

Ecomorphology of Orbit Orientation and the Adaptive Significance of Binocular Vision in Primates and Other Mammals

Christopher P. Heesy

Department of Anatomy, Arizona College of Osteopathic Medicine, Midwestern University, Glendale, Ariz., USA

Key Words

Orbit orientation · Binocular vision · Binocular visual field overlap · Mammals · Primate origins

Abstract

Primates are characterized by forward-facing, or convergent, orbits and associated binocular field overlap. Hypotheses explaining the adaptive significance of these traits often relate to ecological factors, such as arboreality, nocturnal visual predation, or saltatory locomotion in a complex nocturnal, arboreal environment. This study re-examines the ecological factors that are associated with high orbit convergence in mammals. Orbit orientation data were collected for 321 extant taxa from sixteen orders of metatherian (marsupial) and eutherian mammals. These taxa were coded for activity pattern, degree of faunivory, and substrate preference. Results demonstrate that nocturnal and cathemeral mammals have significantly more convergent orbits than diurnal taxa, both within and across orders. Faunivorous eutherians (both nocturnal and diurnal) have higher mean orbit convergence than opportunistically foraging or non-faunivorous taxa. However, substrate preference is not associated with higher orbit convergence and, by extension, greater binocular visual field overlap. These results are consistent with the hypothesis that mammalian predators evolved higher orbit convergence, binocular vision, and stereopsis to counter camouflage in prey inhabiting a nocturnal environment. Strepsirhine primates have a range of orbit convergence val-

ues similar to nocturnal or cathemeral predatory non-primate mammals. These data are entirely consistent with the nocturnal visual predation hypothesis of primate origins.

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Introduction

Large binocular visual fields are a hallmark of the highly specialized visual system of primates [e.g., Allman, 1999]. However, the related trait of high orbit convergence (forward-facing orbits) is perhaps the most controversial trait used to define the Order Primates (fig. 1). The functional significance of orbit orientation has been linked to visual field orientation. Divergent orbits are associated with panoramic (widely encompassing) visual fields with little overlap between each monocular field, whereas convergent orbits are associated with larger binocular (overlapping) visual fields [Cartmill, 1974; Allman, 1977; Ross, 2000; Heesy, 2004; fig. 1]. The relationship between orbit divergence-convergence and binocular visual field overlap in mammals is isometric (i.e., mammals with more convergent orbits have larger zones of binocular visual field overlap), and scales similarly across orders [Heesy, 2004; fig. 1e]. Because of the highly correlated isometric relationship between orbit orientation and degree of binocular visual field overlap, it is robust to utilize orbit orientation as a surrogate variable for binocular visual field overlap.

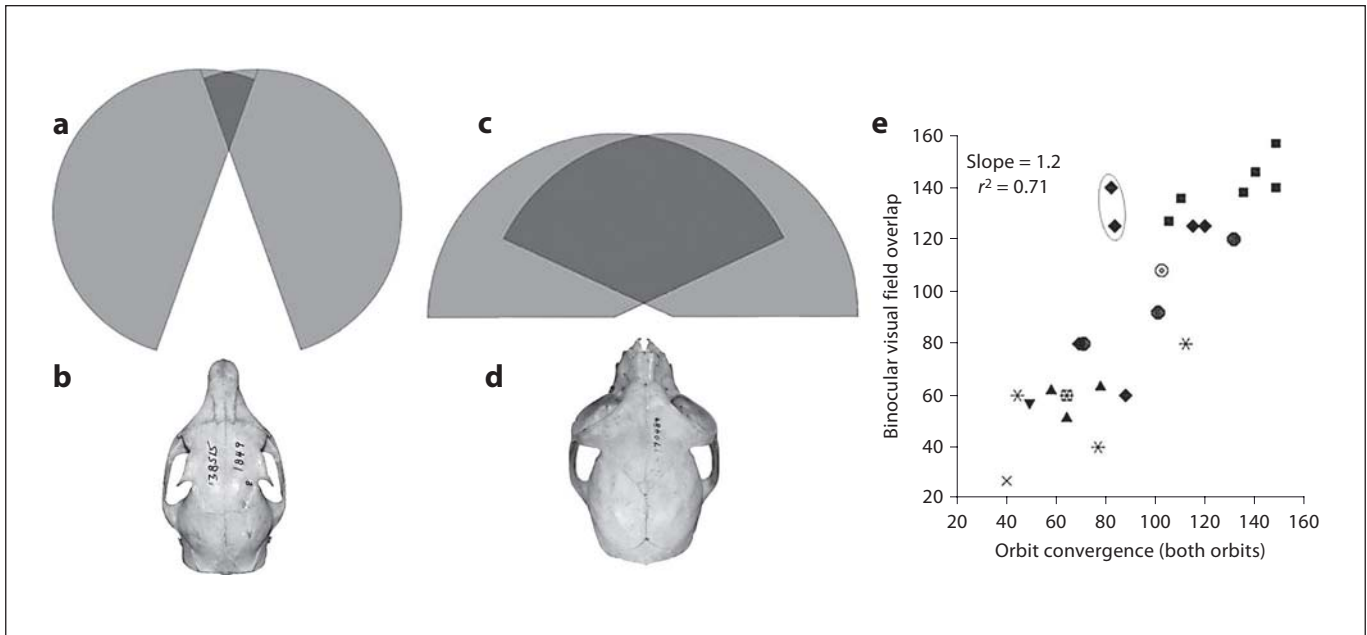


Fig. 1. Relationship between orbit orientation and visual field overlap. **a** Panoramic visual fields are composed of monocular visual fields (lighter shaded regions) that minimally overlap and are associated with small regions of binocular overlap (darker shaded region). **b** Skull of the squirrel *Sciurus carolinensis*, which has laterally facing orbits and a large panoramic visual field. **c** Mammals with substantial binocular visual fields are associated with relatively abbreviated monocular visual fields (lighter shaded regions) compared with the regions of binocular overlap (darker shaded region). **d** Skull of the strepsirhine primate *Propithecus verreauxi*, which has convergent (similarly facing) orbits and possibly a large binocular visual field (skulls not to scale). **e** The cor-

relation between orbit convergence and binocular visual field overlap is significant (Spearman's rho = 0.832, $p < 0.01$, $n = 27$) and the confidence intervals of the reduced major axis slope include isometry [data from Heesy, 2004]. Both variables are presented in degrees. The ellipse denotes the positions of the outliers; *Sminthopsis crassicaudata* and *Dasyurus hallucata* have been related to eye size – orbit size allometry [Heesy, 2004]. Triangle = Artiodactyla, filled circle = Carnivora, double circle = Chiroptera, × = Lagomorpha, diamond = Metatheria, reversed triangle = Perissodactyla, filled square = Primates, star = Rodentia, open square = Scandentia.

