

1 ***Arboreal locomotion and trophic security at the dawn of Euprimate vision***

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5

6 **Abstract**

7 Primate vision is thought to have evolved in connection with life in the trees. However,  
8 several inter-related origins theories—those addressing possible co-evolution with size, predation,  
9 diet, daylight, locomotion, and groups—also provide reasonable explanations of their distinct  
10 cranial-visual morphology. We hypothesized that demand for high-speed arboreal grasp-landing  
11 facilitated predation avoidance thereby reducing the need for lateral facing orbits. To test this  
12 proposed influence, in the context of a likely very multi-causal adaptive landscape, we consolidated  
13 published data on extant primate species including body mass, daily path length, arboreality,  
14 insectivory, frugivory, activity period, leaping, swinging, and group size. Phylogenetically  
15 controlled regressions, on three different taxonomic subsets of the primate order, highlight size and  
16 environmental influences as the most compelling factors explaining higher orbital convergence  
17 [OC]. Moreover, activity period and group size (in anthropoids) as well as arboreality and body  
18 mass (in non-anthropoids) associated convincingly with higher OC. After considering size and path  
19 length, suspensory (and to a lesser extent leaping-based) grasp-landed locomotion co-varied with  
20 OC, primarily in anthropoids. Nocturnality had negative, and leaping mixed, associations with OC  
21 —thus, with the exception of those relating to nocturnal-locomotion, all adaptive origins theories  
22 considered were at least partially corroborated. The conflicting associations of OC with leaping, is  
23 largely attributable to the exceptionally small (and more taxonomically contentious) members of the  
24 order. But prospects otherwise remain bright for our two freshly illuminating theories of grasp-  
25 swing, in anthropoids, and rear attack risk reduction [RARR], more generally, as they provide  
26 compelling alternatives to sized based models (e.g. predation deterrence and allometric scaling) in  
27 explaining deep divisions in the primate order.

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## 1 Introduction

2  
3 Primates have cranial morphology conducive to a binocular focus on the frontal visual field  
4 (Heesy, 2004) as a result of diminished sensory input via smell (Jolly, 1985; Fleagle, 1999;  
5 Cartmill, 2002) and from the rear visual field. While early primates are largely known to us via  
6 fossil dentition, cranial modifications toward larger eyes, a post-orbital septum, and convergent  
7 orbital apertures are the most distinguishing features (Ross and Martin, 2007). Such distinctive  
8 facial changes could have evolved in response to many ecological scenarios: terminal branch  
9 feeding (Sussman, 1991), ripeness detection (Polyak, 1957; Cachel, 1979b), arboreality (Jones,  
10 1916; Smith, 1924), hand emancipation (Jones, 1916), distance judgment (Clark, 1959), masticatory  
11 insulation (Cartmill, 1980), snake detection (Isbell, 2006), predation deterrence (Wheeler, Bradely  
12 and Kamilar, 2011), visual predation (Cartmill, 1972), nocturnal clambering (Allman, 1982),  
13 nocturnal leaping (Crompton, 1995), active fine-branch locomotion (Martin, 1979), and grasp-leap  
14 locomotion (Szalay and Dagosto, 1988), as well as more neutral, allometric effects (Cartmill, 1980).  
15 While entertaining as many of these ideas as possible, we were primarily interested in examining  
16 visual and motor centered explanations—those theories focusing upon the influences of arboreal  
17 grasp landing with an auxiliary tracking of the effects of both body size and group size on both  
18 leaping and predation—of euprimate and anthropoid origins.

19 We recognize origins theories on *euprimates*—ancestors of extant primates—as temporally  
20 distinct from origins theories on *primates*—also inclusive of stem-primates (*Silcox and López-*  
21 *Torres, 2017*). The former origins theories primarily use fossil evidence to piece together how  
22 mammals evolved into primates. The latter theories explore how the common ancestor of these  
23 extinct fossil primate lineages (i.e. stem groups) evolved into the common ancestor of all living  
24 primates (i.e. crown clade). Here we exploratively evaluated multiple theories on primates origins,  
25 using only data on extant primates. We endeavored to test as many of the above theories  
26 simultaneously with an eye towards outlining a rough chronology of adaptation, keeping in mind  
27 their evolution via a likely gradual, “serial accretion” of each component towards this suite of  
28 hallmark traits (Cartmill, 2002). Ideally, an adequate theory ought to be able to explain several, if  
29 not all, of these unique arboreal specializations of early euprimates (Szalay and Dagosto, 1988).  
30 Although we will present evidence favoring a multiplicity of separable causes across the order and  
31 over time.

32 The grasp-leap locomotion theory suggests that a lemuriform-like “rapid successive leaping  
33 and landing with a habitual grasp” best explains the “protoeuprimate form-function complex”  
34 (Szalay and Dagosto, 1988). Grasp-leap, while informative of ancient evolution, primarily only  
35 considers skeletal evidence of leaping as an influence on visual changes in plesiadapiform stem  
36 primates (Szalay and Dagosto, 1988). It does not, for example, address any such continued  
37 evolutionary pressure on OC in anthropoids. Orbital convergence, which enables stereoscopic  
38 vision and visual acuity at the center of the visual field, could have been adaptive in many ways  
39 beyond just leaping. The more fundamental adaptation of primates is arguably hand-eye  
40 coordination (Ross and Martin, 2007), perhaps more generically phrased as *limb placement* or *limb*  
41 *landing*, as it might also be applicable to brachiation. Thus, there is a reasonable case to be made  
42 that rationale for *grasp-leap* theory could be re-purposed into a *grasp-swing* theory, for anthropoids,  
43 or even into a more generalized theory of *precision limb landing*, also encompassing all primates.

44 Uncertainty in grasp placement is an interesting problem relevant to the evolution of near-  
45 stem primates into euprimates. Orbital convergence is thought to improve foraging, climbing, and  
46 leaping along and between terminal branches in alleviation of the incessant visual imperatives of  
47 such locomotion through vegetation (Crompton, 1995). This visual complexity deciphering theory  
48 —whose stereoscopic solution has been described as “camouflage breaking” (Isbell, 2006),  
49 “camouflage countering” (Heesy, 2008), or “x-ray vision” (Changizi and Shimojo, 2008)—  
50 emphasizes the crypsis, or visual confusion, of distinguishing possible targets from background in

1 the fine-branch niche (Crompton, 1995). Crompton’s theory, like many others discussed here, is  
2 typically applied more to early Paleocene stem primates, and has been viewed as less pertinent  
3 towards later OC changes in the euprimate crown group.

4 The visual predation hypothesis (Cartmill, 1972), provides a less substrate-based theory, that  
5 OC evolved to improve insect predation by primates in the “terminal branch milieu” (Cartmill,  
6 1972). Visual predation [VP] is thought to have selected for orbital aperture convergence upon the  
7 mid-sagittal plane (Cartmill, 1970), enabling stereoscopic vision and visual acuity in the center of  
8 the visual field. Visual predation is based on the observation that predators usually have convergent  
9 orbits and the counter-example that there are many non-primates that climb via clawing rather than  
10 grasping. A high degree of OC can also act, instead, to *reduce* depth perception due to reduced  
11 parallax. And because of typical eye closeness of primates, the range of depth perception does not  
12 typically exceed a meter in target distance (Cartmill, 2012). Thus, compelling explanations of OC  
13 should at least recognize selection pressures for focus on close-range targets. Importantly also, is  
14 distinguishing the use of “predation” in VP as relating to *prey capture*, rather than *predator*  
15 *avoidance or deterrence*, a suite of theories we explore in the following paragraphs and  
16 subsequently test in the remainder of the text.

17 The line between theories on the origins of anthropoids, and primate origins theories more  
18 generally, is arguably rather thin, as many adaptations (e.g. for increased size) also trend more  
19 generally throughout the entire order (Clark, 1959). But while OC does correlate with general size  
20 increases, the nearly complete forward rotation of anthropoid orbits constitutes prodigious change  
21 (Clark, 1959), likely associated with diurnality and its effect on relative orbit diameter reduction  
22 (Cartmill, 1970; Kirk, 2006). Most anthropoid origins theories grapple with corresponding effects  
23 on cranio-facial stabilization—including OC, orbital frontation, manifestation of a post-orbital  
24 septum, and fusing of the mandibular symphysis—likely related to the forces of mastication  
25 (Hylander *et al.*, 2000) perhaps in adaptation to frugivory (Polyak, 1957; Cachel, 1979a). The  
26 negative relative orbital allometry (Schultz, 1940) based argument for higher OC in early  
27 anthropoids over ancestral strepsirrhines (Cartmill, 1980; Ravosa *et al.*, 2006) is less applicable to  
28 within-anthropoid changes (Nett and Ravosa, 2019). But this allometry based structural claim,  
29 however, serves fittingly as a reasonable non-adaptive null hypothesis (Ross, 1995; Cartmill, 2002),  
30 as it is well supported by interspecific and ontogenetic data for numerous mammals (Hylander *et*  
31 *al.*, 2000; Noble, Kowalski and Ravosa, 2000; Ravosa and Savakova, 2004; Nett and Ravosa,  
32 2019). We adopt this default, two-part explanation of OC—as a side-effect of decreased relative  
33 orbital diameter in (generally diurnal) anthropoids, and, in counterpoint, as likely adaptive in  
34 several nocturnal non-anthropoids (Cartmill, 1980; Ravosa and Savakova, 2004). Considering this  
35 allometric model, lorises, tarsiers, and anthropoids have the largest relative OC (Kay, Ross and  
36 Williams, 1997) running somewhat counter to leaping based theories. Anthropoids leap less, not  
37 more, than their predecessors (Kay, Ross and Williams, 1997), and lorises do not leap at all  
38 (although the Lorisoidae *Galaginae* do frequently).

