Arboreal locomotion and trophic security at the dawn of Euprimate vision

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Abstract

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

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Introduction

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

We recognize origins theories on *euprimates*—ancestors of extant primates—as temporally distinct from origins theories on *primates*—also inclusive of stem-primates *(Silcox and L*ópez-Torres, 2017). The former origins theories primarily use fossil evidence to piece together how mammals evolved into primates. The latter theories explore how the common ancestor of these extinct fossil primate lineages (i.e. stem groups) evolved into the common ancestor of all living primates (i.e. crown clade). Here we evaluate multiple theories on primates origins, using data on extant primates. We tested most of the above theories to help outline a rough chronology of adaptation, assuming an evolution via a gradual, “serial accretion” of each component towards this suite of hallmark traits (Cartmill, 2002). Ideally, an adequate theory should explain several, if not all, of these unique arboreal specializations of early euprimates (Szalay and Dagosto, 1988). Although we will present evidence favoring a multiplicity of separable causes across the order and over time.

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

Uncertainty in grasp placement is an interesting problem relevant to the evolution of near-stem primates into euprimates. Orbital convergence is thought to improve foraging, climbing, and leaping along and between terminal branches—in alleviation of the incessant visual imperatives of such locomotion through vegetation (Crompton, 1995). This visual complexity deciphering theory —whose stereoscopic solution has been described as “camouflage breaking” (Isbell, 2006), “camouflage countering” (Heesy, 2008), or “x-ray vision” (Changizi and Shimojo, 2008)— emphasizes the crypsis, or visual confusion, of distinguishing possible targets from background in the fine-branch niche (Crompton, 1995). Crompton’s theory, like many others discussed here, is typically applied more to early Paleocene stem primates, and has been viewed as less pertinent towards later OC changes in the euprimate crown group.

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

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

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

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

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

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

Table 1. All primate and anthropoid origins models discussed in the text cross-tabulated by their 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	*hand emancipation*	SLX	Jones, 1916				spa							
primate	*arboreal theory*	SL	Jones, 1916; Smith, 1924				*sp*	*-p-a*						
primate	*distance judgment*	SL	Clark, 1959				*s*	*-p-a*						
primate	*visual predation*	DX	Cartmill, 1972						*p*					
anthropoid	*ripeness detection*	D*	Catchel, 1957; Polyak, 1979							*a*		*a*		
primate	*active fine-branch locomotion*	SLX	Martin, 1979				spa	*-p-a*					spa	a
primate	*masticatory insulation*	D	Cartmill, 1980; Polyak, 1979						*p*	*a*			*p*	
primate	*allometric scaling*	M*	Cartmill, 1980		*a*						*-a*			
primate	*nocturnal clambering*	LX*	Allman, 1982				*p*	*-a-p*			*-a*			
primate	*grasp-leap locomotion*	SLX	Szalay and Dagosto, 1988				*sp*	*-a-p*					*p*	
primate	*angiosperm co-evolution*	SD	Sussman, 1991				*sa*			*sa*				
anthropoid	*dawn monkey*	*	Beard, 1994								*-a*	*a*		
primate	*nocturnal leaping*	L*	Crompton, 1995								*p*		*p*	
anthropoid	*snake detection*	PX	Isbell, 2006								*-a*	*a*		
anthropoid	*(R.A.R.R.) predation deterrence*	PM	Wheeler, 2011		*a*	*a*								
primate	*(R.A.R.R.) predation avoidance*	PSLD	Schruth, 2015				*spa*	*-a*		*a*	*p*	*ap*	*p*	*a*
anthropoid	*grasp-swing locomotion*	SLX	Schruth, 2019				*a*	*-a*						*a*
anthropoid	*anti-parasitic grooming*	X	Schruth, 2019			*a*	*-a*		*a*		*-a*			

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

prediction abbreviations: s=stem-primates, p=non-anthropoids, a=anthropoids ("-" prefix indicates a negative correlation)

R.A.R.R. = rear attack risk reduction

Materials and Methods

Locomotion

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

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

Orbital Convergence

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

Control Variables

We collected variables on vision, activity pattern, and environmental variables (including rain, temperature, latitude, and region) from a prior study (Wheeler, Bradely and Kamilar, 2011). Many of these variables (e.g. rain and temperature) were thought to serve as potential proxy indicators for snake prevalence (Wheeler, Bradely and Kamilar, 2011). We included other control variables such as physiology (body *mass*, *claws*, prehensile *tail*), diet (*fruit*, *insect*), behavior (*nocturnal*, trichromatic [*color*] *vision*, *daily path length [DPL]*), and *group size* as compiled from (Lehmann, Korstjens and Dunbar, 2007; Wheeler, Bradely and Kamilar, 2011; Rowe and Meyers, 2017). As many of these control variables as possible were included in plots and regression models, where the main criterion for rejection was low significance (p-values near one) for estimates from either PGLM or ANOVA in any model. Height estimates were not utilized because there were too few species with height data available. Regression variables were selected based on primate origins theories and constrained by availability of relevant data. From this original pool of 15 total vision evolution relevant predictor variables, we ended up retaining two size related variables, two habitat related variables, two diet variables, two activity period variables, and two locomotion from the larger pool of possible variables. This conveniently well rounded mix of variables helped us to sensibly address the majority of the roughly dozen or so origins models, to some degree, with the unfortunate exception of snake-detection theory which is exceedingly difficult to directly test.

Statistical Methods

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

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

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

In all regressions, we used a nuclear and mitochondrial phylogram (Springer *et al.*, 2012) in order to control for non-independence arising from shared lineage (Felsenstein, 1973). This tree was also used in ancestral character estimation [ACE] (Revell, 2014) to calculate ancient leaping and swinging percentages (Fig 1). Lastly, we should note that values of continuous variables were not transformed for the regression models but were investigated via log-log scale axes in most visualizations.