Although visual field overlap is a continuous variable, contrasts and comparisons are often made between panoramic and binocular visual fields. Panoramic visual fields are qualitatively observed in taxa that are subject to heavy predation, such as artiodactyls, equid and tapirid perissodactyls, and lagomorphs, and are traditionally considered advantageous for identifying approaching predators [e.g., Walls, 1942; Hughes, 1977]. Taxa with large binocular (overlapping monocular) visual fields have narrow or reduced lateral visual fields, but possess three potential visual advantages: greatly enhanced light sensitivity, contrast discrimination, and stereoscopic depth perception. Two eyes that have largely overlapping visual fields have an increased probability of capturing light within the region of overlap by a factor of approximately 1.25 [Pirenne, 1943; Lythgoe, 1979]. Binocularity also improves contrast discrimination (the ability to detect luminance differences in adjacent objects or multiple

parts of the same object) by physical summation of the doubled visual information extracted from the similar images presented to each eye [Campbell and Green, 1965; Lythgoe, 1979; see also Pirenne, 1943]. Summation facilitates distinguishing spurious noise from signal by physiological summation along the visual pathway [Campbell and Green, 1965; Lythgoe, 1979; see also Pirenne, 1943]. Both increased light sensitivity and improved contrast discrimination are important to taxa that inhabit light-limited or highly light-variable environments such as those inhabited by nocturnal or cathemeral taxa [Lythgoe, 1979; Pariente, 1979; Martin, 1990].

The most prominently cited advantage of binocularity for mammals is the potential for stereoscopic depth perception. Binocular visual fields are a prerequisite for stereoscopic depth perception, the cortical computation of object solidity and depth based on binocular disparity cues [e.g., Howard and Rogers, 1995; Schor, 2001]. An im-

portant component of stereopsis is the binocular parallax imparted by the slightly different views of objects projected to the retina of each eye from the binocular field. Stereopsis allows for depth judgments based on calculations from these binocular disparity cues. Additionally, binocular visual fields facilitate binocular fusion, the process that integrates percepts of retinal images from each eye into a singular mental visual image [e.g., Schor, 2001]. The functional utility of stereopsis is for judgments of depth and distance over a short range. The maximum range over which stereopsis functions in amphibians and avians is quite limited (<1 m) based on behavioral data, and mammals probably also have a truncated maximum range over which stereopsis functions [Collett, 1977; McFadden, 1987, 1994].

Orbit Orientation and the Origin of Primates

Adaptive explanations for high orbit convergence in primates have focused on hypothesized benefits that stereoscopic depth perception might grant to animals with specialized locomotor or feeding behaviors. For much of the 20th Century, features of primates, including specializations of the visual system, were explained as adaptations to inhabiting an arboreal niche [Jones, 1917; Collins, 1921; Smith, 1924; Le Gros Clark, 1959; reviewed in Cartmill, 1974]. Only the specializations relevant to orbit convergence and binocular vision are addressed in this study for the purposes of brevity and clarity. The importance of binocularity and hand-eye coordination to primate evolution is reviewed in Ross and Martin [2007]. Collins [1921] was the first to suggest that binocular vision and stereopsis were required for the accurate judgment of distance in arboreal locomotion, in particular during leaping between arboreal substrates. Crompton [1995] expanded on this idea when he suggested that stereoscopic depth perception (and orbit convergence) evolved in early primates to accurately judge distance during nocturnal vertical clinging and leaping, a specialized form of high-speed ricochetal arboreal locomotion found in several taxa of extant primates [Walker, 1974]. The common component to Collins' and Crompton's proposals is the need for accurate judgment of distance among arboreal substrates in order to avoid a catastrophic error in distance estimation during arboreal leaping.

An alternative to the locomotion component of the 'arboreal theory' has been proposed by Cartmill [1972, 1974, 1992], Allman [1977, 1999], and Pettigrew [1978, 1986a] to explain the functional and adaptive advantages of orbit convergence and binocular visual field overlap. The 'visual predation hypothesis' was proposed by Cartmill

[e.g., 1972] to explain an adaptively cohesive suite of morphological, ecological, and behavioral traits of primates. The importance of nocturnality was explicated later by Allman [1977] and Pettigrew [1978]. Hence, the hypothesis is now known as the 'nocturnal visual predation hypothesis' [Cartmill, 1992]. Although Cartmill's hypothesis explains the adaptive significance of multiple traits, only the evolution of the visual system is addressed in this study. High orbit convergence and binocular visual field overlap are hypothesized to be adaptations to the nocturnal visual predatory habits of the last common ancestor of all primates. This hypothesis is based on several key points: the comparative morphology and behavior of arboreal mammals, comparative optics, and the functional attributes of stereopsis.

Comparative Morphology and Behavior of Arboreal Mammals. Arboreality is not unique to primates, and yet other groups of arboreal mammals, such as rodents, pilotans (sloths), and some hyraxes, have divergent orbits and panoramic visual fields [Cartmill, 1972, 1974, 1992; Heesy, 2003, 2004, 2005]. Locomotion in a complex arboreal environment does not require large binocular and stereoscopic fields because many arboreal taxa with panoramic vision successfully move around in this environment [Cartmill, 1972, 1974, 1992]. Nor does arboreal leaping require orbit convergence and expansive binocular visual fields because non-primate arboreal leapers, such as the rodent *Sciurus*, successfully traverse discontinuous arboreal substrates despite divergent orbits and limited binocular visual fields [Cartmill, 1972, 1974, 1992].

Comparative Optics. Allman [1977, 1999] and Pettigrew [1978, 1986a] contributed to the nocturnal predation hypothesis by providing a functional explanation that links orbit convergence to the alignment of the optic and visual axes in nocturnal taxa. Hypothesized optical effects of visual axis alignment in taxa with divergent and convergent orbits are illustrated in figure 2. The optical axis is defined as the axis of symmetry through the cornea and lens, whereas the visual axis is defined as the line that fits through the point of fixation, nodal points, and area centralis (or fovea in taxa that possess one). In taxa with divergent orbits and optic axes (fig. 2, left), when the visual axes converge on an object in front of the animal, these axes also necessarily traverse the most curved portion of the lens of the eye. High curvature of lenses as well as the refractive indices the layers of the lens will alter the path of light depending on the angle of approach of light and degree of curvature of the surface of the lens [Charman, 1991; Smith and Atchison, 1997; Hecht, 2002]. Al-

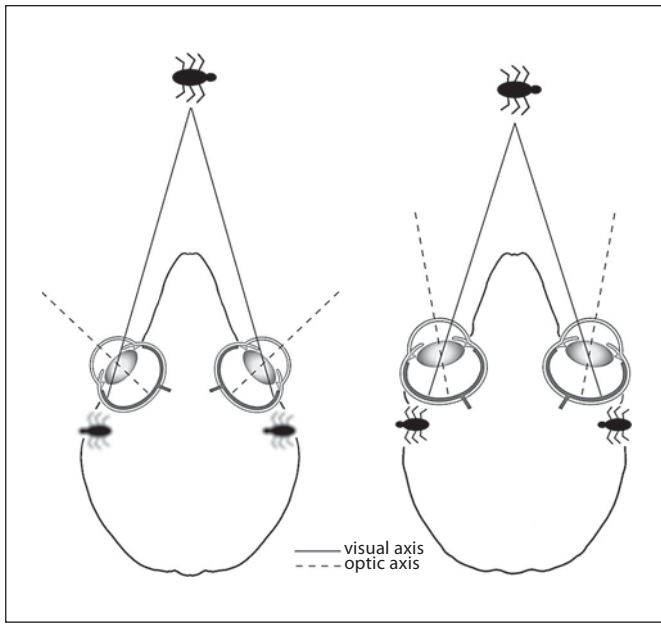


Fig. 2. Visual axis re-orientation. Schematic diagram illustrating relationship between orientation of optic axis, visual axis, and orbits in an animal with divergent orbits (left), and one with convergent orbits (right). See text for a detailed discussion of this figure. Please note that refraction and aberration of the path of light is not detailed in this figure (figure provided by Dr. Callum Ross).