39 Despite the objective appeal of (the null) allometric model, few alternative hypotheses exist  
40 that highlight anthropoid vision improvements. Aside from mastication, two other, more adaptive  
41 theories, explore significant cerebral-thalamic developments, possibly evolutionarily selected via  
42 both snake detection [SD] (Isbell, 2006) and brachiation in gibbons (Isbell, 2009)—the latter being  
43 a *Hylobatidae*-specific form of our anthropoid-general *grasp-swing* construct. On account of  
44 predation-detering effects of group and body size (Wheeler, Bradely and Kamilar, 2011, Table 2)—  
45 we have proposed that reduction in posterior threats more generally could provide an improved,  
46 albeit less disporting, adaptive explanation for increased vision improvements and OC increases,  
47 particularly in anthropoids. This arboreal security (predation avoidance) based theory of *reduced*  
48 *posterior predation*, logically implicates body mass, group size, arboreality, and other means of  
49 avoiding predation (even including nocturnal concealment), as exerting potentially significant  
50 influence on OC, independent of diurnality and allometric effects.

1 Both fore- and hind- limb forms of often rapid, sometimes pendulous, and frequently inter-  
2 substrate grasp-landed locomotion, not only share key hand-eye coordination capabilities essential  
3 to gravitationally time-sensitive limb landing, but this prevalent behavior could have also  
4 influenced many hallmark primate skeletal characteristics. Specifically, we test all three versions of  
5 this overarching theory of precision-limb-landing—that leaping behavior co-evolved with other  
6 skeletal changes observed in early *euprimates* and, further, that swinging could have continued such  
7 a selection pressure on cranial changes in *Hominoidea* and perhaps *Atelidae*. Frontally focused  
8 vision might have enabled close-range acuity for grasp adjustments to secure safe limb-landing  
9 during hazardous, and often high-speed, arboreal locomotion. Both of these precision landed-grasp  
10 forms of locomotion could have been under selection to reduce injuries and prevent death as a result  
11 of falling.

12 Predictions that follow from grasp-swing theory are that hylobatids—who locomote using a  
13 single grasp per bout-cycle and have closer visual access to this (upper body) limb placement—  
14 should have disproportionately higher OC than their neighboring hominids or atelids—who both  
15 tend to arm-swing in a more conservative, attached way. We test these predictions, alongside the  
16 more grasp-leap general prediction that leapers ought to have relatively higher OC. Further  
17 predictive logic can implicate other evolutionary models with several of our tabulated variables—  
18 angiosperm radiation and ripeness detection with color-vision and frugivory, visual predation with  
19 insectivory, as well as other more obvious match-ups such as arboreal theory with less locomotive  
20 ranging (low DPL), predation deterrence with group and body size, and nocturnal locomotion  
21 models with nocturnality and leaping. We take the negative allometric scaling of orbit size (relative  
22 to width) driving OC in diurnal anthropoids as a reasonable null explanation. A more systematic  
23 organization of model predictions in relation to compiled variables is available in Table 1.

24 We harvested the primary literature on primate positional behavior for these locomotor  
25 modes. Many of the estimates of the more specific modes were collapsed down to two categories of  
26 precision limb landed locomotion: leaping and swinging. This re-grouping provides an convenient  
27 amalgamation for subsequent reporting and discussion. A phylogenetically controlled regression,  
28 that also controls for allometry and socio-ecology, helps to demonstrate this co-evolutionary  
29 association between locomotor mode and OC. Size and environmental variables had the strongest  
30 influences on OC. Activity period, group size, and arboreality also associated convincingly. Leaping  
31 and swinging locomotion variables, like those for frugivory, had more mixed results (depending on  
32 sub-order) but still maintain promising predictive power for future model inclusion. A generalistic  
33 grasp-landing theory remains a somewhat challenging prospect, especially considering the handful  
34 of contraindicative cases, but results were more compelling in support of rear attack risk reduction  
35 [RARR]. These new theories constitute formidable alternatives to the existing null models of  
36 allometry in anthropoids and nocturnality in nons.

37

38

1 **Table 1.** All primate and anthropoid origins models discussed in the text cross-tabbed by their  
 2 predicted influence on the collected variables at different points in the evolution of the primate tree.

ORIGINS	MODEL	TYPE	THEORIST(S)	VARIABLES												
				mass	group size	arboreality	path length	insects	fruit	nocturnal	color vision	leaping	swing			
primate	<i>hand emancipation</i>	SX	Jones, 1916			sb										
primate	<i>arboreal theory</i>	S	Jones, 1916; Smith, 1924			sp	pb									
primate	<i>distance judgment</i>	S	Clark, 1959			s										
primate	<i>visual predation</i>	DX*	Cartmill, 1972					p								
anthropoid	<i>ripeness detection</i>	D	Catchel, 1957; Polyak, 1979						ba	-s	a					
primate	<i>active fine-branch locomotion</i>	SLX	Martin, 1979			sp	-p							sp		
primate	<i>masticatory insulation</i>	D	Cartmill, 1980; Polyak, 1979					p	a					p		
primate	<i>allometric scaling</i>	M	Cartmill, 1980	ba					ba	-b						
primate	<i>nocturnal clambering</i>	L*	Allman, 1982							s						
primate	<i>grasp-leap locomotion</i>	SL	Szalay and Dagosto, 1988			sp								p		
primate	<i>angiosperm co-evolution</i>	SD	Sussman, 1991			sba			sba							
anthropoid	<i>dawn monkey</i>	*	Beard, 1994								-ba	ba				
primate	<i>nocturnal leaping</i>	L*	Crompton, 1995							p				p		
anthropoid	<i>snake detection</i>	PLX	Isbell, 2006								-ba					
anthropoid	(R.A.R.R.) <i>predation deterrence</i>	PM	Wheeler, 2011	ba	a											
primate	(R.A.R.R.) <i>predation avoidance</i>	PSLD*	Schruth, 2015			spba	-ba		ba	p				p	a	
anthropoid	<i>grasp-swing locomotion</i>	SLX	Schruth, 2019			a										a
anthropoid	<i>anti-parasitic grooming</i>	(SX)	Schruth, 2019		a	-a		a		-pb						

4 **model type abbreviations:** S=substrate, D=diet, L=locomotion, M=body mass, \*=daylight,  
 5 X=close range stereoscopic

6 **prediction abbreviations:** s=stem-primates, p=non-anthropoids, a=anthropoids, b=both (“-” prefix  
 7 indicates a negative correlation)

## 1 **Materials and Methods**

### 3 **Locomotion**

4 We collected quantitative estimates of leaping and other primate positional behavior data  
5 from the primary literature. The on-line searches enabled by ISI Web of Knowledge (Garfield,  
6 1970), used broad search terms such as “locomot\* position\* primate\*.” More specific searches  
7 were subsequently made, for genera that were not found in the initial search, using Google Scholar  
8 (Acharya and Verstak, 2004). Although some preference was afforded to complete repertoire  
9 studies, we accepted as many studies as possible—the only criteria for rejection being a failure to  
10 report a quantitative estimate for leaping. Relevant tables from the resultant meeting abstracts,  
11 journals articles, and theses, and books chapters (all published before 2015) were extracted and  
12 amalgamated. Averaging across studies (and sites) resulted in estimates for 128 total unique species  
13 (54 genera, from 15 out of the 16 primate families). Locomotor modes were distilled into fewer,  
14 broader locomotion categories from the many possible that were reported and collected.

15 Locomotion within each species’ repertoire was quantified by the number of discrete  
16 movements, or “bouts.” We divided the number of observed bouts for each type of locomotion by  
17 the total number of bouts (across all types) to obtain percentages. Values of zero were used for  
18 certain descriptions (e.g. “strictly terrestrial”), and in other cases, where just a single final value was  
19 available, we merely used this reported percentage. Categories resembling leaping and swinging  
20 ( $n=14$ ) were combined for subsequent analysis. *Swing* included *brachiate*, *semi-brachiate*, *arm-*  
21 *swing*, *tension*, *suspensory*, and *torso-orthograde* and *leap* included: *leap*, *vertical cling leap*,  
22 *bound leap*, *jump*, *drop*, *leap/drop*, and *airborne*. If a study split locomotor bouts across different  
23 field sites or classified them functionally (e.g. travel vs. foraging), we weighed the locomotion  
24 percentages by bout counts and then averaged them. Although brachiation estimates were nearly  
25 entirely from non-captive studies, leaping percentages were derived 1/4<sup>th</sup> from captive studies—  
26 although a captivity effect on locomotion was determined to be insignificant. All relevant data have  
27 been uploaded to <https://osf.io/cd68q/>

### 29 **Orbital Convergence**

30 We collected OC values as measured by two primary studies (Ross, 1995; Heesy, 2003).  
31 Measures of orbit orientation were collected by Ross (1995) on 88 species using a dihedral  
32 goniometer (Cartmill, 1970) and by Heesy (2003) on 93 species using a MicroScribe 3DX  
33 coordinate data stylus. Though different tools were used, the measurements of OC had a strong  
34 correlation ( $|\text{Spearman's } \rho| = 0.966, p < 0.001, n = 41$ ) (Heesy, 2003). In both studies, the  
35 measurements were taken on primate crania on loan from various museums in the United States.  
36 The values used in subsequent analyses were obtained by averaging together the OC values from  
37 these two studies. Case-wise deletion was inevitable after including control variables. These  
38 missing control variable values resulted in dropping nearly half of the initial species from analysis,  
39 resulting in 60 species that were included in the final regression model.

