.600	0.291	0.109	0.235	0.841
Dromaius_novaehollandiae	Mesopic	no	0.174	0.729	0.097	1.110	2.107
Falco_mexicanus	Mesopic	yes	0.356	0.313	0.331	1.047	0.628
Gallinago_gallinago	Mesopic	yes	0.380	0.093	0.527	0.991	-0.570
Lagopus_lagopus	Mesopic	yes	0.660	0.310	0.030	-0.364	1.398
Larus_argentatus	Mesopic	yes	0.517	0.386	0.097	0.328	1.176
Larus_californicus	Mesopic	yes	0.510	0.389	0.101	0.356	1.169
Larus_canus	Mesopic	yes	0.452	0.410	0.138	0.573	1.126
Lophura_bulweri	Mesopic	yes	0.418	0.413	0.169	0.709	1.077
Perdix_perdix	Mesopic	yes	0.786	0.173	0.040	-0.453	0.742
Phoebastria_immutabilis	Mesopic	no	0.153	0.847	0.000	-1.854	5.293
Rallus_limicola	Mesopic	yes	0.677	0.170	0.154	0.212	0.214
Stercorarius maccormicki	Mesopic	yes	0.558	0.411	0.031	-0.201	1.683
Struthio_camelus	Mesopic	no	0.426	0.430	0.144	0.636	1.170
Aegolius_acadicus	Scotopic	no	0.091	0.035	0.874	1.902	-1.039
Aegotheles_cristatus	Scotopic	yes	0.409	0.398	0.193	0.774	0.998
Asio_otus	Scotopic	no	0.161	0.050	0.789	1.576	-0.915
Bubo_bubo	Scotopic	no	0.140	0.079	0.781	1.742	-0.489
Caprimulgus_ridgwayi	Scotopic	no	0.054	0.044	0.902	2.280	-0.653

Caprimulgus_rufigena	Scotopic	no	0.119	0.059	0.822	1.808	-0.683
Caprimulgus_vociferus	Scotopic	no	0.132	0.093	0.776	1.805	-0.332
Corucia_zebrata	Scotopic	yes	0.957	0.024	0.019	-1.263	-0.593
Eublepharis_maculatus	Scotopic	no	0.287	0.055	0.658	1.164	-0.978
Eublepharis_sp	Scotopic	no	0.385	0.114	0.501	0.997	-0.390
Gekko_gecko	Scotopic	no	0.120	0.052	0.828	1.787	-0.788
Gekko_ulikovskii	Scotopic	no	0.143	0.049	0.809	1.657	-0.904
Lialis_burtoni	Scotopic	no	0.329	0.003	0.668	0.586	-3.277
Ninox_novaeseelandiae	Scotopic	no	0.147	0.117	0.736	1.757	-0.165
Nyctibius_jamaicensis	Scotopic	no	0.094	0.193	0.713	2.104	0.421
Nyctidromus_albicollis	Scotopic	no	0.077	0.069	0.854	2.124	-0.400
Otus_asio	Scotopic	no	0.198	0.052	0.751	1.437	-0.944
Phalaenoptilus_nuttallii	Scotopic	no	0.128	0.081	0.790	1.804	-0.438
Podargus_strigoides	Scotopic	no	0.310	0.236	0.453	1.216	0.321
Rhacodactylus_auriculatus	Scotopic	no	0.227	0.062	0.711	1.360	-0.830
Rhacodactylus_ciliatus	Scotopic	no	0.197	0.072	0.730	1.485	-0.663
Steatornis_caripensis	Scotopic	yes	0.271	0.598	0.131	0.930	1.652
Strix_occidentalis	Scotopic	no	0.074	0.057	0.869	2.114	-0.558
Teratoscincus_przewalskii	Scotopic	no	0.193	0.044	0.763	1.427	-1.076
Teratoscincus_sp	Scotopic	no	0.236	0.049	0.714	1.297	-1.034
Tyto_alba	Scotopic	no	0.404	0.119	0.477	0.954	-0.355