Results

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

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

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

	model size:	**full**	**intermediate**	**reduced**	AIC weighted average
non-anthropoids	*variable count:*	***v*=7**	***v*=6**	***v*=3**	
	tree transform:		κ=0.66; λ=0.33; δ=2.4		
	model perform:	R^2=0.815; AIC=85	R^2=0.78; AIC=83	R^2=0.713; AIC=82	
	mass, Kg	**1.33 (0.037)** *	**1.49 (0.012)** *	**1.32 (0.004)** **	**1.26**
	nocturnal	**-4.01 (0.210)** _	**-2.92 (0.293)** _		**-1.34**
	fruit	-2.11 (0.313) _			-1.81
	insect	**4.39 (0.240)** _	**4.33 (0.218)** _		**3.02**
	arboreal	**4.60 (0.242)** _	**3.38 (0.329)** _		**2.86**
	path length, km	**-4.72 (0.014)** *	**-4.83 (0.005)** **	**-3.68 (0.001)** **	**-4.20**
	leap, %	**-13.34 (0.016)** *	**-12.17 (0.006)** **	**-10.01 (0.007)** **	**-9.76**
anthropoids	*variable count:*	***v*=10**	***v*=6**	***v*=4**	
	tree transform:		κ=0.87; λ=0.385; δ=2		
	model perform:	R^2=0.391; AIC=291	R^2=0.384; AIC=283	R^2=0.369; AIC=281	
	mass, Kg	**0.13 (0.010)** *	**0.14 (0.001)** **	**0.14 (0.001)** ***	**0.14**
	group size	**0.10 (0.191)** _	**0.10 (0.152)** _	**0.10 (0.078)** .	**0.09**
	nocturnal	**-4.44 (0.491)** _	**-5.01 (0.394)** _		**-4.87**
	color vision	1.18 (0.748)		3.35 (0.159) _	2.55
	fruit	**-1.56 (0.582)**	**-2.58 (0.237)** _		**-2.72**
	insect	-0.93 (0.768)			-2.69
	arboreal	-0.75 (0.834)			-0.07
	path length, km	**-1.03 (0.482)** _	**-0.92 (0.405)** _		**-0.42**
	leap, %	0.52 (0.957)			-3.26
	swing, %	**5.05 (0.456)** _	**6.06 (0.238)** _	**4.30 (0.370)** _	**4.39**
all primates	*variable count:*	***v*=10**	***V*=6**	***v*=4**	
	tree transform:		K=2.0; λ=0.5; δ=0.6		
	model perform:	R^2=0.325; AIC=393	R^2=0.315; AIC=388	R^2=0.282; AIC=385	
	mass, Kg	**0.14 (0.003)** **	**0.14 (0.001)** **	**0.15 (0.001)** ***	**0.15**
	group size	**0.12 (0.074)** .	**0.14 (0.019)** *	**0.13 (0.024)** *	**0.11**
	nocturnal	**-4.07 (0.161)** _	**-3.57 (0.177)** _	**-4.07 (0.123)** _	**-3.86**
	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
	arboreal	1.50 (0.569)			1.39
	path length, km	**-1.07 (0.302)** _	**-1.09 (0.226)** _	**-1.27 (0.150)** _	**-1.04**
	leap, %	-3.74 (0.496) _			-3.35
	swing, %	**3.16 (0.591)**	**5.17 (0.273)** _		**4.53**

Table 2. Highest R^2 OC models for full, intermediate, and reduced variable compositions.

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

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

		predominantly frugivorous			
		NO		**YES**	
		color vision		***color vision***	
predominantly arboreal	***nocturnal***	***no***	***yes***	***no***	***yes***
NO	***yes***	NA	NA	NA	NA
	no	56 (1)	82 (6)	NA	80 (7)
YES	***yes***	54 (7)	NA	58 (4)	NA
	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-frugivors (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).

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

	frequent leaping			
	no		**yes**	
	daily path length			
Anthropoid	***long***	***short***	***long***	***short***
yes	77 (27)	76 (8)	68 (11)	82 (19)
no	55 (1)	56 (9)	50 (3)	57 (5)

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*, *Piliocolobus*, 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.

Discussion

Primates' specialized neuroanatomy prioritizing vision over smell is echoed by their enlarged crania and convergent orbits—and active locomotion implied by fossils with powerfully long hind legs, and claw-less grasping hands (Cartmill, 2002; Silcox *et al.*, 2007; Gebo, 2013). The fossil evidence for such forms of substrate grasping origins has been corroborated by quantification of analogous mechanics in other arboreal mammals (Rasmussen, 1990; Lemelin, 1999). These specializations towards full-time tree dwelling serve as compelling testimony to an over-arching evolution towards arboreal avoidance of predational encounters (Crompton, 1995; Isbell, 2006). It is unclear, however, when these morphological changes happened evolutionarily along other possible evolutionary events in the late Cretaceous and early Paleogene. The relative contribution of individual ecological forces in shaping the euprimate morphotype is similarly unclear. No one-size-fits-all explanation to the question of primate or anthropoid origins is likely to suffice. Instead, evolutionary explanations should ultimately endeavor to be "multifactorial"—tracking vision changes, diet, and locomotion in a diversity of arboreal contexts (Crompton, 1995). Indeed, many leading theories—angiosperm co-evolution, VP, and terminal branch locomotion—share considerable overlaps with each other (Rasmussen, 1990). Here we outline over a dozen consequential primate origins theories and evaluate their cogency in light of these new results with an eye toward relevance to anthropoid origins.

Stem-anthropoids were small primates that endured their likely reclusive existence via scrounging for insects in dusky foliage (Beard *et al.*, 1994; Ross, 1995). Correspondingly, researchers have frequently considered nocturnality as determinative of [a light-intake maximizing function for] OC (Allman, 1977; Kay and Cartmill, 1977; Heesy, 2008; Wheeler, Bradely and Kamilar, 2011), perhaps in combination with locomotion (Cartmill, 1980; Allman, 1982). Activity period related vision changes (toward tricromatic vision for haplorhines) proved to be a consistently important factor associated with higher OC, especially when comparing anthropoids to nons (*nocturnal;* -4; p<0.2). Our results agree that activity period and color-vision are important factors overall, as found in a previous study (Wheeler, Bradely and Kamilar, 2011). Nocturnality and color vision had similar effect sizes, of around four degrees, but were rarely both significant in the same model (Table 2). Daylight, admittedly however, did seem to provide an important setting in which color vision could have co-evolved with frugivory to bring about the precipitous increase of OC ranging from 4° to 12° (Table 3). This conclusion is supported by transitional fossil taxa such as the Omomyidae who exhibit a mix of both dietary (insectivory and frugivory) and activity period (diurnal and nocturnal) traits (Kay and Covert, 1984). But nocturnal locomotion theories, including leaping (Crompton, 1995), clambering (Allman, 1982), and nocturnal visual predation [NVP] (Cartmill, 1972) were not supported here despite possible relevance in stem-primates, for whom we have no data.