### 41 **Control Variables**

42 We collected variables on vision, activity pattern, and environmental variables (including  
43 rain, temperature, latitude, and region) from a prior study (Wheeler, Bradely and Kamilar, 2011).  
44 Many of these variables (e.g. rain and temperature) were thought to serve as potential proxy  
45 indicators for snake prevalence (Wheeler, Bradely and Kamilar, 2011). We additionally included  
46 other control variables such as physiology (*body mass*, *claws*, *prehensile tail*), diet (*fruit*, *insect*),  
47 behavior (*nocturnal*, *trichromatic [color] vision*, *daily path length [DPL]*), and *group size* as  
48 compiled from (Lehmann, Korstjens and Dunbar, 2007; Wheeler, Bradely and Kamilar, 2011; Rowe  
49 and Meyers, 2017). As many of these control variables as possible were included in plots and  
50

1 regression models, where the main criterion for rejection was low significance ( $p$ -values near one)  
2 for estimates from either PGLM or ANOVA in any model. Height estimates were not utilized  
3 because there were too few species with height data available. Regression variables were selected  
4 based on primate origins theories and constrained by availability of relevant data. From this original  
5 pool of 15 total predictor variables, (by chance) we ended up retaining two size related variables,  
6 two habitat related variables, two diet variables, two activity period variables, and two locomotion  
7 from the larger pool of possible variables—all potentially related to vision evolution. This  
8 conveniently well rounded mix of variables helped us to sensibly address the majority of the  
9 roughly dozen or so origins models, to some degree, with the unfortunate exception of snake-  
10 detection theory which is exceedingly difficult to directly test.

11

## 12 **Statistical Methods**

13 We used phylogenetic regression to assess the evolutionary association of leaping with  
14 vision changes in the primate cranium (specifically OC). Generally speaking, this method provides  
15 for tests of associations between evolved traits in extant species in a phylogenetic tree while  
16 controlling for their shared lineage (Felsenstein, 1985). We used phylogenetic generalized least  
17 squares (PGLM) regression. In PGLM, the parameters of the evolutionary model—lambda, delta,  
18 and kappa—can be co-estimated with the regression parameters (using the R package caper v 1.0)  
19 the branch lengths parameters (Orme et al., 2013) on a model by model basis. In our case, we  
20 iterated over all possible variable combinations and performed ML estimates on each of the tree  
21 transformation parameters to obtain a complete matrix of possible values. We performed the ML  
22 estimation with the following pre-specified ranges—lambda from 0.3 to 0.8, kappa from 0.4 to 2.7,  
23 delta from 0.4 to 2.7—which helped avoid algorithmic convergence issues. The average ML values  
24 for each of the three subsets (including the entire tree) were used to establish fixed values for  
25 subsequent OC predictor parameter estimations. The highest  $R^2$  for each model’s variable count  
26 group was selected, this incidentally also had the side-effect of maximizing the AIC for each. A  
27 generalized version of this procedure is published on-line at protocols.io (Schruth, 2021). To  
28 independently corroborate final model parameters (both directionality and composition), we  
29 supplementally employed an information theoretic workflow (Garamszegi, 2011) whereby AICc  
30 was used to both rank and weight averages of parameter estimates of all possible variable  
31 combinations (Symonds and Moussalli, 2011).

32 These regression models were further compared against plots and cross-tabulations on OC  
33 using our continuous and categorical variables, respectively. Categorical cross tabulation tables  
34 were constructed to further investigate both angiosperm co-evolution and grasp-leap theory. The  
35 2x2x2x2 angiosperm table was constructed by creating binary variables from (trichromatic) *color*  
36 *vision* and *nocturnal* as well as from our ‘predominantly’ frugivorous and ‘predominantly’ arboreal  
37 variables, resulting in 16 total cells, 7 of which contained empty sets. The 2x2x2 grasp-leap table  
38 was created by splitting two continuous variables into roughly equally sized halves: the leaping  
39 percentages above and below 25% and the daily path length distances above and below  $1/3^{\text{rd}}$  of max  
40 DPL (1.34 km), with a final division between anthropoids and non-anthropoids for 8 total cells.

41 While the use of the grade term “prosimian” is an out-dated, aphylogenetic term, we find  
42 this division quite useful here not only for our allometric tests, but because it neatly divides the  
43 distribution of primate OC values into two mutually exclusive groups. This division, between  
44 anthropoid and nons, partitions OC values above and below 64 degrees, respectively—the only  
45 possible split by taxonomic rank, incidentally, that does not produce distributional overlaps. These  
46 allometric tests were carried out both via PGLM as well as by using *evomap* and running the  
47 *gls.ancova* function on our dataset by comparing models of the effect of the independent variable on  
48 the dependent variable while controlling for interaction terms (Smaers and Rohlf, 2016).

49 In all regressions, we used a nuclear and mitochondrial phylogram (Springer *et al.*, 2012) in  
50 order to control for non-independence arising from shared lineage (Felsenstein, 1973). This tree was

1 also used in ancestral character estimation [ACE] (Revell, 2014) to calculate ancient leaping and  
2 swinging percentages (Fig 1). Lastly, we should note that values of continuous variables were not  
3 transformed for the regression models but were investigated via log-log scale axes in most  
4 visualizations.

5

6

## 7 **Results**

8

9 The PGLM regressions found size and ecological variables to be significant predictors of  
10 orbital convergence (Table 2) after controlling for several other variables. Body *mass* (+0.14 and  
11 +1.3, per Kg, in anthropoids and nons, respectively) and *group size* (+0.1° per indiv. in anthropoids)  
12 had strongly positive and somewhat significant relationships with OC ( $p < 0.05$  and  $p < 0.1$ ). Also,  
13 while *swinging* had marginal (+4.5°) associations ( $p < 0.5$ ) with OC (Fig. 1: middle), *leaping* had  
14 only mixed associations—significantly negative in non-anthropoids by itself (Table 2) and  
15 significantly positive after controlling for its interaction with body mass (Table 2; Figs. 1 & 2).  
16 *Daily path length* traveled (-0.4 to -4° per km) and *nocturnal* (-4°) were the only strongly negatively  
17 associated variables, more significantly so in non-anthropoids (Fig. 1). *Color vision* (+3°) was  
18 positively associated in anthropoids and overall ( $p < 0.15$ ). Not surprisingly, *leaping* and *path length*  
19 are highly inter-related variables with interactions that obscured straightforward interpretation of  
20 effects (Table 2). *Insectivory* was understandably positive in non-anthropoids ( $p < 0.25$ ) and negative  
21 in anthropoids ( $p < 0.75$ ). Surprisingly, *fruit* eating was negatively correlated ( $p < 0.6$ ) in all models.

22 These results are mostly consistent with previous studies (Wheeler, Bradely and Kamilar,  
23 2011) that found body mass, arboreal ranging, and vision sense variables to be the most  
24 convincingly co-varying with OC (see Table 2). Many of our discoveries, in anthropoids, however,  
25 were in impressive contrast to previous studies. For example, we see a moderate and significant  
26 group size effect on OC. This effect is particularly pronounced in anthropoids and especially for  
27 groups over ten individuals—in solid support of predation deterrence theory. We also uncovered a  
28 correspondence of frugivory and color vision to large differences in OC ( $> 12^\circ$ ) in a categorically  
29 partitioned analysis (Table 3)—arguably supportive of an angiosperm co-evolution model that could  
30 be extended to ripeness detection faculties at the emergence of basal anthropoid diurnality. A  
31 similar, cross-tabulation based, examination, of grasp-leap variables, revealed the highest average  
32 OC as occurring via the combination of low-path-length and frequent leaping, within both  
33 anthropoids and non-anthropoids alike (Table 4). These additional tables, along with our numerous  
34 multivariate plots, proved invaluable for independently substantiating various aspects of the results  
35 of the PGLM and AIC weighted model averaging analyses.

36 Our *anthropoid* indicator variable (results un-tabulated) also helped to confirm, in  
37 agreement with previous research (Ravosa and Savakova, 2004), that the anthropoid subset of  
38 primates deviate significantly from the acute predictions of allometric theory—that negative scaling  
39 of eye and orbit size primarily drives OC in anthropoids. These findings open up new possibilities  
40 for viewing OC changes in anthropoids as more adaptive (swing-grasp, frugivory, snake detection,  
41 and other possible group size related models) rather than as chance side-effects. Thus there appears  
42 to be evidence for almost all (ten) variables reasonably influencing OC, and in a way that lends  
43 support to most of the dozen plus origins theories considered. The conflicting results between the  
44 PGLM and aggregative cross-tabulations for both the binary indicators of *nocturnal* and *fruit* as  
45 well as the continuous locomotion variables are discussed—and hopefully somewhat deconvoluted  
46—in various tables (Tables 3 & 4), figures (Figs. 1-3), and multiple paragraphs in the subsequent  
47 discussion. Ancestral character estimation for leaping (32%) and swinging (24%) are also depicted  
48 (Figs. 4 & 5) and serve to further bolster evolutionary chronologies in the context of limited fossil  
49 evidence.



1 **Table 2. Highest R<sup>2</sup> OC models for full, intermediate, and reduced variable compositions.**