teration of the light path through the more curved portions of the lens produces spherical aberration [Smith and Atchison, 1997; Hecht, 2002]. Spherical aberration reduces image quality in optical systems and has a potentially detrimental affect on visual acuity by decreasing image focus on the retina [Hughes, 1977; Land and Nilsson, 2002; see also Smith and Atchison, 1997; Hecht, 2002]. The drop-off in image quality is reduced in taxa like rats, in which the lens has a pronounced spherical shape and uniform angle of approach [Hughes, 1972, 1977, 1979]. It is additionally possible that differences in the refractive indices between the center and periphery of the lens may also produce aberration, but the comparative data are limited at present [Hughes, 1977]. Diurnal taxa can avoid image aberration and poor visual acuity due to spherical aberration by reducing the diameter of the pupil, thereby allowing light to pass only through the center of the lens. The lens center is optically superior because it is the least curved and allows light to pass through this paraxial zone with less re-orientation of the light path than is caused by light passing through the peripheral portion of the lens [Smith and Atchison, 1997; Hecht, 2002; Land

and Nilsson, 2002]. Nocturnal taxa cannot reduce pupil size because they need to capture as much light as possible from the environment to produce a sufficiently bright image on the retina [Allman, 1977; Pettigrew, 1978, 1986a; Land, 1981; Hall and Ross, 2007]. The alternative is to re-orient the eyes and orbits such that the visual and optic axes are more closely aligned, thereby allowing light from the object of interest to pass through the center of the lens (fig. 2, right). This is the orientation of the optic and visual axes that best allows nocturnal animals to view objects or prey within binocular fields without compromising light-gathering capabilities.

Functional Attributes of Stereopsis. Another line of evidence that supports the nocturnal visual predation hypothesis is that stereopsis counters camouflage-based crypsis, the camouflage patterning that matches the luminance, coloration, and textures of an animal's exterior to the background [Julesz, 1971; van der Willigen et al., 1998; Merilaita, 2003]. Camouflage crypsis is typical of heavily preyed upon taxa that inhabit complex visual environments [Julesz, 1971; van der Willigen et al., 1998; Merilaita, 2003]. The crypsis-countering effect of stereopsis is a natural product of the retinal disparity of viewing three-dimensional objects in a binocular field: the two-dimensional presentations of three-dimensional objects on each retina differ by the distance between each eye [Julesz, 1971; Howard and Rogers, 1995; Schor, 2001]. Disparity between a cryptic prey animal, which is nearer to the viewer, differs from that of the background on which it sits, which is relatively further away. Therefore, stereopsis allows the depth ordering of these objects, and the relative and absolute distances between the prey and background to be computed. Because prey animals typically evolve camouflage, stereopsis was suggested by Julesz [1971] to be a predatory adaptation to counter camouflage-based crypsis. Expanding the binocular and stereoscopic field also widens the zone over which cryptic prey can be detected. In addition, enhanced binocularity increases the ability to gauge the distance to cryptic or evasive prey items without unnecessary head movements, which could alert a prey animal to the presence of the predator prior to ambush [Cartmill, 1974].

Testing Orbit Orientation Hypotheses

The arboreal locomotion component of the 'arboreal theory' suggests that arboreal substrate utilization is the predominant factor that affects orbit convergence, whereas the 'nocturnal visual predation hypothesis' suggests that both activity pattern and diet affect convergence. Neither the predictions of arboreal locomotion nor noc-

turnal visual predation have been sufficiently analyzed for the effects of activity pattern, diet, and substrate utilization on orbit convergence and other measures of orbit orientation. Primates are often compared with nocturnal visual predators that also exhibit high orbit convergence, such as small-sized felid carnivores and owls. Such studies are often cited as corroborating evidence for the nocturnal visual predation hypothesis for primate origins [Cartmill, 1972, 1974, 1992; Allman, 1977, 1999; Pettigrew, 1978, 1986a; but see Martin, 1999, and Martin and Katzir, 1999 for alternative interpretations for the functions of binocularity in birds]. However, Cartmill's dataset was small, and the correlations of all the ecological factors with orbit orientation were not investigated quantitatively. Ravosa and Savakova [2004] supported the predictions of nocturnal visual predation in a study that included carnivores and euarchontans (primates, tree shrews, and dermopterans), but the effects of dietary factors were not treated quantitatively, and substrate utilization was not included.

This study aims to evaluate the functional and adaptive hypotheses for orbit convergence in mammals using a large, ecologically diverse dataset of mammals. Univariate and multivariate comparisons of orbit orientation are made among mammals of known activity pattern, diet, and locomotor preferences to determine which of these factors explains more variance in orbit orientation. For arboreal locomotion to be supported as the more likely scenario driving increased orbit convergence, arboreal substrate preference must be the most significant factor explaining variance in orbit convergence. For nocturnal visual predation to be supported, nocturnal activity pattern and faunivorous diet must explain significantly more variance in orbit convergence than substrate preference.

Materials and Methods

Taxa Sampled

Mammals that broadly span a range of orbit orientation, activity pattern, diet and locomotor repertoire were chosen for this study. Data were collected on 1,324 specimens of 331 taxa from 16 orders of extant mammals [classification of taxa largely follows McKenna and Bell, 1997]. Raw morphometric data are available as an online supplement to Heesy [2005]. These orders include (number of taxa in parentheses): Artiodactyla (23), Carnivora (83), Chiroptera (32; megachiropterans only), Cingulata (3), Dermoptera (2), Dasyuromorphia (1), Didelphimorphia (15), Diprotodontia (13), Erinaceomorpha (5), Hyracoidea (4), Macroscelidea (7), Perissodactyla (6), Pilosa (4), Primates (96; 35 strepsirhines, 61 haplorhines), Rodentia (26), Scandentia (11). The samples are housed in the Departments of Mammalogy of the American Mu-

seum of Natural History, Smithsonian Institution, and the Museum of Comparative Zoology (Harvard).

Data Collection and Analysis

Three-dimensional coordinate data were collected for 22 landmarks on the skull with a MicroScribe-3DX coordinate data stylus (Immersion Corp., San Jose, Calif., USA). Each specimen was mounted on an elevated clay base so that all coordinate data could be collected in a single series [e.g., Lockwood et al., 2002]. Each specimen sits within its own three-dimensional coordinate data space with this arrangement.

Convergence is measured as the dihedral angle (an angle between two planes) between the orbital margin plane and the midsagittal plane (fig. 3). Convergence can be used as a surrogate variable for degree of binocular visual field overlap because of the isometric relationship between these variables (fig. 1) [Heesy, 2004]. Frontation is defined as the angle between the nasion-inion chord and the orbital plane as it crosses the sagittal plane (fig. 3). Verticality is defined as the dihedral angle between the orbital margin plane and palatal plane (plane containing prosthion and points taken on alveolar margin directly above the middle of each M^1). Both verticality and frontation measure the degree to which the orbits face the end of the rostrum, and reflect postural orientation of the skull during locomotion [e.g., Strait and Ross, 1999]. Differences between verticality, which is measured relative to the palate, and frontation, which is measured relative to the braincase, are probably based on differences in orientation between the face and braincase, the angle between which can differ among mammals [Cartmill, 1970, 1974; Ross and Ravosa, 1993; Ross et al., 2004; see Heesy, 2005].