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

Aside from such vision-impaired leap-landing, there are other visually challenging targets that could be considered to have selective influence on primate orbits. Predation upon insects in the "fine-branch milieu" via VP (Cartmill, 1972) is possibly a second core selective influence following arboreal grasping and perhaps preceding (Heesy, 2009) dietary preference for flowering plants (Cartmill, 1972, 2012). Here, *insect*ivory was only a marginally significant factor in non-anthropoids (*p*<0.2), but this fact conforms well directionally (positive in non-anthropoids and negative in anthropoids) to insect predation theories. This evidence for a dietary selection effect on non-anthropoids is consistent with the high levels of variation in dietary indicators in fossil teeth—a mix between frugivory and insectivory—seen in Eocene *Omomyidae*, a stem group of tarsiiformes (Rasmussen, 2007). Locomotion-wise, our examination confirms evidence favoring an adaptive VP model as differing from neutral allometric predictions—by highlighting the exceptional case of (high OC) lorises who similarly dive forward with their forelimbs (sans leaping) to capture flying insect prey. Thus it is important to understand both the nature of landing targets as well as the form and mode of associated positional behaviors involved.

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

In this study, body mass was by far the most significant variable. Estimates of ancestral primate body mass range from rather small (< 1 Kg) (Silcox and López-Torres, 2017) to extremely small (15g) (Gebo, 2013). And a primary distinguishing feature of anthropoids is the great discrepancy in sizes, ranging from 50 g all the way up to 250 Kg. As smaller early anthropoids grew, a reasonable null suggests that relatively smaller orbits may have relieved constraints on lateral facing orbital apertures (Cartmill, 1970). And despite the fact that Lorises do provide confirmation of the adaptiveness of such unusually high OC compared with a default two-part (activity period meets allometry) model, they are exceptional amongst non-anthropoids. Body mass, for example, is still highly (10-fold larger effect size) predictive of OC in highly *nocturnal* non-anthropoids who have no such diurnality to support the case for allometric scaling driving OC. Considering that group-size effects are the second most consistently significant effect on OC in differentiating anthropoids (*p*<0.03), an agglomerate evolutionary constraint-relaxation mechanism via predation-aversion emerges as rather promising.

Organisms can avoid predation by evading, fleeing, out-growing, out-competing, mobbing, freezing, or deploying spines or armor (Morse, 1976). The "arboreal theory," in line with the first two of these forms of non-confrontation, suggests that trees were the most formative of primates. Because arboreal complexity requires distance judgments related to climbing (Jones, 1916; Smith, 1924; Clark, 1959) and for more accurate locomotor bout landing behavior, primates may have further developed stereoscopic vision and increased OC. Due to numerous examples from rodents and squirrels as well as felids and raptors, we know that arboreality does not by itself necessitate OC (Cartmill, 1972; Heesy, 2009) and that binocular vision, regardless of habitat, tends to evolve in predators (Allman, 1977; Pettigrew, 1986). And despite primates largely inheriting arboreality from their euarchonton predecessors, other extant orders (e.g. tree shrews) are only semi-arboreal (Fuchs and Corbach-Söhle, 2010), suggesting primates may have initially been more steadfast arborealists. And even today, those that aren't protected on islands or by larger size (e.g. African and Malay primates) tend to maintain a strict arboreality (e.g. New World monkeys) (Napier and Napier, 1985). Furthermore, hazardous forms of arboreal locomotion (e.g. leaping), might also co-associate with increased fall risk, especially on terminal branches. The idea that inter-substrate gap-spanning drives primate cranial evolution is at least partially supported by positive leap percentages (and negative DPL) associating with OC, especially if mass is also considered (Fig. 2). Our binary arboreal measure alone, however, suggests evolutionary influence (+4°) in non-anthropoids (p<0.3), and perhaps between sub-ordinal clades (Table 2). Thus, OC could be quite influenced by arboreal refuges, presumably as part of alleviating predation pressures. Arboreal locomotion, like arboreality itself, appears to have been a foremost adaptive influence (Crompton and Sellers, 2007) to counteract terrestrial carnivores. Additionally, inter-tree leaping could have been important part of maintaining a strict arboreality—essential for continued predation avoidance and maintenance of a high trophic level—thereby eliminating any need for constant posterior vigilance.

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

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

Eocene primates, as they experienced diminishing pressure for concealment from predation, especially via the cover of night, may have subsequently found themselves under an entirely new array of selection pressures via daylight. As mentioned formerly in this section, *nocturnal*ity had a negative relationship with OC under all taxonomic subsets and variable compositions. This suggests that diurnality could have been a strong factor in driving orbital convergence in primates resembling *Eosimiidae*, the aptly designated ‘dawn monkey’ (Beard, 2004). A dual curiosity remains, however, of not only why these primates were able to risk predation by forgoing the protective cover of night, but also why, in braving the light, they evolutionarily forfeited posterior peripheral vision used for detecting such attacks. Although foraging upon the colorful terminuses of branches, instead of for insects, could have also provided positive selection for OC (Sussman, 1991). Oddly, Haplorhines—which includes modern (low OC) tarisers *(Beard et al.*, 1994)—were (e.g. *Archicebidae*) initially diurnal *(Ni et al.*, 2013) before returning to a nocturnal (and insectivorous) lifestyle. This last fact is rather illustrative of just how potent adaptations for color vision may have been in empowering cathemeral, and even diurnal, primates that began consuming the flowering terminal branches of angiosperms.