		full	intermediate	reduced	AIC weighted average
<i>model size:</i>					
non-anthropoids	<i>variable count:</i>	<b>v=7</b>	<b>v=6</b>	<b>v=3</b>	
	<i>tree transform:</i>		$\kappa=0.66; \lambda=0.33; \delta=2.4$		
	<i>model perform:</i>	$R^2=0.815; AIC=85$	$R^2=0.78; AIC=83$	$R^2=0.713; AIC=82$	
	<b>mass, Kg</b>	<b>1.33 ( 0.037 ) *</b>	<b>1.49 ( 0.012 ) *</b>	<b>1.32 ( 0.004 ) **</b>	<b>1.26</b>
	<b>nocturnal</b>	<b>-4.01 ( 0.210 ) _</b>	<b>-2.92 ( 0.293 ) _</b>		<b>-1.34</b>
	fruit	-2.11 ( 0.313 ) _			-1.81
	<b>insect</b>	<b>4.39 ( 0.240 ) _</b>	<b>4.33 ( 0.218 ) _</b>		<b>3.02</b>
	<b>arboreal</b>	<b>4.60 ( 0.242 ) _</b>	<b>3.38 ( 0.329 ) _</b>		<b>2.86</b>
	<b>path length, km</b>	<b>-4.72 ( 0.014 ) *</b>	<b>-4.83 ( 0.005 ) **</b>	<b>-3.68 ( 0.001 ) **</b>	<b>-4.20</b>
	<b>leap, %</b>	<b>-13.34 ( 0.016 ) *</b>	<b>-12.17 ( 0.006 ) **</b>	<b>-10.01 ( 0.007 ) **</b>	<b>-9.76</b>
anthropoids	<i>variable count:</i>	<b>v=10</b>	<b>v=6</b>	<b>v=4</b>	
	<i>tree transform:</i>		$\kappa=0.87; \lambda=0.385; \delta=2$		
	<i>model perform:</i>	$R^2=0.391; AIC=291$	$R^2=0.384; AIC=283$	$R^2=0.369; AIC=281$	
	<b>mass, Kg</b>	<b>0.13 ( 0.010 ) *</b>	<b>0.14 ( 0.001 ) **</b>	<b>0.14 ( 0.001 ) ***</b>	<b>0.14</b>
	<b>group size</b>	<b>0.10 ( 0.191 ) _</b>	<b>0.10 ( 0.152 ) _</b>	<b>0.10 ( 0.078 ) .</b>	<b>0.09</b>
	<b>nocturnal</b>	<b>-4.44 ( 0.491 ) _</b>	<b>-5.01 ( 0.394 ) _</b>		<b>-4.87</b>
	color vision	1.18 ( 0.748 )		3.35 ( 0.159 ) _	2.55
	<b>fruit</b>	<b>-1.56 ( 0.582 )</b>	<b>-2.58 ( 0.237 ) _</b>		<b>-2.72</b>
	insect	-0.93 ( 0.768 )			-2.69
	arboreal	-0.75 ( 0.834 )			-0.07
all primates	<i>variable count:</i>	<b>v=10</b>	<b>V=6</b>	<b>v=4</b>	
	<i>tree transform:</i>		$\kappa=2.0; \lambda=0.5; \delta=0.6$		
	<i>model perform:</i>	$R^2=0.325; AIC=393$	$R^2=0.315; AIC=388$	$R^2=0.282; AIC=385$	
	<b>mass, Kg</b>	<b>0.14 ( 0.003 ) **</b>	<b>0.14 ( 0.001 ) **</b>	<b>0.15 ( 0.001 ) ***</b>	<b>0.15</b>
	<b>group size</b>	<b>0.12 ( 0.074 ) .</b>	<b>0.14 ( 0.019 ) *</b>	<b>0.13 ( 0.024 ) *</b>	<b>0.11</b>
	<b>nocturnal</b>	<b>-4.07 ( 0.161 ) _</b>	<b>-3.57 ( 0.177 ) _</b>	<b>-4.07 ( 0.123 ) _</b>	<b>-3.86</b>
	color vision	1.09 ( 0.767 )	3.04 ( 0.284 ) _		2.91
	fruit	-1.19 ( 0.560 )			-1.73
	insect	-1.21 ( 0.644 )			-2.86
	<b>arboreal</b>	<b>1.50 ( 0.569 )</b>			<b>1.39</b>
<b>path length, km</b>	<b>-1.07 ( 0.302 ) _</b>	<b>-1.09 ( 0.226 ) _</b>	<b>-1.27 ( 0.150 ) _</b>	<b>-1.04</b>	
leap, %	-3.74 ( 0.496 ) _			-3.35	
<b>swing, %</b>	<b>3.16 ( 0.591 )</b>	<b>5.17 ( 0.273 ) _</b>		<b>4.53</b>	

2 Insectivory was only significant in non-anthropoids, supportive of visual predation theory. The  
3 combination of significance and directionality of nocturnal, arboreality, and color vision are  
4 supportive of ripeness detection or angiosperm co-evolution, but only if terrestrial (yet fruit-eating)  
5 macaca are left out. Group size had mixed effect directions (- in reduced and + in full) amongst  
6 non-anthropoids and was left out of the final PGLM. Swinging and group size had credibly positive  
7 associations with OC in anthropoids. Body mass was the single most consistently significant factor  
8 determining higher OC at all levels, even in the most reduced model compositions. These last two  
9 results are supportive of rear attack risk reduction [RARR] theory over more neutral allometric  
10 hypotheses. AIC-weighted means of parameter estimates, over all possible models, appear in the  
11 rightmost column. Significance codes: '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 '\_' 0.5 ' ' 1

1

2 **Table 3. Angiosperm relevant variable cross-aggregations for OC means (and species counts).**

		predominantly frugivorous				
		NO		YES		
		color vision		color vision		
		no	yes	no	yes	
predominantly arboreal	NO	nocturnal yes	NA	NA	NA	NA
		nocturnal no	56 (1)	82 (6)	NA	80 (7)
	YES	nocturnal yes	54 (7)	NA	58 (4)	NA
		nocturnal no	59 (5)	79 (9)	71 (27)	77 (15)

The largest positive differences in OC, between angiosperm relevant categorical variables, occurs between color-blind non-frugivores (far left column) and the other combinations of frugivory (right most columns) and trichromatic vision (sub-right columns). Out of many possible comparisons, the OC discrepancies associated with change in fruit-eating status between non-trichromatic arborealists (sub-left lower columns) seems most telling. Although the +4° convergence seen in nocturnals (third row) is somewhat small, the +12° difference in convergence between

those with dichromatic vision towards frugivory (lemurs vs. callitrichids) is more supportive of co-evolution scenarios involving incisor-initiated consumption of hard, colorful fruit (Cachel, 1979a) as well as flowering vegetation more generally (Sussman, 1991).

20

21

22 **Table 4. Grasp-leap relevant variable cross-aggregations for OC means (and species counts).**

		frequent leaping			
		no		yes	
		daily path length			
		long	short	long	short
Anthropoid	yes	77	76	68	82
	no	55	56	50	57

The primates with the highest OC are those with short daily path length (< 1.4 km) and frequent leaping (> 25%) behaviors (far right column). Such primates include several anthropoids: *Colobus*, *Ptilocolobus*, and *Presbytis* (top row), as well as non-anthropoids: *Tarsius*, *Hapalemur*, *Eulemur*, *Indri*, and *Propithecus* (bottom row). This combination might suggest that primates with high OC are merely more proficient vertical tree-trunk climbers who are perhaps spending more time locomoting vertically rather than horizontally. It could also alternatively suggest that efficient canopy gap-crossing OC selected for

landing of associated long-distance leaps or that such elevationally protected canopy inhabitants have much less need for peripheral view of attacks from predators. Also see the continuous versions of this analysis in Figures 1 through 3.

36

37

### 38 Discussion

39

40 Primates' specialized neuroanatomy prioritizing vision over smell is echoed by their  
 41 enlarged crania and convergent orbits—and active locomotion implied by fossils with powerfully  
 42 long hind legs, and claw-less grasping hands (Cartmill, 2002; Silcox *et al.*, 2007; Gebo, 2013). The  
 43 fossil evidence for such forms of substrate grasping origins has been corroborated by quantification  
 44 of analogous mechanics in other arboreal mammals (Rasmussen, 1990; Lemelin, 1999). These  
 45 specializations towards full-time tree dwelling serve as compelling testimony to an over-arching  
 46 evolution towards arboreal avoidance of predational encounters (Crompton, 1995; Isbell, 2006). It  
 47 is unclear, however, when these morphological changes happened evolutionarily along other  
 48 possible evolutionary events in the late Cretaceous and early Paleogene. The relative contribution of  
 49 individual ecological forces in shaping the euprimate morphotype is similarly unclear. No one-size-

1 fits-all explanation to the question of primate or anthropoid origins is likely to suffice. Instead,  
2 evolutionary explanations should ultimately endeavor to be “multifactorial”—tracking vision  
3 changes, diet, and locomotion in a diversity of arboreal contexts (Crompton, 1995). Indeed, many  
4 leading theories—angiosperm co-evolution, VP, and terminal branch locomotion—share  
5 considerable overlaps with each other (Rasmussen, 1990). Here we outline over a dozen  
6 consequential primate origins theories and evaluate their cogency in light of these new results with  
7 an eye toward relevance to anthropoid origins.

8 Stem-anthropoids were small primates that endured their likely reclusive existence via  
9 scrounging for insects in dusky foliage (Beard *et al.*, 1994; Ross, 1995). Correspondingly,  
10 researchers have frequently considered nocturnality as determinative of [a light-intake maximizing  
11 function for] OC (Allman, 1977; Kay and Cartmill, 1977; Heesy, 2008; Wheeler, Bradely and  
12 Kamilar, 2011), perhaps in combination with locomotion (Cartmill, 1980; Allman, 1982). Activity  
13 period related vision changes (toward trichromatic vision for haplorhines) proved to be a consistently  
14 important factor associated with higher OC, especially when comparing anthropoids to nons  
15 (*nocturnal*;  $-4$ ;  $p < 0.2$ ). Our results agree that activity period and color-vision are important factors  
16 overall, as found in a previous study (Wheeler, Bradely and Kamilar, 2011). Nocturnality and color  
17 vision had similar effect sizes, of around four degrees, but were rarely both significant in the same  
18 model (Table 2). Daylight, admittedly however, did seem to provide an important setting in which  
19 color vision could have co-evolved with frugivory to bring about the precipitous increase of OC  
20 ranging from  $4^\circ$  to  $12^\circ$  (Table 3). This conclusion is supported by transitional fossil taxa such as the  
21 Omomyidae who exhibit a mix of both dietary (insectivory and frugivory) and activity period  
22 (diurnal and nocturnal) traits (Kay and Covert, 1984). But nocturnal locomotion theories, including  
23 leaping (Crompton, 1995), clambering (Allman, 1982), and nocturnal visual predation [NVP]  
24 (Cartmill, 1972) were not supported here despite possible relevance in stem-primates, for whom we  
25 do not have data.