Angular data can potentially be non-normally distributed due to the constraints of circular dimensions [Fisher, 1993]. Departures from normality for angular and linear data were tested using the Kolmogorov-Smirnov test with Lillefors modification [Sokal and Rohlf, 1995; Green et al., 2000]. In three groups angular measures deviated moderately from normality, but not to a degree that required a specialized statistical distribution [e.g., Fisher, 1993]. In the cases of the MANOVA and ANOVA analyses, they were run both including and excluding these three groups and the results compared. The results did not differ, and the more inclusive MANOVA and ANOVA results are presented with all post-hoc comparisons.

The variance in orbit orientation that is attributable to activity pattern, locomotor substrate, and relative degree of faunivory was evaluated using multifactorial multivariate analysis of variance (MANOVA). The coding of individual taxa for these variables and the sources from which these were derived are presented in Heesy [2003]. Both main effects and interactive effects, and the difference between groups on one independent variable that varies depending on the level of the second independent variable [Hair et al., 1998], were examined. Follow-up univariate analyses of variance (ANOVA) were conducted to assess whether there are differences among population means for significant independent variables. The Bonferroni method of correction to control for Type I error was used for the follow-up ANOVAs. Both Dunnett's C and Games-Howell post-hoc pairwise comparisons were made to determine the impact of independent variables on orbit orientation.

Separate univariate comparisons among composite categories were conducted as an alternative to analyzing ecological catego-

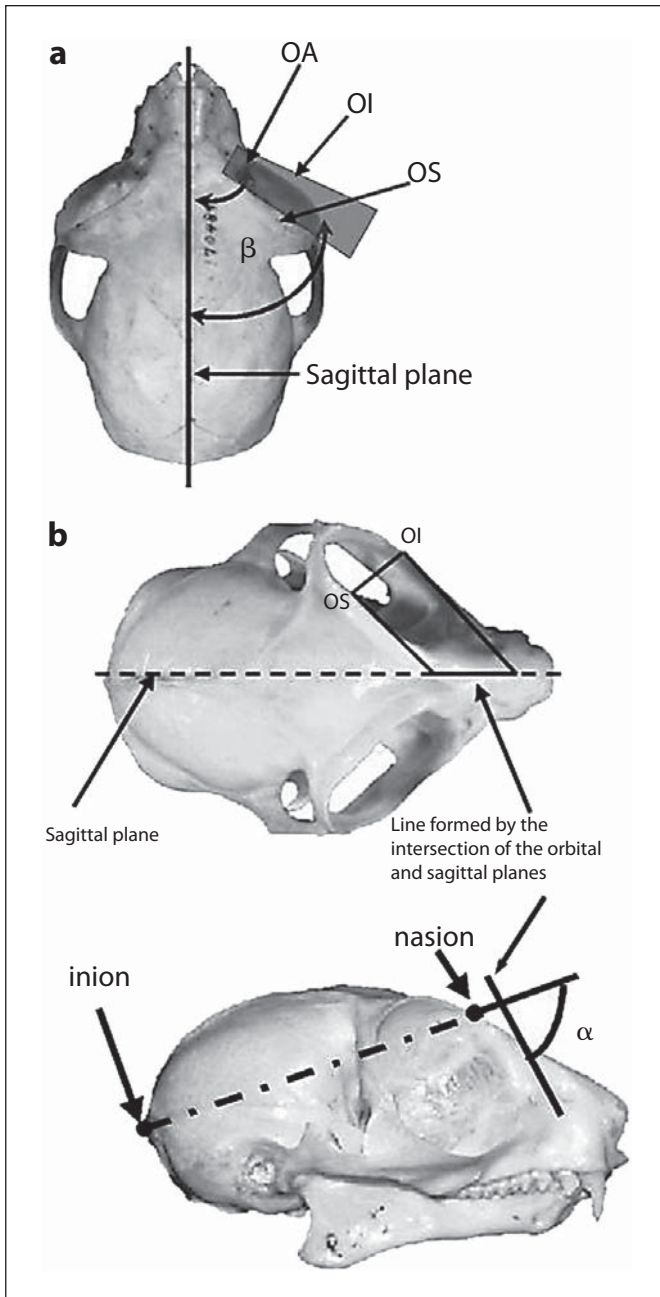


Fig. 3. Angular measurements. **a** Convergence is the dihedral angle between the orbital and sagittal planes. Note that verticality (not shown) is similar in that it is the dihedral angle between the orbital and palatal planes (plane containing prosthion and points taken along the alveolar margin directly above the middle of each M^1). **b** Frontation is the angle between the nasion-inion chord and the line formed by the intersection of the orbital and sagittal planes. OS = Orbitale superius, point on the orbital margin furthest from the toothrow; OI = orbitale inferius, point on the bony orbital margin closest to the toothrow; OA = orbitale anterior, point on the bony margin most distant from inion; OL = orbitale lateralis, lateralmost point on the bony margin; α = frontation angle; β = convergence angle. Skulls not to scale.

ries separately. Taxa were sorted by considering activity pattern, degree of faunivory, and locomotor substrate together. These comparisons focus solely on convergence because this is the single measure of orbit orientation that is expected to covary with binocular field overlap. There are four states for degree of faunivory (faunivore, omnivore, variable/opportunistic faunivory, and non-predator). These were coded by the following: faunivore (animal matter greater than 75% of the diet), omnivore (animal matter between 11 and 74% of the diet), opportunistic/variable faunivore (animal matter occasionally taken, but less than 10%), and non-predatory (no animal matter in the diet). There are three states for activity pattern (nocturnal, cathemeral, and diurnal), and three for substrate use (arboreal, terrestrial, and aerial – based on predominant substrate preference). There are 36 potential categories, 23 of which are occupied by taxa in this study.

Continuous biological data potentially violate standard statistical assumptions of independence due to phylogenetic relatedness [Felsenstein, 1985; Harvey and Pagel, 1991]. Specialized phylogenetically based statistical methods for comparative analyses have been devised to evaluate the contribution of relatedness to variance in the variables of interest [Felsenstein, 1985; Martins and Hansen, 1997; Rohlf, 2001]. Although useful, these methods cannot be applied in this study because they are designed for bivariate and simple multivariate analyses. The multivariate MANOVA analyses conducted in this study include three discrete and three continuous variables. At present, the phylogenetically controlled method that allows the inclusion of discrete variables can only analyze one discrete and one continuous variable, and this discrete variable is binary (i.e., can only have two states) [Purvis and Rambaut, 1995]. However, previous studies that utilized bivariate statistics [Heesy, 2003, 2005] have successfully analyzed these continuous orbit orientation variables in a phylogenetic context utilizing phylogenetic generalized least squares [Martins and Hansen, 1997; Rohlf, 2001], and found equivalent or heightened significance than results from raw (not phylogenetically corrected) data alone.