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

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

It is thought that body mass increases associated with suspensory locomotion (and a shift toward terrestriality) could drive OC (Isbell, 2006). But it is also possible that grasp-swing by itself acts as (an admittedly more proximate) selection pressure, analogous to the way grasp-leap or arboreal clambering might require accuracy in limb landing for fall-avoidance in other arboreal primates. Despite hylobatids having a higher than expected OC given their *group size* (Fig. 3), *swing*ing was admittedly only marginally significantly correlated with OC in PGLM. Understandably, *swing*ing has a less pronounced evolutionary signature on OC, perhaps due to its rarity. Also, it tends to include more substrate connectivity, and presumably entails less risk, but potentially more skill than leaping. Swinging—when along the same branch, tree, and orientation—is more predictable, but per-limb landing-accuracy risks are higher, than in leap-landing. Nevertheless, it appears that a grasp-swing form of generalized precision limb-landing—an extrapolation of grasp-leap—is still somewhat (albeit weakly) supported, but surprisingly more so in gibbons over prehensile tail wielding spider-monkeys (Fig. 3). More puzzling, however, is what this marginal association of OC with (our theoretical extension into) swinging implies about ancestral grasp-leap theory itself. If precision limb landing via swinging is perhaps only a minor factor amongst hominoids (only 26% ancestrally; see Fig. 4) in determining OC, then logically, it is also perhaps similarly so for other more challenging forms of locomotion in primates more generally. This low (yet non-negligible) percentage may approximate the ancestral condition for *Hominoidea*—in concurrence with the evidence for suspensory locomotor behavior as ancient as 20mya in fossil genus *Morotopithecus* (MaClatchy et al., 2000). This is in spite the existence of several non-suspensory fossil apes that emerged after the 18mya split with hylobatids—17myo *Proconsul,* a putative ancestor to modern chimpanzees (Ward, 1993), and 12myo *Sivapithecus,* a putative ancestor to orangutans (Pilbeam *et al.*, 1990). Our results, therefore, are reasonably in line with a deep ancestry of (at least a modicum of) suspensory behavior that may have subsequently been substantially diminished in the taxonomic branches running conterminously with *Hominidea*.

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

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

Conclusion

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

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

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

Penultimately, we declare a need for overhaul of measurement approaches with prioritization of continuous ecological indexes. Binary indicator variables (with huge effect sizes in the two-by-two analysis), for example, seem to be statistically overshadowed by their continuous neighbors in PGLM, which tended to show much greater statistical significance. Likewise, instead of more ideal measures of canopy height, trophic level, and home range, we have resorted to using imperfect, but more readily measurable, variables such as path length and leaping frequency to detect merely signatures of our proposed elevated trophic rank of full-time arboreal primates. More ultimate causative evolutionary phenomena such as predation, arboreality, fall risk, competition, and territoriality—each of which is currently too ambiguously delineated—could also similarly be re-construed to serve as indirect indicators of many of our more ultimate influences. Further issues include taxonomic quandaries, case-wise species deletions between mismated datasets, as well as the known deficiency of ecological controls. Measurements of predation, in particular, are nearly entirely unprocurable, and research into comparisons of such effects on OC in primates to other (predator and non-predator) mammals is merited.

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

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REFERENCES

Acharya, A. and Verstak, A. (2004) *Google Scholar*. Available at: http://scholar.google.com.

Allman, J. (1977) ‘Evolution of the visual system in early primates’, in *Progress in psychobiology and physiological psychology*. New York: Academic Press, pp. 1–53.

Allman, J. (1982) ‘Reconstructing the Evolution of the Brain in Primates Through the Use of Comparative Neurophysiological and Neuroanatomical Data’, in Armstrong, E. and Falk, D. (eds) *Primate Brain Evolution*. Boston, MA: Springer US, pp. 13–28. doi:10.1007/978-1-4684-4148-2_2.

Beard, C. (2004) *The Hunt for the Dawn Monkey: Unearthing the Origins of Monkeys, Apes, and Humans*. Berkeley: University of California Press.

Beard, K.C. *et al.* (1994) ‘A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China’, *Nature*, 368(6472), pp. 604–609. doi:10.1038/368604a0.

Boyer, D.M., Toussaint, S. and Godinot, M. (2017) ‘Postcrania of the most primitive euprimate and implications for primate origins’, *Journal of Human Evolution*, 111, pp. 202–215. doi:10.1016/j.jhevol.2017.07.005.

Cachel, S. (1979a) ‘A functional analysis of the primate masticatory system and the origin of the anthropoid post-orbital septum’, *American Journal of Physical Anthropology*, 50(1), pp. 1–17. doi:10.1002/ajpa.1330500102.

Cachel, S. (1979b) ‘A paleoecological model for the origin of higher primates’, *Journal of Human Evolution*, 8(3), pp. 351–359. doi:10.1016/0047-2484(79)90058-7.

Cartmill, M. (1970) *The orbits of arboreal mammals: a reassessment of the arboreal theory of primate evolution*. Ph.D. University of Chicago.

Cartmill, M. (1972) ‘Arboreal adaptations and the origin of the order Primates.’, in Tuttle, R. (ed.) *The Functional and Evolutionary Biology of Primates*. Chicago: Aldine-Atherton, pp. 97–122.

Cartmill, M. (1980) ‘Morphology, Function, and Evolution of the Anthropoid Postorbital Septum’, in Ciochon, R.L. and Chiarelli, A.B. (eds) *Evolutionary Biology of the New World Monkeys and Continental Drift*. Boston, MA: Springer US, pp. 243–274. doi:10.1007/978-1-4684-3764-5_12.

Cartmill, M. (1992) ‘New views on primate origins’, *Evolutionary Anthropology: Issues, News, and Reviews*, 1(3), pp. 105–111. doi:10.1002/evan.1360010308.

Cartmill, M. (2002) ‘Explaining primate origins’, in *Physical anthropology: original readings in method and practice*. Upper Saddle River, NJ: Pearson Education, pp. 42–52.

Cartmill, M. (2012) ‘Primate origins, human origins, and the end of higher taxa’, *Evolutionary Anthropology: Issues, News, and Reviews*, 21(6), pp. 208–220. doi:10.1002/evan.21324.

Changizi, M.A. and Shimojo, S. (2008) ‘“X-ray vision” and the evolution of forward-facing eyes’, *Journal of Theoretical Biology*, 254(4), pp. 756–767. doi:10.1016/j.jtbi.2008.07.011.

Clark, W. (1959) *The Antecedents of Man*. Chicago: Quadrangle Books.

Crompton, R.H. (1995) ‘“Visual Predation,” Habitat Structure, and the Ancestral Primate Niche’, in Alterman, L., Doyle, G.A., and Izard, M.K. (eds) *Creatures of the Dark: The Nocturnal Prosimians*. 11-30.

Crompton, R.H. and Sellers, W.I. (2007) ‘A Consideration of Leaping Locomotion as a Means of Predator Avoidance in Prosimian Primates’, in Gursky, S.L. and Nekaris, K.A.I. (eds) *Primate Anti-Predator Strategies*. Boston, MA: Springer US, pp. 127–145. doi:10.1007/978-0-387-34810-0_6.

Felsenstein, J. (1973) ‘Maximum-likelihood estimation of evolutionary trees from continuous characters’, *American Journal of Genetics*, 25(5), pp. 471–492.