26 Tarsiers, relatedly, are known to orally catch their insect prey before landing with freed  
27 limbs—a task which could require (nocturnal) vision to be undisturbed by such mid-flight  
28 mastication. It posits that ocular motor stability—rather than stress (Nakashige, Smith and Strait,  
29 2011) from chewing—could be responsible for the emergence of the post orbital septum, a cranial  
30 feature adjacent to the orbits. It is possible that OC and the post-orbital septum evolved in order to  
31 brace the highly-interconnected visual-mastication apparatus while chewing food (Cartmill, 1980;  
32 Ravosa *et al.*, 2006). This masticatory-visual stabilization theory (Noble, Kowalski and Ravosa,  
33 2000) is quite compelling, but no combination of *leap* and *insectivory* was statistically supported,  
34 and thus any consideration of interactivity was excluded from final models. The related, but more  
35 specific, incisor-bite facial-twist buttressing theory (Rosenberger, 1986) is only slightly more  
36 supported as it identifies harder fruits as instigative (Table 3). Our examination, however, is  
37 admittedly quite limited, not only just to extant primate data-points, but to orbital convergence data  
38 as an outcome variable, instead of potentially more appropriate alternatives, such as those relating  
39 post-orbital bar strength. However, OC did at least associate positively with *insectivory*, perhaps  
40 indicating that preying upon insects could play a role in primate cranial evolution.

41 Aside from such vision-impaired leap-landing, there are other visually challenging targets  
42 that could be considered to have selective influence on primate orbits. Predation upon insects in the  
43 “fine-branch milieu” via VP (Cartmill, 1972) is possibly a second core selective influence following  
44 arboreal grasping and perhaps preceding (Heesy, 2009) dietary preference for flowering plants  
45 (Cartmill, 1972, 2012). Here, *insectivory* was only a marginally significant factor in non-  
46 anthropoids ( $p < 0.2$ ), but this fact conforms well directionally (positive in non-anthropoids and  
47 negative in anthropoids) to insect predation theories. This evidence for a dietary selection effect on  
48 non-anthropoids is consistent with the high levels of variation in dietary indicators in fossil teeth—a  
49 mix between frugivory and insectivory—seen in Eocene *Omomyidae*, a stem group of tarsiiiformes  
50 (Rasmussen, 2007). Locomotion-wise, our examination confirms evidence favoring an adaptive VP

1 model as differing from neutral allometric predictions—by highlighting the exceptional case of  
2 (high OC) lorises who similarly dive forward with their forelimbs (sans leaping) to capture flying  
3 insect prey. Thus it is important to understand both the nature of landing targets as well as the form  
4 and mode of associated positional behaviors involved.

5 To save time and energy during foraging or evasion, leapers can avoid long path lengths  
6 between trees (Crompton et al., 1993). Leaping theories such as these, more generally, were most  
7 strongly supported in our results via daily locomotion *path length*, and moderately so via *leaping*  
8 (Table 2) provided that encumbrances with other factors (e.g. body mass and substrate type) are  
9 taken into account (Figure 2). Frequent vertical, and likely elevationally risky, leaping in particular,  
10 corresponded to high OC (Table 4). This aligns well with both fossil and modern data analyses that  
11 corroborate ancestral leaping as a quite common (>32%) locomotor activity (Schruth, 2015; Boyer,  
12 Toussaint and Godinot, 2017) suggestive of leaping being frequent enough to play a role in ancient  
13 evolution, but potentially more for motor-control cognition than committed skeletal changes.  
14 However, the evidence presented here (Table 2) suggests leaping has an opposite association in non-  
15 anthropoids (-) vs anthropoids (+). Perhaps the former practice a more horizontal form of leaping  
16 with unplanned, and sometimes terrestrial, landings (e.g. low-height, habitual *evasion* in galagos).  
17 The latter could practice a more deliberate vertical leaping onto relatively narrower, branch or trunk  
18 landings (e.g. high-canopy *avoidance* in *Proboscis* or *Indri*). In either case, frequent leaping  
19 behavior (Fig. 5) is broadly evidenced by post-cranial fossils in nearly all early primates, but not  
20 other euarchontans (Fleagle, 2013)—and thus likely influenced changes in euprimate vision,  
21 skeletally manifested or not. A primary confounding factor in leaping frequency, however, is the  
22 mass of the leaping primate insofar as heavier primates tend to leap less.

23 In this study, body mass was by far the most significant variable. Estimates of ancestral  
24 primate body mass range from rather small (< 1 Kg) (Silcox and López-Torres, 2017) to extremely  
25 small (15g) (Gebo, 2013). And a primary distinguishing feature of anthropoids is the great  
26 discrepancy in sizes, ranging from 1 Kg all the way up to 1000 Kg. As smaller early anthropoids  
27 grew, a reasonable null suggests that relatively smaller orbits may have relieved constraints on  
28 lateral facing orbital apertures (Cartmill, 1970). And despite the fact that Lorises do provide  
29 confirmation of the adaptiveness of such unusually high OC compared with a default two-part  
30 (activity period meets allometry) model, they are exceptional amongst non-anthropoids. Body mass,  
31 for example, is still highly (10-fold larger effect size) predictive of OC in highly *nocturnal* non-  
32 anthropoids who have no such diurnality to support the case for allometric scaling driving OC.  
33 Considering that group-size effects are the second most consistently significant effect on OC in  
34 differentiating anthropoids ( $p < 0.03$ ), an agglomerate evolutionary constraint-relaxation mechanism  
35 via predation-aversion emerges as rather promising.

36 Organisms can avoid predation by evading, fleeing, out-growing, out-competing, mobbing,  
37 freezing, or deploying spines or armor (Morse, 1976). The “arboreal theory,” in line with the first  
38 two of these forms of non-confrontation, suggests that trees were the most formative of primates.  
39 Because arboreal complexity requires distance judgments related to climbing (Jones, 1916; Smith,  
40 1924; Clark, 1959) and for more accurate locomotor bout landing behavior, primates may have  
41 further developed stereoscopic vision and increased OC. Due to numerous examples from rodents  
42 and squirrels as well as felids and raptors, we know that arboreality does not by itself necessitate  
43 OC (Cartmill, 1972; Heesy, 2009) and that binocular vision, regardless of habitat, tends to evolve in  
44 predators (Allman, 1977; Pettigrew, 1986). And despite primates largely inheriting arboreality from  
45 their euarchontan predecessors, other extant orders (e.g. tree shrews) are only semi-arboreal (Fuchs  
46 and Corbach-Söhle, 2010), suggesting primates may have initially been more steadfast arborealists.  
47 And even today, those that aren’t protected on islands or by larger size (e.g. African and Malay  
48 primates) tend to maintain a strict arboreality (e.g. New World monkeys) (Napier and Napier, 1985).  
49 Furthermore, hazardous forms of arboreal locomotion (e.g. leaping), might also co-associate with  
50 increased fall risk, especially on terminal branches. The idea that inter-substrate gap-spanning

1 drives primate cranial evolution is at least partially supported by positive leap percentages (and  
2 negative DPL) associating with OC, especially if mass is also considered (Fig. 2). Our binary  
3 arboreal measure alone, however, suggests evolutionary influence (+4°) in non-anthropoids ( $p < 0.3$ ),  
4 and perhaps between sub-ordinal clades (Table 2). Thus, OC could be quite influenced by arboreal  
5 refuges, presumably as part of alleviating predation pressures. Arboreal locomotion, like arboreality  
6 itself, appears to have been a foremost adaptive influence (Crompton and Sellers, 2007) to  
7 counteract terrestrial carnivores. Additionally, (infant-laden) inter-tree leaping could have been  
8 important part of maintaining a strict arboreality—essential for continued predation avoidance and  
9 maintenance of a high trophic level—thereby eliminating any need for constant posterior vigilance.

10 After arboreality, a co-radiation with large-gape, constricting snakes could have brought  
11 about further predatory selection pressures that likely influenced vision-related improvements—  
12 perhaps due to being recruited for detection of them (Isbell, 2006). Primates are known to execute  
13 specialized locomotor bouts to avoid predators (Legreneur *et al.*, 2012), and snakes have been a  
14 perennial evolutionary influence for hundreds of millions of years (Silcox and López-Torres, 2017).  
15 Although no snake-specific proxy variables were significant here, or previously, in a study testing  
16 SD (Wheeler, Bradely and Kamilar, 2011)—we suggest not ruling out serpentine predation pressure  
17 until more direct measures are developed. Regardless of the inconclusive evidence relating reaching  
18 and grasping with stereoscopic vision (Watt and Bradshaw, 2000), locomotion based theories are  
19 not necessarily exclusive of snake-predation theories. However, the various environmental proxy  
20 variables associated with snake habitats—such as rainfall, temperature, and latitude—did not lend  
21 promising support for snake detection theory. Barring development of improved methods, which  
22 might more directly track certain predators, we will likely not be able to do better than testing more  
23 generalistic predation theories.

24 It is possible that predation (specifically lack thereof) still indirectly drives OC, as apex  
25 predators, who are prey to no predators themselves, are known to have highly convergent orbits  
26 (Cartmill, 1972; Pettigrew, 1986; Wheeler, Bradely and Kamilar, 2011). Although few primates are  
27 apex predators, their avoidance of being the prey of any carnivores improves their trophic level by  
28 default. Consequently, primates may have much less impulsion to flee when threatened, perhaps due  
29 to a consistently reduced risk of predation that spanned epochs. Surviving radiations of primates  
30 increased in body mass and, consequently, further reduced their predation threats (Isbell, 2006). The  
31 significance of body mass (as a mechanical deterrent to prey potential) however also provides  
32 strong evidence of something other than predation by snakes driving OC (Wheeler, Bradely and  
33 Kamilar, 2011). It is possible that, in frugivorous anthropoids, such a high calorie, growth enabling  
34 diet could have propelled such a continued explosion in size. This form of (gross mass) size  
35 dominance-based predator deterrence could have further allowed for converging orbits due to a  
36 relaxed need for peripheral vision as defense from predators or competitors. Trees likely provided a  
37 barrier partitioning clusters of closely related kin from conspecific as well as predation-based  
38 threats, thus relaxing any rear-attack risk, and consequently also any peripheral constraints on OC.  
39 Thus reduced posterior predation could be broadly construed as *rear attack risk reduction* [RARR],  
40 to also accommodate conspecific attack risks.