Therefore, because the usual phylogenetic correction statistical methods were unavailable, alternate methods for this study were required. The variation in orbit orientation in two groups of mammals, metatherians (marsupials) and anthropoid primates (monkeys and apes), required additional statistical treatment in order to evaluate the variance components of the groups on both the MANOVA and ranked ecological ANOVAs. Orbit convergence values in metatherian mammals are relatively high and orbit frontation and verticality are very low [Heesy, 2005] (fig. 4). Cartmill's [1970, 1972] data indicate that there is a negative scaling relationship between convergence and frontation in metatherians, and he hypothesized that very low frontation is influenced by the spatial constraints of head and body positioning during early ontogeny in the marsupial pouch. Regardless of the influences on orbit frontation, the negative relationship between marsupial orbit convergence and frontation results in convergence values that are necessarily high because the orbits are constrained to a directly dorsal orientation. In addition, the robust morphology of the metatherian anterior zygomatic arch, which forms the inferior orbital margin, also has an allometric relationship with orbit convergence; increases in anterior zygomatic arch sizes lead to higher orbit convergence values [Cartmill, 1972; Derby et al., 2003]. Both of these allometric scaling factors considered together suggest that visual ecology might have less influence on orbit

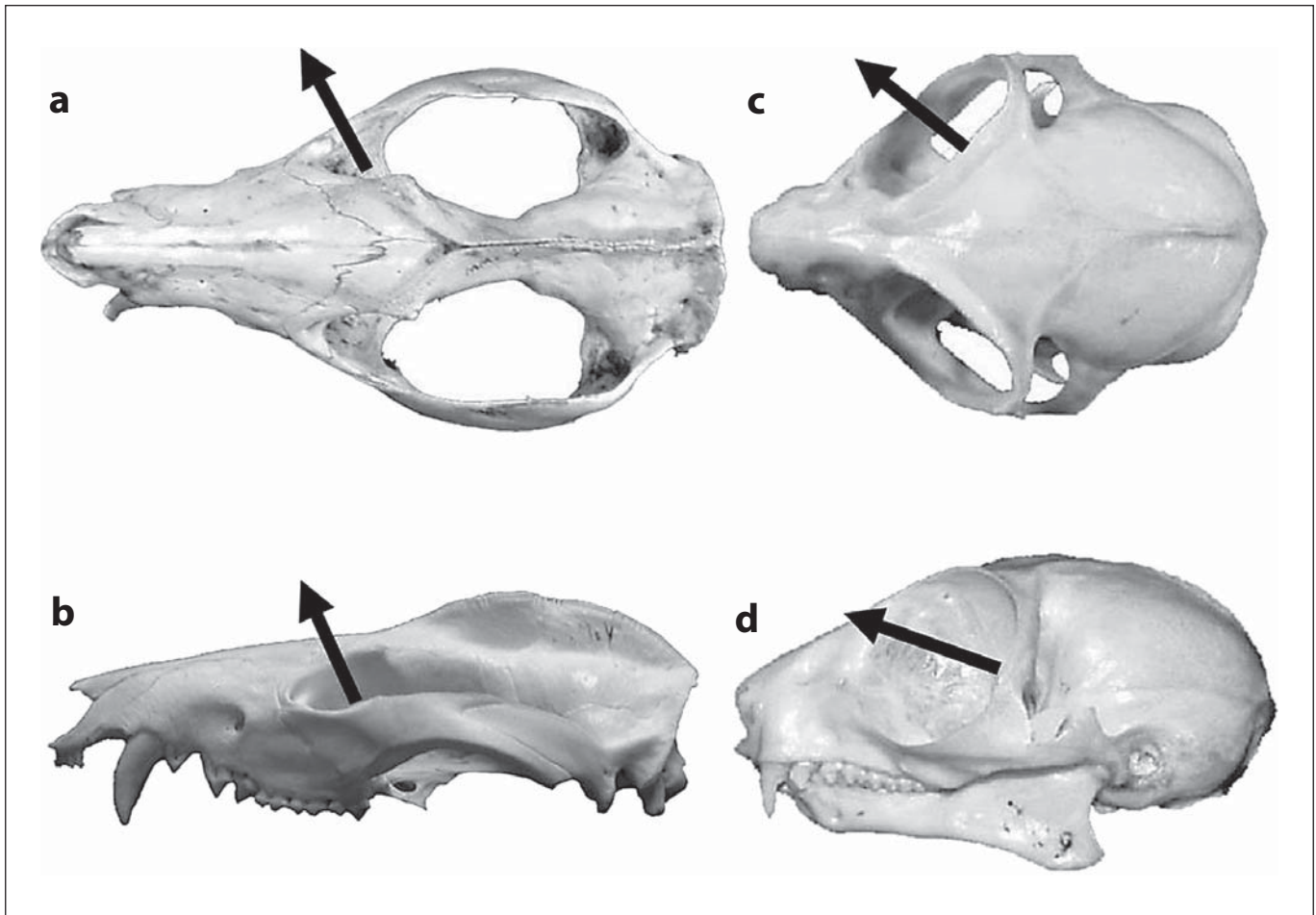


Fig. 4. Constraints on marsupial vertical orbit orientation. Marsupial convergence and frontation **a, b** compared to similar measures in a primate, *Otolemur* **c, d**. Cartmill [1970, 1972] suggested that very low frontation is influenced by the spatial constraints of head and body positioning in the marsupial pouch in early ontogeny. The robust morphology of the metatherian anterior zygomatic arch and inferior orbital margin has an allometric relationship with orbit convergence [Cartmill, 1972; Derby et al., 2003]. Allometric scaling might have greater influence on marsupial orbit orientation than visual ecology.

orientation and morphology than allometric factors associated with marsupial skull construction.

Anthropoid primates differ from strepsirhine and tarsiid primates (e.g., lemurs, lorises, galagos, and *Tarsius*) as well as all other mammals in that anthropoids have the absolutely highest orbit convergence values – anthropoids can be considered ‘hyper’-convergent compared to all other mammals. The very high orbit convergence in anthropoid primates has been explained as an allometric increase in both orbit convergence and frontation at a small body size during the transition to diurnality at the origin of the anthropoid lineage [Cartmill, 1980; Ross, 1995, 1996, 2000]. Pertinent to this discussion is the fact that orbit convergence in anthropoids increased from a strepsirhine-like morphotype, which is high compared to many other mammals [Cartmill, 1980; Ross, 1995, 1996, 2000].

Two different sets of statistical analyses were employed in this study. Firstly, all groups were analyzed together in order to allow for intergroup comparisons. Secondly, because the usual phylogenetic correction methods are unavailable, groups were separated from each other and analyzed individually as well. In order to evaluate the effects of contributed variance in both the MANOVA and ranked ecological ANOVAs by metatherians and primates, three sets of taxa were compiled and analyses were conducted in stepwise fashion on increasingly more exclusive groups. Separating the groups for individual re-analysis allows for data interpretation without the groups exerting undue phylogenetic influence on the analysis as a whole, and without allowing trends in the larger dataset to obscure patterns in smaller groups. The first set included all mammals available in the morphometric dataset of Heesy [2005] for which ecological variables could be coded. A second set, called Eutherian Set 1, that excluded both metatheri-

ans and anthropoid primates was tabulated, and the MANOVA and ANOVAs were conducted again. A third set, called Eutherian Set 2, was tabulated that excluded metatherians as well as anthropoid, strepsirhine, and tarsiiiform primates, and the MANOVA and ANOVAs were conducted for a third time.

Results

Ecological Variables and Orbit Orientation

Metatheria, Epitheria, and Eutheria. A multifactorial multivariate analysis of variance (MANOVA) was conducted to determine the effects of activity pattern, degree of faunivory, and locomotor substrate on orbit convergence, frontation, and verticality for all taxa included in the dataset for which all ecological factors could be coded. All three factors contribute to variance in orbit orientation (table 1). The summed multivariate $\eta^2 = 0.453$ indicates 45% of multivariate variance of the orbit orientation (dependent) variables is associated with the ecological grouping factors. Activity pattern explains approximately 15% of the variance, followed by substrate preference (approximately 8%), and degree of faunivory (approximately 5%). There is a statistically significant series of interaction effects among the factors as well, which together contribute to approximately 15% of the variance. The interaction effect among all three factors simultaneously is not significant.