Felsenstein, J. (1985) ‘Phylogenies and the Comparative Method’, *The American Naturalist*, 125(1), pp. 1–15. doi:10.1086/284325.

Fleagle, J.G. (1999) *Primate Adaptation and Evolution*. New York: Academic Press.

Fleagle, J.G. (2013) *Primate Adaptation and Evolution*. 3rd edn. New York: Academic Press.

Fuchs, E. and Corbach-Söhle, S. (2010) ‘Tree shrews’, in *The UFAW handbook on the care and management of laboratory and other research animals*. John Wiley & Sons, pp. 262–275.

Garamszegi, L.Z. (2011) ‘Information-theoretic approaches to statistical analysis in behavioural ecology: an introduction’, *Behavioral Ecology and Sociobiology*, 65(1), pp. 1–11. doi:10.1007/s00265-010-1028-7.

Garfield, E. (1970) ‘Citation Indexing for Studying Science’, *Nature*, 227(5259), pp. 669–671. doi:10.1038/227669a0.

Gebo, D.L. (2013) ‘Primate Locomotion’, *Nature Education Knowledge*, 4(8), p. 1.

Heesy, C.P. (2003) *The evolution of orbit orientation in mammals and the funciton of the primate postorbital bar*. Ph.D. Stony Brook University.

Heesy, C.P. (2004) ‘On the relationship between orbit orientation and binocular visual field overlap in mammals’, *The Anatomical Record*, 281A(1), pp. 1104–1110. doi:10.1002/ar.a.20116.

Heesy, C.P. (2008) ‘Ecomorphology of Orbit Orientation and the Adaptive Significance of Binocular Vision in Primates and Other Mammals’, *Brain, Behavior and Evolution*, 71(1), pp. 54–67. doi:10.1159/000108621.

Heesy, C.P. (2009) ‘Seeing in stereo: The ecology and evolution of primate binocular vision and stereopsis’, *Evolutionary Anthropology: Issues, News, and Reviews*, 18(1), pp. 21–35. doi:10.1002/evan.20195.

Hylander, W.L. *et al.* (2000) ‘Symphyseal fusion and jaw adductor muscle force: An EMG study’, *American Journal of Physical Anthropology*, 112(4), pp. 469–492. doi:10.1002/1096-8644(200008)112:4<469::AID-AJPA5>3.0.CO;2-V.

Isbell, L.A. (2006) ‘Snakes as agents of evolutionary change in primate brains’, *Journal of Human Evolution*, 51(1), pp. 1–35. doi:10.1016/j.jhevol.2005.12.012.

Isbell, L.A. (2009) *The Fruit the Tree and the Serpent*. Cambridge, MA: Harvard University Press.

Jarrell, H.M. (2011) *Associations between Skeletal Fractures and Locomotor Behavior, Habitat Use, and Body Mass in Nonhuman Primates*. Ph.D. Ohio State University. Available at: http://rave.ohiolink.edu/etdc/view?acc_num=osu1306432619.

Jolly, A. (1985) *The Evolution of Primate Behavior*. New York: Macmillan Publishing Company.

Jones, F.W. (1916) *Arboreal Man*. Longmans.

Kay, R.F. and Cartmill, M. (1977) ‘Cranial morphology and adaptations of Palaechthon nacimienti and other paromomyidae (Plesiadapoidea, ? primates), with a description of a new genus and species’, *Journal of Human Evolution*, 6(1), pp. 19–53. doi:10.1016/S0047-2484(77)80040-7.

Kay, R.F. and Covert, H.H. (1984) ‘Anatomy and Behaviour of Extinct Primates’, in Chivers, D.J., Wood, B.A., and Bilsborough, A. (eds) *Food Acquisition and Processing in Primates*. Boston, MA: Springer US, pp. 467–508. doi:10.1007/978-1-4757-5244-1_21.

Kay, R.F., Ross, C.F. and Williams, B.A. (1997) ‘Anthropoid origins’, *Science*, 275, pp. 797–804.

Kirk, E. (2006) ‘Effects of activity pattern on eye size and orbital aperture size in primates’, *Journal of Human Evolution*, 51(2), pp. 159–170. doi:10.1016/j.jhevol.2006.02.004.

Legreneur, P. *et al.* (2012) ‘Convergent exaptation of leap up for escape in distantly related arboreal amniotes’, *Adaptive Behavior*, 20(1), pp. 67–77. doi:10.1177/1059712311426797.

Lehmann, J., Korstjens, A.H. and Dunbar, R.I.M. (2007) ‘Group size, grooming and social cohesion in primates.’, *Animal Behaviour*, 74(6), pp. 1617–1629.

Lemelin, P. (1999) ‘Morphological correlates of substrate use in didelphid marsupials: implications for primate origins’, *Journal of Zoology*, 247(2), pp. 165–175. doi:10.1111/j.1469-7998.1999.tb00980.x.

MaClatchy, L. *et al.* (2000) ‘Postcranial functional morphology of Morotopithecus bishopi, with implications for the evolution of modern ape locomotion’, *Journal of Human Evolution*, 39(2), pp. 159–183. doi:10.1006/jhev.2000.0407.

Martin, R.D. (1979) ‘Phylogenetic aspects of prosimian behavior’, in Doyle, G.A. and Martin, R.D. (eds) *The Study of Prosimian Behavior*. Academic Press, pp. 45–78.

Morse (1976) *Behavioral Mechanisms in Ecology*. Cambridge: Harvard University Press.

Nakashige, M., Smith, A.L. and Strait, D.S. (2011) ‘Biomechanics of the macaque postorbital septum investigated using finite element analysis: implications for anthropoid evolution: Postorbital septum biomechanics’, *Journal of Anatomy*, 218(1), pp. 142–150. doi:10.1111/j.1469-7580.2010.01316.x.

Napier, J.R. and Napier, P.H. (1985) *The natural history of the primates*.

Nett, E.M. and Ravosa, M.J. (2019) ‘Ontogeny of Orbit Orientation in Primates’, *The Anatomical Record* [Preprint]. doi:10.1002/ar.24193.

Ni, X. *et al.* (2013) ‘The oldest known primate skeleton and early haplorhine evolution’, *Nature*, 498(7452), pp. 60–64. doi:10.1038/nature12200.

Noble, V.E., Kowalski, E.M. and Ravosa, M.J. (2000) ‘Orbit orientation and the function of the mammalian postorbital bar’, *Journal of Zoology*, 250(3), pp. 405–418. doi:10.1111/j.1469-7998.2000.tb00784.x.