41 Eocene primates, as they experienced diminishing pressure for concealment from predation,  
42 especially via the cover of night, may have subsequently found themselves under an entirely new  
43 array of selection pressures via daylight. As mentioned formerly in this section, *nocturnality* had a  
44 negative relationship with OC under all taxonomic subsets and variable compositions. This suggests  
45 that diurnality could have been a strong factor in driving orbital convergence in primates resembling  
46 *Eosimiidae*, the aptly designated ‘dawn monkey’ (Beard, 2004). A dual curiosity remains, however,  
47 of not only why these primates were able to risk predation by forgoing the protective cover of night,  
48 but also why, in braving the light, they evolutionarily forfeited posterior peripheral vision used for  
49 detecting such attacks. Although foraging upon the colorful terminuses of branches, instead of for  
50 insects, could have also provided positive selection for OC (Sussman, 1991). Oddly, Haplorhines—

1 which includes modern (low OC) tarsiers (*Beard et al.*, 1994)—were (e.g. *Archicebidae*) initially  
 2 diurnal (*Ni et al.*, 2013) before returning to a nocturnal (and insectivorous) lifestyle. This last fact is  
 3 rather illustrative of just how potent adaptations for color vision may have been in empowering  
 4 cathemeral, and even diurnal, primates that began consuming the flowering terminal branches of  
 5 angiosperms.

6 Subsistence in the form of terminal-branch foraging (Sussman, Rasmussen and Raven,  
 7 2013) is argued to have driven the very first defining adaptations of primates, eventually favoring  
 8 dental despecialization, claw loss, and grasping improvements (Silcox *et al.*, 2007). Indeed, fossil  
 9 teeth of early primates suggest an omnivorous diet including insects as well as fruit (Silcox and  
 10 López-Torres, 2017). Frugivory was even more compelling as a selective force, perhaps as part of  
 11 angiosperm co-radiation (Rasmussen, 1990; Sussman, 1991), during the Eocene (Silcox and López-  
 12 Torres, 2017). In our PGLM analysis, frugivory was inversely associated with OC (Table 2), but the  
 13 negative effect size is substantially reduced with removal of the three terrestrial yet frugivorous  
 14 macaca species, who perhaps forage less fastidiously in the trees. Furthermore, frugivory was able  
 15 to be rectified as confirmative in our categorical analysis (Table 3). The apparent effect on OC of  
 16 differences in fruit eating between color-blind (non-trichromatic) primates was striking (+12°),  
 17 suggestive of a possibly (positively selected) adaptive evolution. We correspondingly suggest that  
 18 vision related changes, perhaps for improved foraging, could be key in differentiating these two  
 19 sub-ordinal clades, partly in confirmation of others' findings of OC and frugivory (Heesy, 2003).  
 20 This large effect size conjures imagery of cathemeral and dichromatic primates experimentally  
 21 sampling the varied ripeness of fruits (Polyak, 1957) as earnest arborealists—eventually partitioning  
 22 the (unsuccessful) strepsirrhines from the (successful) platyrrhines and catarrhines. The more  
 23 compelling possibility of such an inter-related co-evolution between color vision, frugivory, and  
 24 diurnality (Cachel, 1979b), in turn, also renders the neutral allometry model less compelling as a  
 25 solitary instructive explanation for OC in anthropoids.

26 *Group size* was another variable strongly associated with OC, primarily in anthropoids but  
 27 also overall, perhaps highlighting a major difference between anthropoids and nons. Others have  
 28 suggested that group size could have evolved in relation with snake predation as a way to *detect*  
 29 them pre-encounter (Isbell, 2006) or *mob* them during (Wheeler, Bradely and Kamilar, 2011). We  
 30 have suggested, instead here, that size has stronger statistical link to group defensibility as a  
 31 predation *deterrent* well before any detection. Unlike during individualized pursuit of more solitary  
 32 primates, those that live in large groups are much less likely to be attacked from behind due to the  
 33 *possibility* of group counter-attack—and therefore such protections may have contributed to an  
 34 atrophy in maintenance of laterally oriented eyes. Other than rear-facing disincentives, however,  
 35 many other forward-facing incentives of group life are also possible including: anti-parasitic  
 36 grooming, group member recognition, and interpretation of facial gestures. In addition to  
 37 arboreality, size, and grasp-landing, anthropoids may have increasingly employed suspensory-based  
 38 feeding to enable further increases in OC—as habitual swinging comprises nearly 80% of all  
 39 locomotor types amongst the largest frugivores.

40 It is thought that body mass increases associated with suspensory locomotion (and a shift  
 41 toward terrestriality) could drive OC (Isbell, 2006). But it is also possible that grasp-swing by itself  
 42 acts as (an admittedly more proximate) selection pressure, analogous to the way grasp-leap or  
 43 arboreal clambering might require accuracy in limb landing for fall-avoidance in other arboreal  
 44 primates. Despite hylobatids having a higher than expected OC given their *group size* (Fig. 3),  
 45 *swinging* was admittedly only marginally significantly correlated with OC in PGLM.  
 46 Understandably, *swinging* has a less pronounced evolutionary signature on OC, perhaps due to its  
 47 rarity. Also, it tends to include more substrate connectivity, and presumably entails less risk, but  
 48 potentially more skill than leaping. Swinging—when along the same branch, tree, and orientation—  
 49 is more predictable, but per-limb landing-accuracy risks are higher, than in leap-landing.  
 50 Nevertheless, it appears that a grasp-swing form of generalized precision limb-landing—an

1 extrapolation of grasp-leap—is still somewhat (albeit weakly) supported, but surprisingly more so  
2 in gibbons over prehensile tail wielding spider-monkeys (Fig. 3). More puzzling, however, is what  
3 this marginal association of OC with (our theoretical extension into) swinging implies about  
4 ancestral grasp-leap theory itself. If precision limb landing via swinging is perhaps only a minor  
5 factor amongst hominoids (only 26% ancestrally; see Fig. 4) in determining OC, then logically, it is  
6 also perhaps similarly so for other more challenging forms of locomotion in primates more  
7 generally. This low (yet non-negligible) percentage may approximate the ancestral condition for  
8 *Hominoidea*—in concurrence with the evidence for suspensory locomotor behavior as ancient as  
9 20mya in fossil genus *Morotopithecus* (MaClatchy et al., 2000). This is in spite the existence of  
10 several non-suspensory fossil apes that emerged after the 18mya split with hylobatids—17myo  
11 *Proconsul*, a putative ancestor to modern chimpanzees (Ward, 1993), and 12myo *Sivapithecus*, a  
12 putative ancestor to orangutans (Pilbeam et al., 1990). Our results, therefore, are reasonably in line  
13 with a deep ancestry of (at least a modicum of) suspensory behavior that may have subsequently  
14 been substantially diminished in the taxonomic branches running conterminously with *Hominidea*.

15 Our observed locomotion influences on OC were primarily only significant under scenarios  
16 that explicitly split the primate tree in two. Analyses that focus on either anthropoids or non-  
17 anthropoids, each by themselves, help distinguish the many interactions (e.g. mass with locomotion)  
18 in various clades—pivotal, evidently, for resolving independent evolutionary chronologies. Archaic  
19 non-anthropoids, for example, were small but likely leapt more frequently, and perhaps with less  
20 concern for accurate landing. Derived anthropoids, however, likely leapt less frequently, but perhaps  
21 more conservatively to avoid an elevated risk of injury—as is associated with larger falling bodies  
22 (Sawyer et al., 2000; Jarrell, 2011). Our advocacy for the adaptive nature of improvements in hand-  
23 eye coordination for arboreal landing tasks—is unfortunately only conflictingly supported by our  
24 locomotion data. And while this locomotion model is graphically supported (Fig. 3), parameter  
25 estimates via PGLM suggest only marginal significance in anthropoids (Table 2). Adaptive changes  
26 in OC, however, could more likely originate from an alternative driver of reduction in posterior  
27 predation, that of predation-detering general size increases.

28 Taken together, the changes primates have achieved in motor-control for visually guided  
29 limb-landing may have evolved in response to indirect pressures via locomotion—albeit  
30 increasingly for anthropoid, rather than non-anthropoid, primate evolution. Theories such as anti-  
31 parasitic grooming, face recognition, or even terrestrial mobbing deterrence, are difficult to test, but  
32 they do seem to merit intriguing promise for future inquiry. Angiosperm coevolution and ripeness  
33 detection have strong support in our categorical analysis (Table 3) but are conflicted by (terrestrial  
34 fruit-eating macaca in) the PGLM, an inconsistency due perhaps to diet being more labile or due to  
35 it only being a binary measure of a still poorly defined trait. Clearly however, daylight decidedly  
36 appears to have played a role, regardless of the specific evolutionary sequence of trait acquisition.  
37 Diurnality likely radically empowered solitary primates via illumination of their grasp-landing  
38 targets, perhaps because, as arborealists, they were no longer actively evading predators, but  
39 preventatively avoiding them entirely. Serpentine predation presents testing difficulties, but our  
40 results are not entirely inconsistent with most such predation scenarios. Snakes are one of the few  
41 predators who can pursue primates arboreally and similarly exceed the typical allometric limits of  
42 locomotion in such topologies. Although not an explicitly significant effect as studied here in  
43 isolation, a more broadly re-construed influence of long-term arboreality—maintained via terrestrial  
44 predation and enabled via angiosperm dependence—is still conceivably congruous with our results.  
45 While insectivory clearly has a positive effect on OC (in support of VP and ocular stability)  
46 *nocturnal* did not increase with OC—with the important exception of Lorises (Fig. 3)—ruling out  
47 the applicability of such primate origins theories to most primate sub-taxa.  
48

## 1 Conclusion

2

3 Primates can out-maneuver, out-position, or out-grow predators by leaping away from them,  
4 dwelling in trees, or increasing in size. While our finding regarding size appears to be consistently  
5 true throughout primate evolution, our findings on locomotion are more complicated and mixed. In  
6 confirmation of rapid grasp-landed locomotion being a convincing influence on cranial evolution,  
7 most anthropoids, and some lemurs, had positive associations of leaping with OC. More  
8 compellingly, however, terminal branch frugivory, perhaps in conjunction with visual-perceptual  
9 adaptations to increasing diurnality, seems to have most strongly effected OC—establishing this  
10 most prodigious division of the primate order. This is possibly a result of the survival enhancing  
11 nature of full-time frugivory in enabling long-term arboreal predation avoidance. Considerations of  
12 both body and group size, together through the illuminating lens of trophic-rank modeling, evokes  
13 measurable support for our argument for overall predation and competition reduction indirectly  
14 driving increases in OC. That is, many primates seem to have eliminated posterior threats by  
15 becoming bigger or more numerous, and consequently reduced the need for lateral facing orbits.