Analyses of variance (ANOVA) on each dependent variable were conducted as follow-up tests to the MANOVA (table 1). Using the Bonferroni method of correction to control for Type I error, each ANOVA was tested at the 0.01 level (3 dependent variables, α of $0.05/3 = 0.016$ or 0.01). Significant tests are shown in table 1. The significant main and interactive effects differ among convergence, frontation, and verticality with the exception of the interaction between activity pattern and degree of faunivory. This effect contributes to variance in all three dependent variables.

Post-hoc analyses to the univariate ANOVAs for the independent variables, each of which contributes to at least one of the measures of orbit orientation, were conducted to examine differences among groups. Only significant results on main factors are discussed. Orbit convergence and frontation are significantly greater in arboreal taxa than in both aerial and terrestrial taxa (Dunnett's $C < 0.01$). Orbit frontation and verticality are also greater in faunivorous and omnivorous taxa than in opportunistic and non-predatory taxa (Dunnett's $C < 0.01$).

Eutherian Mammals Excluding Anthropoid Primates. Another multifactorial MANOVA was conducted simi-

lar to the first but excluding metatherian and anthropoid taxa. The summed multivariate $\eta^2 = 0.369$ indicates 37% of multivariate variance of the orbit orientation (dependent) variables is associated with the ecological grouping factors (table 1). Locomotor substrate explains approximately 11% of the variance in orbit orientation, followed by degree of faunivory (approximately 7%) and activity pattern (approximately 6%). Degree of faunivory and locomotor substrate as well as activity pattern and faunivory also have statistically significant interaction effects on orbit orientations, contributing approximately 5 and 6% of the variance, respectively.

Post-hoc analyses to the univariate ANOVAs for the independent variables were conducted to examine differences among groups. Nocturnal and cathemeral taxa have significantly higher orbit convergence than diurnal taxa (Dunnett's $C < 0.01$). However, nocturnal and cathemeral taxa are not significantly different. All categories of diet differ significantly for orbit convergence; faunivorous taxa have the most convergent orbits, followed by, in ranked order, omnivorous, opportunistic, and non-predatory taxa (Dunnett's $C < 0.01$). In addition, arboreal taxa have significantly more of the high orbit frontation values than terrestrial taxa (Dunnett's $C < 0.01$).

Non-Primate Eutherian Mammals. One MANOVA was performed on eutherians excluding strepsirhine, tarsiiiform and anthropoid primates. Significant differences were found among the three ecological categories for the measures of orbit orientation (table 1). The summed multivariate $\eta^2 = 0.443$ indicates that 44% of the multivariate variance of orbit orientation (dependent) variables is associated with the ecological grouping factors. Locomotor substrate explains approximately 15% of the variance in orbit orientation, followed by degree of faunivory (approximately 8%) and activity pattern (approximately 7%). The degree of faunivory and locomotor substrate also have a statistically significant interaction effect on the orbit orientations of non-primate eutherians, contributing approximately 6% of the variance.

ANOVAs on each dependent variable were again conducted as follow-up tests to the MANOVA. Using the Bonferroni method of correction, each ANOVA was tested at the 0.01 level. Significant factors are shown in table 1. Significant factors were found only for convergence and verticality.

Post-hoc analyses to the univariate ANOVAs for the independent variables were conducted to examine differences among groups. Nocturnal and cathemeral taxa have significantly higher orbit convergence than diurnal taxa (Dunnett's $C < 0.01$). However, nocturnal and cath-

Table 1. Results of multifactorial MANOVAs of ecological factors and measures of orbit orientation (only significant factors are shown)

Set	Factor	Wilk's Λ	Test	η^2
All mammals	Activity pattern	0.71	F (6, 600) = 18.22, $\rho < 0.001$	0.15
	Degree of faunivory	0.86	F (9, 730) = 5.15, $\rho < 0.001$	0.05
	Substrate	0.86	F (6, 600) = 8.11, $\rho < 0.001$	0.08
	Activity * faunivory	0.80	F (18, 849) = 3.93, $\rho < 0.001$	0.07
	Activity * substrate	0.92	F (6, 600) = 4.46, $\rho < 0.001$	0.04
	Faunivory * substrate	0.89	F (12, 794) = 3.10, $\rho < 0.001$	0.04
<i>Follow-up</i>				
Convergence	Substrate		F (2, 302) = 18.10, $\rho < 0.001$	0.11
	Activity * faunivory		F (2, 302) = 2.95, $\rho < 0.001$	0.11
Frontation	Degree of faunivory		F (3, 302) = 4.81, $\rho < 0.003$	0.03
	Substrate		F (2, 302) = 4.69, $\rho < 0.01$	0.03
Verticality	Activity * faunivory		F (6, 302) = 2.95, $\rho < 0.008$	0.06
	Activity		F (2, 302) = 40.69, $\rho < 0.001$	0.21
	Degree of faunivory		F (3, 302) = 11.91, $\rho < 0.001$	0.11
	Activity * faunivory		F (6, 302) = 2.95, $\rho < 0.008$	0.08
	Activity * substrate		F (2, 302) = 12.05, $\rho < 0.001$	0.07
	Act * faun * substrate		F (2, 302) = 12.05, $\rho < 0.005$	0.04
<hr/>				
Eutheria Set 1	Activity pattern	0.83	F (9, 672) = 4.69, $\rho < 0.001$	0.06
	Degree of faunivory	0.81	F (9, 540) = 5.51, $\rho < 0.001$	0.07
	Substrate	0.80	F (9, 444) = 8.87, $\rho < 0.001$	0.11
	Activity * faunivory	0.84	F (18, 662) = 2.19, $\rho < 0.003$	0.06
	Faunivory * substrate	0.87	F (12, 587) = 2.77, $\rho < 0.001$	0.05
<i>Follow-up</i>				
Convergence	Activity pattern		F (3, 246) = 7.82, $\rho < 0.001$	0.10
	Degree of faunivory		F (3, 246) = 5.86, $\rho < 0.001$	0.07
	Substrate		F (2, 246) = 7.34, $\rho < 0.001$	0.06
	Activity * faunivory		F (6, 246) = 3.07, $\rho < 0.007$	0.08
Frontation	Activity pattern		F (3, 246) = 4.15, $\rho < 0.007$	0.05
	Degree of faunivory		F (3, 246) = 6.53, $\rho < 0.001$	0.08
Verticality	Activity pattern		F (3, 246) = 4.09, $\rho < 0.007$	0.05
	Degree of faunivory		F (3, 246) = 11.68, $\rho < 0.001$	0.14
	Substrate		F (2, 246) = 5.59, $\rho < 0.004$	0.05
<hr/>				
Eutheria Set 2	Activity pattern	0.87	F (6, 365) = 4.17, $\rho < 0.001$	0.07
	Degree of faunivory	0.78	F (9, 433) = 5.10, $\rho < 0.001$	0.08
	Substrate	0.73	F (6, 356) = 10.19, $\rho < 0.001$	0.15
	Faunivory * substrate	0.83	F (12, 471) = 2.96, $\rho < 0.001$	0.06
<i>Follow-up</i>				
Convergence	Activity pattern		F (2, 180) = 10.44, $\rho < 0.001$	0.10
	Degree of faunivory		F (3, 180) = 10.11, $\rho < 0.001$	0.14
Verticality	Degree of faunivory		F (3, 180) = 8.71, $\rho < 0.001$	0.13
	Substrate		F (2, 180) = 5.79, $\rho < 0.001$	0.06
	Activity * faunivory		F (6, 180) = 3.48, $\rho < 0.003$	0.10

* Denotes an interaction effect. Wilk's Λ tests the overall significance of the MANOVA by testing the null hypothesis that samples come from populations with equal means. The sample sizes, significance, and level of significance of the F tests are shown. η^2 is an estimate of the variance explained by each factor.