Pettigrew, J. (1986) ‘Flying primates? Megabats have the advanced pathway from eye to midbrain’, *Science*, 231(4743), pp. 1304–1306.

Pilbeam, D. *et al.* (1990) ‘New Sivapithecus humeri from Pakistan and the relationship of Sivapithecus and Pongo’, *Nature*, 348(6298), pp. 237–239. doi:10.1038/348237a0.

Polyak, S. (1957) *The Vertebrate Visual System*. Chicago: University of Chicago Press.

Rasmussen, D.T. (1990) ‘Primate origins: Lessons from a neotropical marsupial’, *American Journal of Primatology*, 22, pp. 263–277.

Rasmussen, D.Tab. (2007) ‘Fossil record of the primates from the Paleocene to the Oligocene’, in *Handbook of Paleoanthropology*. Berlin: Springer, pp. 889–920.

Ravosa, M.J. *et al.* (2006) ‘Adaptive plasticity in mammalian masticatory joints’, in Bonse, U. (ed.). *SPIE Optics + Photonics*, San Diego, California, USA, p. 63180D. doi:10.1117/12.680580.

Ravosa, M.J. and Savakova, D.G. (2004) ‘Euprimate origins: the eyes have it’, *Journal of Human Evolution*, 46(3), pp. 355–362. doi:10.1016/j.jhevol.2003.12.002.

Revell, L.J. (2014) ‘Ancestral character estimation under the threshold model from quantitative genetics: ancestral states’, *Evolution*, 68(3), pp. 743–759. doi:10.1111/evo.12300.

Rosenberger, A.L. (1986) ‘Platyrrhines, catarrhines and the anthropoid transition’, in Wood, B., Martin, L., and Andrews, P. (eds) *Major Topics in Primate and Human Evolution*. Cambridge, UK: Cambridge University Press.

Ross, C.F. (1995) ‘Allometric and functional influences on primate orbit orientation and the origins of the Anthropoidea’, *Journal of Human Evolution*, 29(3), pp. 201–227. doi:10.1006/jhev.1995.1057.

Ross, C.F. and Martin, R.D. (2007) ‘The role of vision in the origin and evolution of primates.’, in *Evolution of Nervous Systems Volume 4: The Evolution of Primate Nervous Systems.* Oxford: Elsevier, pp. 59–78.

Rowe, N. and Meyers, M. (2017) *All the World’s Primates*. Charlestown, RI: Pogonias Press.

Sawyer, J.R. *et al.* (2000) ‘Fracture Patterns in Children and Young Adults Who Fall from Significant Heights’, *Journal of Pediatric Orthopaedics*, 20(2), pp. 197–202.

Schruth, D.M. (2015) ‘Testing the origins of primate anterior orbital convergence as a function of evasive leap landing and reduced posterior predation.’, in *American Society of Primatologists*. *38th Annual Meeting*, Bend, OR: American Journal of Primatology. doi:10.1002/ajp.22494.

Schruth, D.M. (2021) *A global variable-permutation based approach for estimating tree transformation parameters used in phylogenetically controlled multivariate regression*. Available at: http://doi.org/dx.doi.org/10.17504/protocols.io.bzdhp236.

Schultz, A.H. (1940) ‘The size of the orbit and of the eye in primates’, *American Journal of Physical Anthropology*, 26(1), pp. 389–408. doi:10.1002/ajpa.1330260138.

Silcox, M.T. *et al.* (2007) ‘1 Primate Origins and Supraordinal Relationships: Morphological Evidence’, in Henke, W. and Tattersall, I., *Handbook of Paleoanthropology*. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 831–859. doi:10.1007/978-3-540-33761-4_29.

Silcox, M.T. and López-Torres, S. (2017) ‘Major Questions in the Study of Primate Origins’, *Annual Review of Earth and Planetary Sciences*, 45(1), pp. 113–137. doi:10.1146/annurev-earth-063016-015637.

Smaers, J.B. and Rohlf, F.J. (2016) ‘Testing species’ deviation from allometric predictions using the phylogenetic regression’, *Evolution*, 70(5), pp. 1145–1149. doi:10.1111/evo.12910.

Smith, G.E. (1924) *The Evolution of Man*. London: Oxford University Press.

Springer, M.S. *et al.* (2012) ‘Macroevolutionary Dynamics and Historical Biogeography of Primate Diversification Inferred from a Species Supermatrix’, *PLoS ONE*. Edited by R. Stanyon, 7(11), p. e49521. doi:10.1371/journal.pone.0049521.

Sussman, R.W. (1991) ‘Primate origins and the evolution of angiosperms’, *American Journal of Primatology*, 23(4), pp. 209–223. doi:10.1002/ajp.1350230402.

Sussman, R.W., Rasmussen, T. and Raven, P.H. (2013) ‘Rethinking Primate Origins Again: Primate Origins Again’, *American Journal of Primatology*, 75(2), pp. 95–106. doi:10.1002/ajp.22096.

Symonds, M.R.E. and Moussalli, A. (2011) ‘A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion’, *Behavioral Ecology and Sociobiology*, 65(1), pp. 13–21. doi:10.1007/s00265-010-1037-6.

Szalay, F.S. and Dagosto, M. (1988) ‘Evolution of hallucial grasping in the primates’, *Journal of Human Evolution*, 17(1–2), pp. 1–33. doi:10.1016/0047-2484(88)90047-4.

Ward, C.V. (1993) ‘Torso morphology and locomotion in Proconsul nyanzae’, *American Journal of Physical Anthropology*, 92(3), pp. 291–328. doi:10.1002/ajpa.1330920306.

Watt, S.J. and Bradshaw, M.F. (2000) ‘Binocular cues are important in controlling the grasp but not the reach in natural prehension movements’, *Neuropsychologia*, 38(11), pp. 1473–1481. doi:10.1016/S0028-3932(00)00065-8.

Wheeler, B.C., Bradely, B.J. and Kamilar, J.M. (2011) ‘Predictors of orbital convergence in primates: A test of the snake detection hypothesis of primate evolution’, *Journal of Human Evolution*, 61, pp. 233–242.