16 Our primary test of an order-wide, precision-limb-landing theory to extend the logic of  
17 *grasp-leap*, to something we have companion termed *grasp-swing*, should also apply to more rapid  
18 forms of suspensory locomotion (e.g. ricochet brachiation), although data on speed of locomotion  
19 is currently still quite limited. Likewise, one of our proposed associations of OC with improvised  
20 predation-evasive leaping in smaller early primates has presented such a grasp-leap origins theory  
21 with some reproval, as primarily the larger-bodied, grasp-landing anthropoids seem to have higher  
22 degrees of OC. Despite this complication, grasp-swing has fared better, however, as Hylobatids  
23 have higher orbital convergence, even compared with comparably-sized Atelids, and especially after  
24 consideration of *group size* effects (Fig. 3). Improvements in ecological data collection, analytical  
25 methodologies, and phylogenetic control should help to untangle the highly inter-connected causal  
26 complexities underlying the origins of grasp-landing in primates.

27 Admittedly, this work depends on many methodological and theoretical assumptions that  
28 have heretofore largely not been addressed. The modestly compelling results on leaping also appear  
29 to be highly sensitive to selection of ecological control variables, their interactions, and  
30 phylogenetic-tree transformation assumptions. We captured such deeply inobservable events (e.g.  
31 angiosperm co-evolution) only under more extreme tree transformations, which we have  
32 confirmationally salvaged chiefly by virtue of the categorical analysis. There are also major limits  
33 to such a comparative approach, namely that we consider fossil evidence, or known irregularities in  
34 the paleogeologic histories, only in passing. Along these lines, we should note that the PGLM tends  
35 to only capture more gradualistic, pan-taxon evolutionary changes over time (within taxonomic  
36 subsets) and may neglect more punctuated changes between such subsets. Furthermore, we are  
37 reminded that OC is only one of many possible measures of visual potentialities, as *neurological*  
38 restructuring likely also heavily influences (even nocturnal) locomotor capabilities. Without trees,  
39 and corresponding symbiosis to feed (and disperse) their full-time arboreal residents, eyes locked in  
40 an anterior direction by bony post-orbital septa might better indicate overall reduced posterior risks  
41 (from predators or competitors) than improved ability for detection of anterior visual detail.

42 Penultimately, we declare a need for overhaul of measurement approaches with  
43 prioritization of continuous ecological indexes. Binary indicator variables (with huge effect sizes in  
44 the two-by-two analysis), for example, seem to be statistically overshadowed by their continuous  
45 neighbors in PGLM, which tended to show much greater statistical significance. Likewise, instead  
46 of more ideal measures of canopy height, trophic level, and home range, we have resorted to using  
47 imperfect, but more readily measurable, variables such as path length and leaping frequency to  
48 detect merely signatures of our proposed elevated trophic rank of full-time arboreal primates. More  
49 ultimate causative evolutionary phenomena such as predation, arboreality, fall risk, competition,  
50 and territoriality—each of which is currently too ambiguously delineated—could also similarly be



1 re-construed to serve as indirect indicators of many of our more ultimate influences. Further issues  
2 include taxonomic quandaries, case-wise species deletions between mismatched datasets, as well as  
3 the known deficiency of ecological controls. Measurements of predation, in particular, are nearly  
4 entirely unprocurable, and research into comparisons of such effects on OC in primates to other  
5 (predator and non-predator) mammals is merited.

6 Finally, while these proposed theories are typically only applied to origins of primates in  
7 contrast to supra-ordinal stem clades (an analysis currently hindered by our extant primate dataset),  
8 we have found them to be surprisingly useful in explaining the evolutionary shifts both within and  
9 between suborders. Specifically, we have found evidence that the four predator deterrents of  
10 arboreality initially, size in all primates, vertical leap *landing* in larger non-anthropoids, and  
11 potentially even brachiational hand placement in hylobatids, could all serve to maintain trophic  
12 dominance in particular ecosystems and thereby reduce the requirement for peripheral visual input  
13 for prolonged vigilance. Most notably, we recommend a broader reconsideration of at least half of  
14 conventional primate origins theories that could also equally, if not more appropriately, be applied  
15 to anthropoid origins.

16

17

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19

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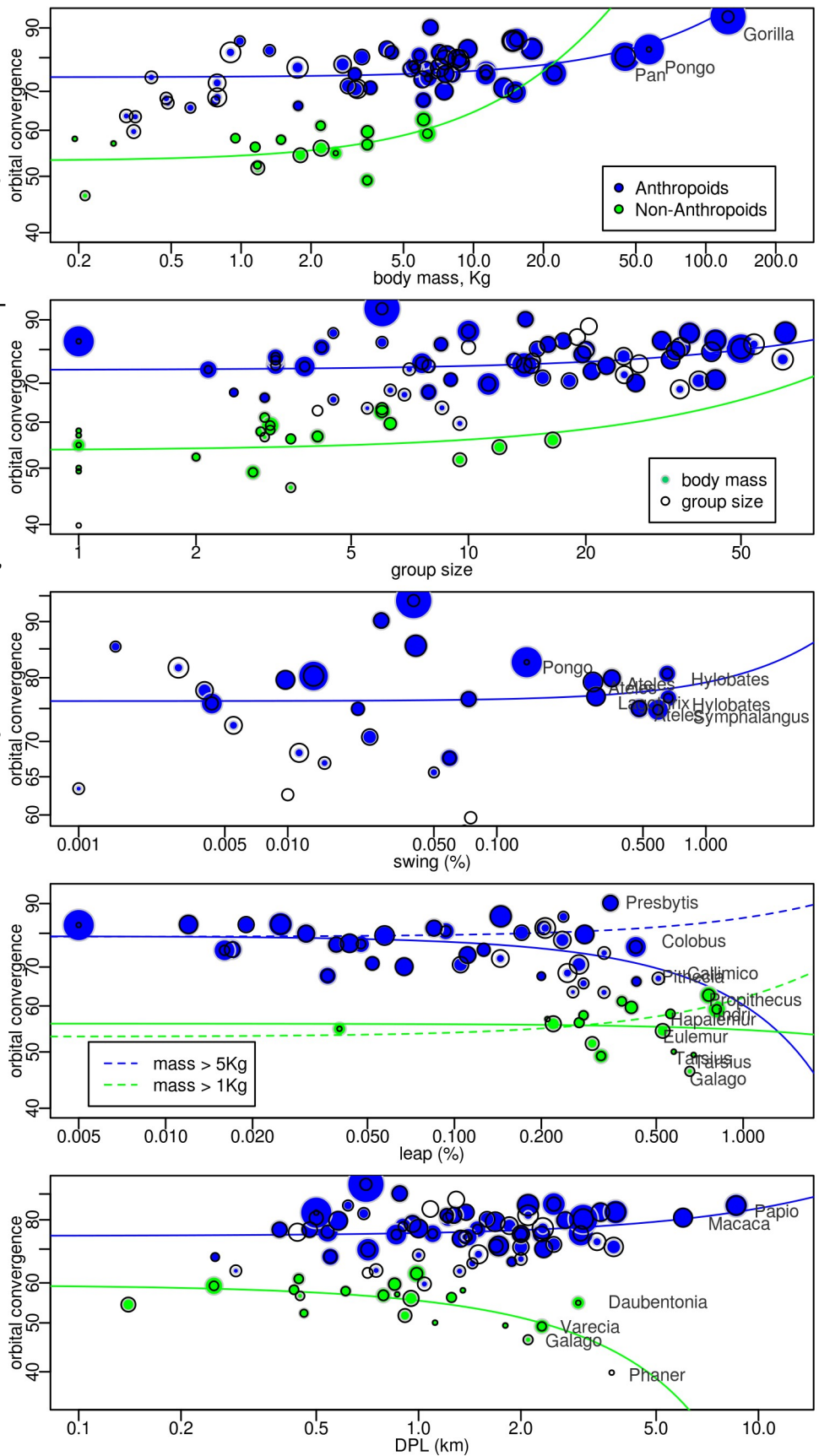
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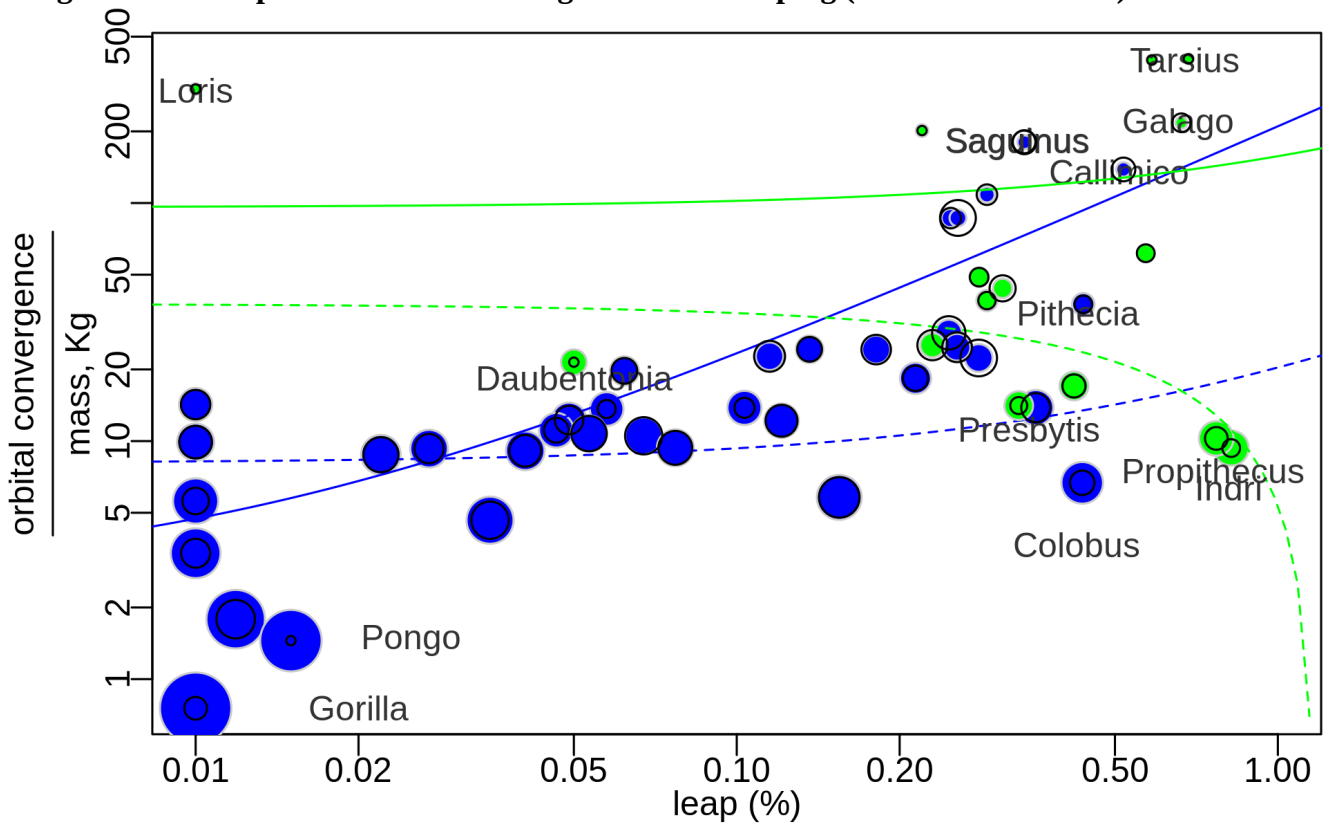
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1 **Figure 1. Scatterplots of**  
 2 **orbital convergence versus**  
 3 **continuous predictors.** Each  
 4 of the continuous predictor  
 5 variables (x-axis) are plotted in  
 6 decreasing directionality of  
 7 correlation with OC.  
 8 The size of both body (scaled colored dots)  
 9 and group (scaled black rings)  
 10 appear to correlate with OC in  
 11 both anthropoids (blue) and non-  
 12 anthropoids (green). Swinging  
 13 appears to correspond with  
 14 higher OC after taking group  
 15 and body size into account.  
 16 Leaping has a negative  
 17 relationship with OC in  
 18 anthropoids unless the handful  
 19 of outlier small bodied primates  
 20 (bottom right) are accounted for,  
 21 which reverses this association  
 22 in anthropoids, specifically, and  
 23 primates, more generally. Daily  
 24 path length was negatively  
 25 correlated with OC in non-  
 26 anthropoids. Note that linear fits  
 27 of each variable to OC are  
 28 plotted on logarithmic axes and  
 29 thus have the appearance of  
 30 being non-linear.