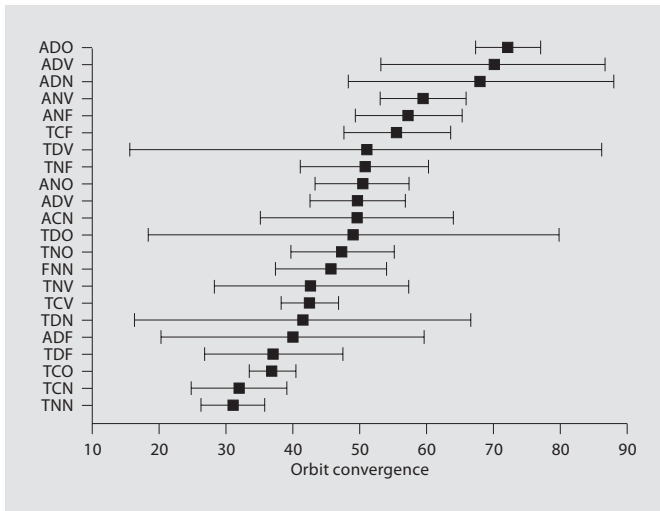


Fig. 5. Ranked ecological composite categories based on orbit convergence (all mammals). Groups are ranked by mean orbit convergence. Top, beginning with ADO, has the highest mean convergence, and bottom, TNN, the lowest mean convergence. Filled squares indicate mean bracketed by error bars. Abbreviations for group codes are as follows: ADO = Arboreal diurnal omnivore; ANF = arboreal nocturnal faunivore; TCF = terrestrial cathemeral faunivorous; ANO = arboreal nocturnal omnivore; ANN = arboreal nocturnal non-predator; TNO = terrestrial nocturnal omnivore; AND = arboreal diurnal non-predator; FNN = aerial/flying nocturnal non-predator; TNV = terrestrial nocturnal variably faunivorous; TCV = terrestrial cathemeral variably faunivorous; ADF = arboreal diurnal faunivore; TDF = terrestrial diurnal faunivore; TCO = terrestrial cathemeral omnivore; TCN = terrestrial cathemeral non-predator; TDN = terrestrial diurnal non-predator; TNN = terrestrial nocturnal non-predator; TDV = terrestrial diurnal variable faunivorous; ADV = arboreal diurnal variably faunivorous.

emeral taxa are not significantly different. In addition, faunivorous taxa have more convergent orbits than non-predatory taxa (Dunnett's $C < 0.01$), but omnivorous and opportunistic taxa do not differ from any other category.

Univariate Comparisons Among Composite Categories. As an alternative to analyzing ecological categories separately, taxa were sorted by considering activity pattern, degree of faunivory, and locomotor substrate together. These comparisons focus solely on convergence because this measure of orbit orientation has been hypothesized to covary with binocular field overlap. Departures from normality for orbit convergence were tested among these composite categories using the Kolmogorov-Smirnov test with Lillefors modification [Sokal and Rohlf, 1995]. For the 'all taxa' comparisons, three of 22

groups deviated somewhat from normality. One-way ANOVAs, parametric statistics for which normality within groups is an assumption, were conducted both including and excluding these three groups and the results compared. These results did not differ, and the ANOVA results with all taxa are presented with all significant post-hoc comparisons.

A one-way ANOVA was conducted with an all-mammal dataset to evaluate the relationship of composite ecological factors on orbit convergence. Composite ecological categories differ significantly for orbit convergence ($F_{(21, 300)} = 10.65$, $p < 0.001$; adjusted $\eta^2 = 0.39$). Composite ecological groups are ranked by mean orbit convergence (fig. 5). The ecological composite categories with the highest mean orbit convergence values share arboreal substrate use as a common factor (fig. 5), just as with the 'all taxa' MANOVA analyses described above. Both Dunnett's C and Games-Howell post-hoc comparisons between composite ecological categories are summarized in table 2.

A second one-way ANOVA was conducted with a eutherian mammal dataset that excluded anthropoid primates but retained strepsirhine and tarsiiiform primates. Composite ecological categories differ significantly for orbit convergence ($F_{(20, 242)} = 7.06$, $p < 0.001$; adjusted $\eta^2 = 0.39$). Composite ecological groups are ranked by mean orbit convergence (fig. 6). The ecological composite categories with the highest mean orbit convergence values inhabit light-limited environments (are either nocturnal or cathemeral) and four of the five highest groups are faunivorous or omnivorous. On the other hand, six of seven of the composite groups with the lowest mean orbit convergence values are non-predatory or opportunistically faunivorous.

A final one-way ANOVA was conducted with a non-primate eutherian dataset. Composite ecological categories differ significantly for orbit convergence ($F_{(17, 182)} = 9.03$, $p < 0.001$; adjusted $\eta^2 = 0.41$). As with the larger taxonomic sample, ecological groups are ranked by mean orbit convergence (fig. 7). Five of the top seven groups are either faunivorous or omnivorous, whereas the bottom six taxa are all non-predatory or rarely faunivorous. In addition, these top seven taxa are also all either nocturnal or cathemeral. Most faunivorous groups differ significantly from those that are rarely faunivorous (table 2).

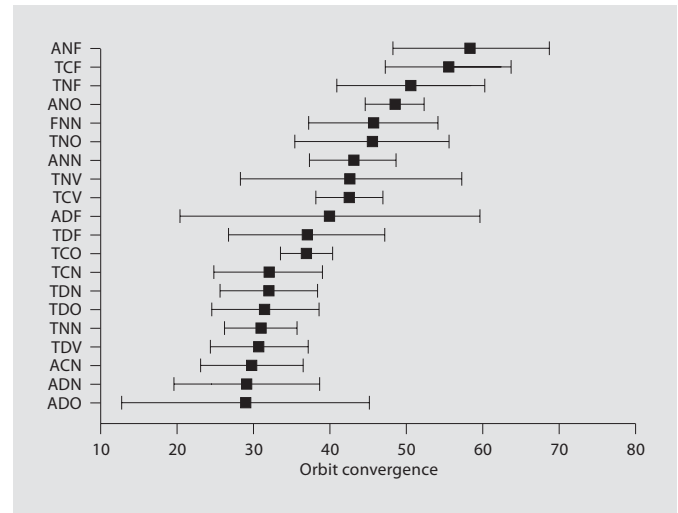
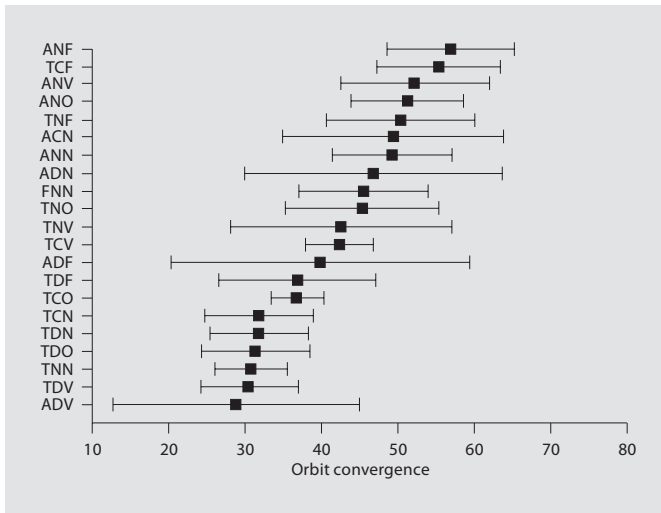


Fig. 6. Ranked ecological composite categories based on orbit convergence (eutherian mammals excluding anthropoid primates). Groups are ranked by mean orbit convergence. Top, beginning with ANF, has the highest mean convergence, and bottom, ADV, the lowest mean convergence. Filled squares indicate mean bracketed by error bars. Abbreviations follow those given for figure 5.