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Figure 1. Scatterplots of orbital convergence versus continuous predictors. Each of the continuous predictor variables (x-axis) are plotted in decreasing directionality of correlation with OC. The size of both body (scaled colored dots) and group (scaled black rings) appear to correlate with OC in both anthropoids (blue) and non-anthropoids (green). Swinging appears to correspond with higher OC after taking group and body size into account. Leaping has a negative relationship with OC in anthropoids unless the handful of outlier small bodied primates (bottom right) are accounted for, which reverses this association in anthropoids, specifically, and primates, more generally. Daily path length was negatively correlated with OC in non-anthropoids. Note that linear fits of each variable to OC are plotted on logarithmic axes and thus have the appearance of being non-linear.

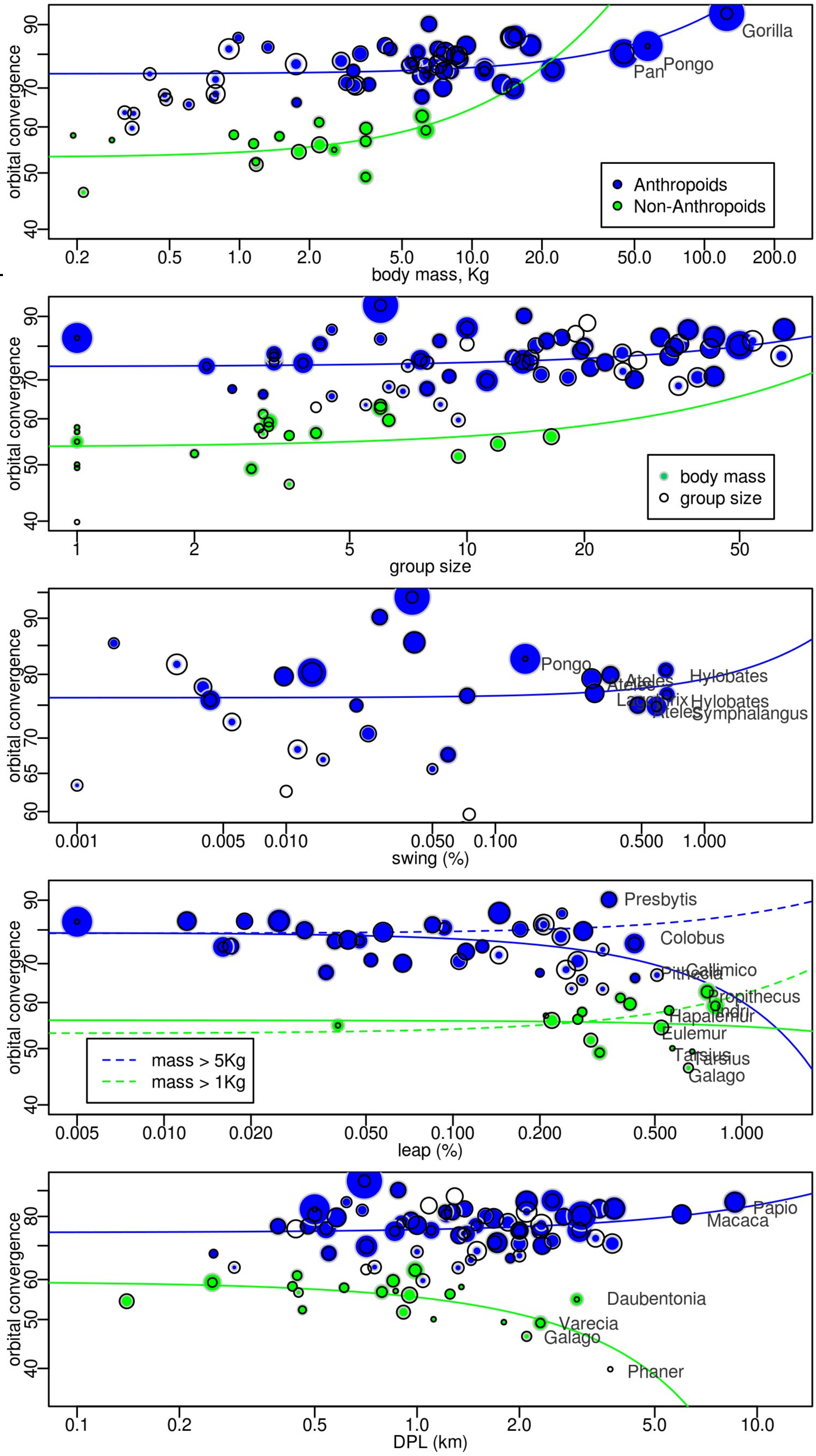
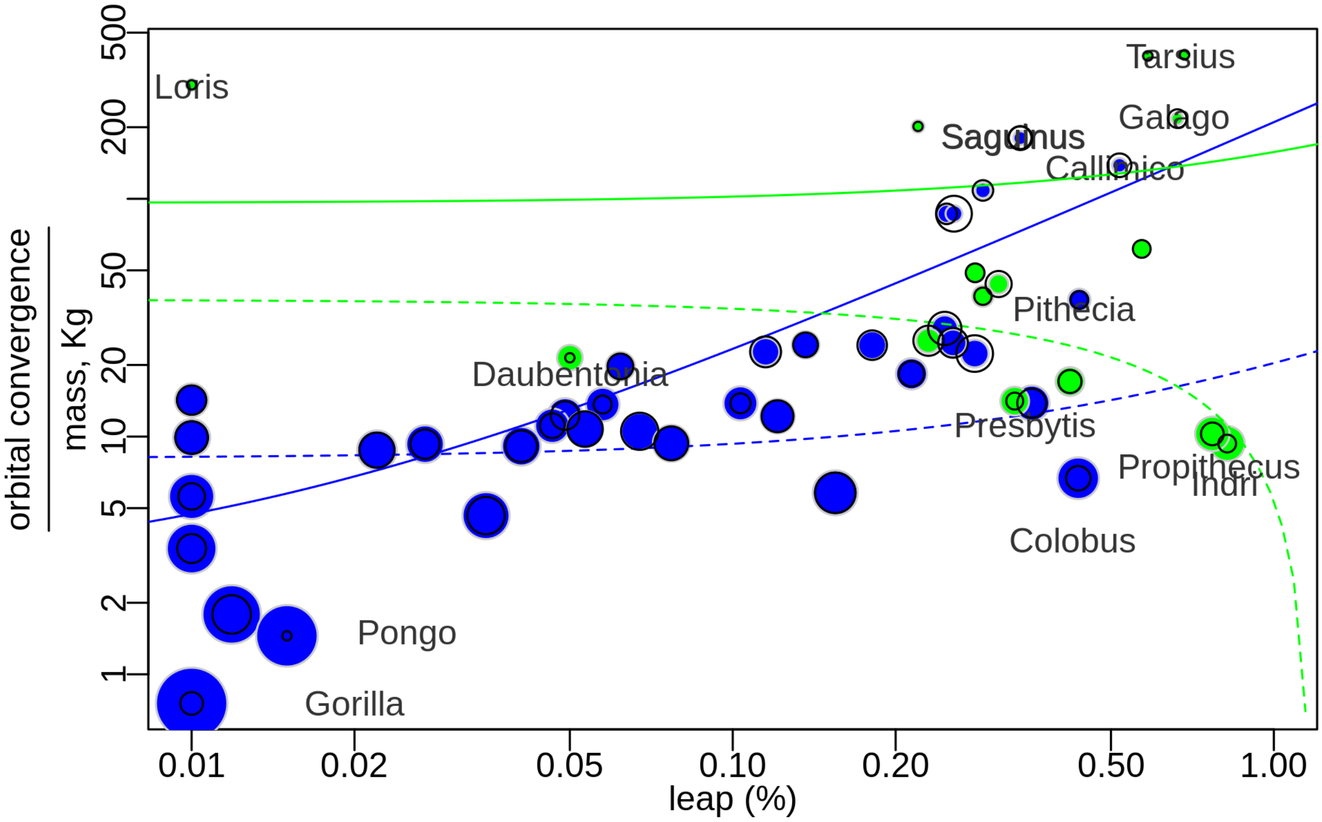