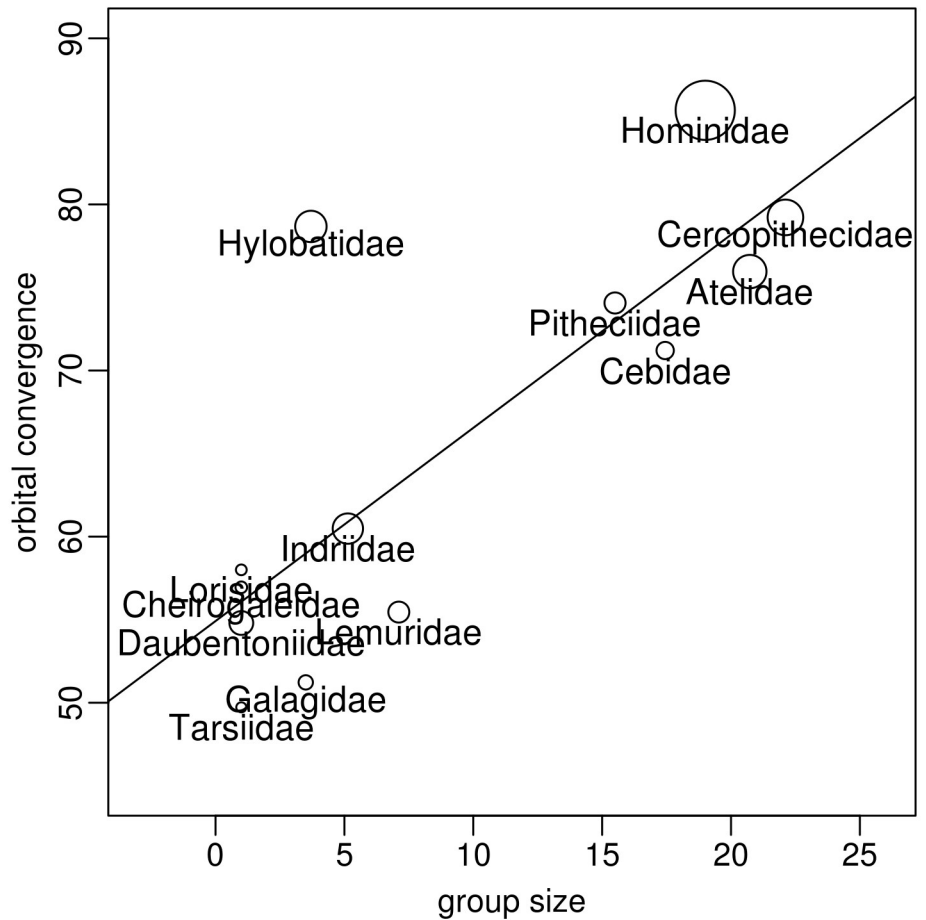


1 **Figure 2. Scatterplots of orbital convergence versus leaping (controlled for mass).**

2 Orbital convergence has a rather complex relationship with both leaping and body mass (and group size). In  
 3 this plot illustrating the effects of leaping on orbital convergence, we attempt to account for body mass both  
 4 by dividing OC by *mass* but also by employing low *mass* cut-offs (dashed lines) and splitting into anthropoid  
 5 (blue) and non-anthropoids (green) subgroups (see legends in figure 3). The solid lines (no cut-off) both  
 6 indicate positive relationships as is mirrored by the PGLM interaction term between *leaping* and *mass*. The  
 7 dashed lines here echo the findings in the independent variable approach of the full exploratory model in the  
 8 PGLM regressions (Table: 1: top). This significant disassociation in *leaping* on OC in non-anthropoids is  
 9 largely driven by the two Indriidae species in the lower right. A reminder, however that this outlier effect  
 10 could perhaps mostly be driven by their unusual amount of leaping given their mass or possibly from small-  
 11 group size effects (see gorilla in lower left). Conversely, the exceptional Loris genera in the upper left most  
 12 corporates an adaptive nature of extreme prosimian OC, given their small size—perhaps on account of their  
 13 built in protective responses of toxic biting and freezing, in lieu of locomotion, to prevent predation or to their  
 14 unique form of (non-leaping) nocturnal visual predation (Cartmill, 1970, 1972, 1992). As in Fig. 2, Linear  
 15 fits of each variable to OC are plotted on logarithmic axes and thus have the appearance of non-linear curves.

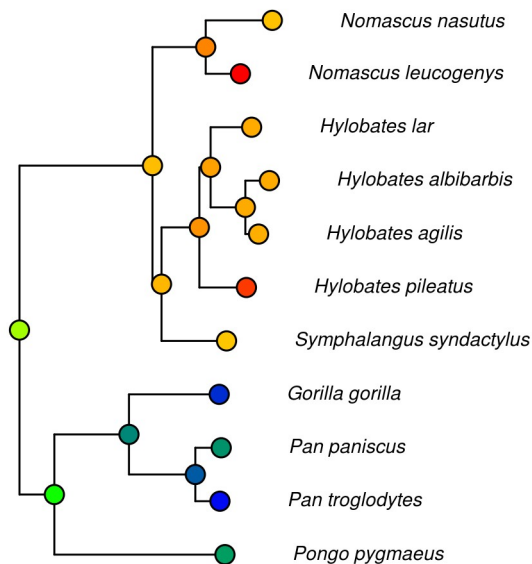


1 **Figure 3. Scatterplot of**  
 2 **orbital convergence versus**  
 3 **group size aggregated at**  
 4 **the family level.** As *group*  
 5 *size* and *body mass* (relative  
 6 *circle size*) are the primary  
 7 uniquely predictive influences  
 8 of orbital convergence in  
 9 anthropoids we plotted each  
 10 family aggregates of mean OC  
 11 (versus *group size*) in order to  
 12 look for family level outliers.  
 13 As predicted, gibbons are  
 14 unusually convergent for  
 15 having such small group sizes.  
 16 This combination of one limb-  
 17 landing and no prehensile tail  
 18 likely makes such locomotion  
 19 exceedingly risky and thus  
 20 positively selective of  
 21 accommodating vision  
 22 improvements.



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35 **Figure 4. A phylogenetic tree of swinging**  
 36 **in Hominoidea.** Ancestral character estimation  
 37 calculated internal nodes by averaging terminal  
 38 nodes (values from extant homonoids).  
 39 Estimates for ancient hominoids was 24%  
 40 *swinging* for all apes (compared with, for  
 41 example, 68% for all gibbons)



1 **Figure 5. A**  
2 **phylogenetic**  
3 **tree of**  
4 **leaping in**  
5 **Primates.**

6 Ancestral  
7 character  
8 estimation  
9 calculated  
10 internal nodes  
11 by averaging  
12 terminal nodes  
13 (values from  
14 extant  
15 primates).  
16 Estimates for  
17 the ancestral  
18 euprimate  
19 node was 32%  
20 *leaping*.