Figure 2. Scatterplots of orbital convergence versus leaping (controlled for mass).



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

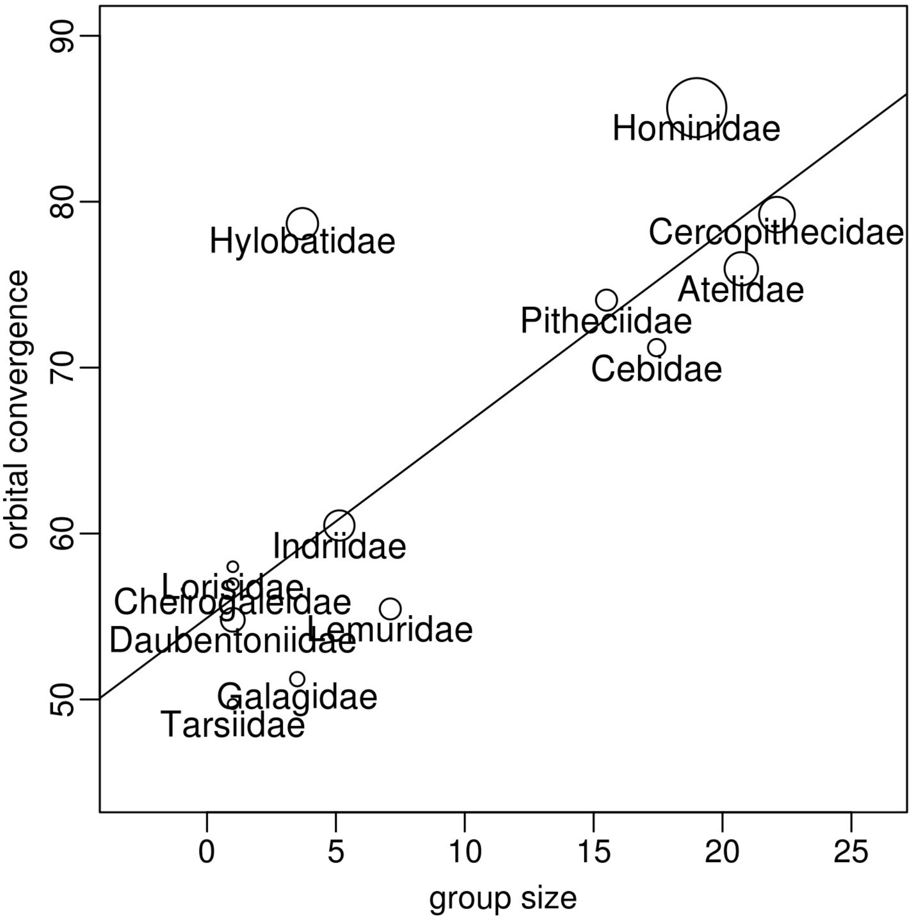


Figure 3. **Scatterplot of orbital convergence versus group size aggregated at the family level**. As *group size* and body *mass* (relative circle size) are the primary uniquely predictive influences of orbital convergence in anthropoids we plotted each family aggregates of mean OC (versus *group size*) in order to look for family level outliers. As predicted, gibbons are unusually convergent for having such small group sizes. This combination of one limb-landing and no prehensile tail likely makes such locomotion exceedingly risky and thus positively selective of accommodating vision improvements.

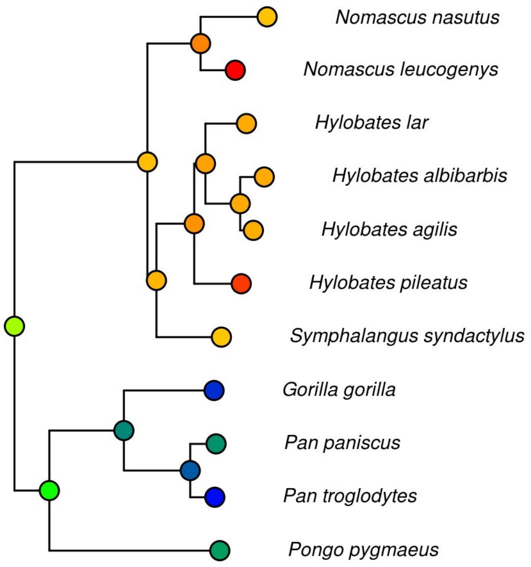


Figure 4. **A phylogenetic tree of swinging in Hominoidea**. Ancestral character estimation calculated internal nodes by averaging terminal nodes (values from extant homonoids). Estimates for ancient hominoids was 24% *swinging* for all apes (compared with, for example, 68% for all gibbons)

Figure 5. **A phylogenetic tree of leaping in Primates**. Ancestral character estimation calculated internal nodes by averaging terminal nodes (values from extant primates). Estimates for the ancestral euprimate node was 32% *leaping*.