Fig. 7. Ranked ecological composite categories based on orbit convergence (non-primate eutherian mammals). Groups are ranked by mean orbit convergence. Top, beginning with ANF, has the highest mean convergence, and bottom, ADO, the lowest mean convergence. Abbreviations follow those given for figure 5.

Table 2. Results of Dunnett's C/Games-Howell post hoc comparisons between means of composite ecological categories for orbit convergence

Set	Composite ecological category	Differs from (computed at $p < 0.05$)	
All mammals	ANV	FNN, TDF, TCN, TDN, TNN	
	ANF	FNN, TDF, TCN, TDN, TNN	
	TCF	FNN, TDF, TCN, TDN, TNN	
	TNF	TDF, TCN, TDN, TNN	
	ANO	TDF, TCN, TDN, TNN	
	ANN	TDF, TCN, TDN, TNN	
	TNO	TCN, TDN, TNN	
	FNN	TCN, TDN, TNN	
	Eutheria Set 1	ANF	ADV, FNN, TNN, TCN, TDF, TDN
		TCF	TNN, TCN, TDF, TDN
ANO		TNN, TCN, TDF, TDN	
TNF		TNN, TCN, TDF, TDN	
ACN		TCN, TDN	
ANN		TCN, TDN	
ADN		TDN	
FNN		ANF, TDF, TDN	
Eutheria Set 2	ANF	FNN, TDF, TCO, TCN, TDN, TNN, TDV, ADN, ADV	
	TCF	TDF, TCO, TCN, TDN, TNN, TDV, ADN, ADV	
	TNF	TDF, TCN, TDN, TNN, TDV	
	ANO	TDF, TCO, TCN, TDN, TNN, TDV, ADN, ADV	
	ANN	TCN, TDN, TNN	
	FNN	TDF, TCN, TDN, TNN	

Only significant differences are shown.

Discussion

Ecological Influences on Mammalian Orbit Orientation

The arboreal locomotion component of the 'arboreal theory' predicts that arboreal substrate utilization is the predominant factor that affects orbit convergence, whereas the 'nocturnal visual predation hypothesis' predicts that both a nocturnal activity pattern and faunivorous diet affect convergence. The multifactorial multivariate analyses of variance (MANOVA) demonstrate that activity pattern, substrate use, and degree of faunivory all influence orbit orientation, including convergence. Roughly 43% of the variance in orbit orientation is explained by these individual factors for all taxa in this analysis when the variance explained by these factors is summed (table 1). This analysis demonstrates that ecological factors have a strong influence on orbit orientation and by extension visual ecology in mammals, and suggest that the analyses of orbit convergence are warranted.

Because there are no phylogenetic comparative methods that are currently capable of the MANOVA and composite ANOVA statistics required by this study, by removing first the marsupials and anthropoids, and finally the strepsirhines, from the data set and re-performing the statistical analyses at each step, this allows for the included groups to be analyzed individually and therefore bring to light which groups drive the different aspects of the analysis. It is generally true for all mammals in this analysis that arboreal taxa tend to have relatively higher orbit convergence than aerial or terrestrial taxa. This result is driven by the inclusion of marsupials, which I argued above might have constraints on their circumorbital morphology, and anthropoid primates, which possess highly derived circumorbital morphology when compared to strepsirhine primates as well as all other mammals [Cartmill, 1980; Ross, 1995, 1996, 2000]. The degree of faunivory is a significant factor when the analysis is restricted to non-anthropoid eutherian mammals (eutheria set 1 in table 2). Nonetheless, substrate preference is still a significant factor explaining variance in orbit convergence when strepsirhine primates remain within the dataset. It is only when strepsirhines are removed so that the other animals in the study can be individually examined statistically that substrate preference is no longer a significant factor. The implications of these results to primate orbit evolution are discussed below.

Nocturnal and cathemeral eutherian taxa have relatively higher orbit convergence than diurnal taxa. In addition, as shown by the post-hoc tests to the ANOVAs,

faunivorous or omnivorous eutherians are more convergent than opportunistic or non-faunivorous taxa. These general conclusions are further supported by ANOVA comparisons among the composite ecological categories, among which five of the top seven groups are either faunivorous or omnivorous and are also all either nocturnal or cathemeral (fig. 6 and 7). These composite 'niche' categories explain approximately 39% of the variance in orbit convergence among all taxa in this study, and approximately 41% among eutherians.

Adaptive Significance of Primate Orbit Convergence and Binocular Vision

Arboreality does not explain a significant portion of the variance in convergence among non-primate eutherians (see table 1), as would be expected if distance estimation for arboreal locomotion, especially leaping, was the dominant factor selecting for binocularity [Collins, 1921; Crompton, 1995]. This result is perhaps not unexpected. If the maximum range over which mammalian stereopsis is effective is as limited as those of amphibians and avians (<1 m: Collett, 1977; McFadden, 1987, 1994), then this form of depth perception alone would be inadequate for leaping locomotion, as small-sized leaping strepsirhines often jump over 5 m and larger-sized strepsirhines leap distances greater than 10 m [Cartmill, 1974; Demes et al., 1991]. The difference between the possible maximum stereoscopic range and maximum leaping distances suggests that stereopsis would only be functionally effective for the shortest leaps that are part of the vertical clinging and leaping cycle and not for the complete range of leap distances [Crompton et al., 1993], the longer ones of which are presumably the most dangerous to an arboreal animal. As was noted by Cartmill [1974], numerous arboreal taxa with laterally directed orbits and low binocular visual field overlap exist, such as *Sciurus*, which are quite capable of rapid acrobatic arboreal locomotion including leaping. Arboreal leaping taxa presumably use monocular distance cues such as interposition (one object in front of another), head-based motion parallax, and perspective [reviewed in Kandel, 1991]. However, the results to the follow-up ANOVAs for eutherian set 1, which includes strepsirhines, demonstrate that substrate preference does account for a small but significant amount of variance in orbit convergence. Nevertheless, activity pattern (specifically nocturnality), degree of faunivory, as well as the interaction between the two variables, explains over four times the variance in orbit convergence. This might be due to the specialized vertical clinging and leaping behavior found in a number of strep-

sirhine primates, which is not found in any of the other animals included in this study.

The data that support the influence of substrate preference on orbit convergence does not include leapers, but fliers (megachiropteran or fruitbats) and gliders (dermopterans or 'flying lemurs') (FNN in fig. 5–7). These flying and gliding taxa rank below the faunivorous and omnivorous taxa for comparative orbit convergence and above the majority of the taxa in this study. Superficial similarities between orbit orientation and morphology as well as the construction of the primary visual pathways between megachiropterans and primates have been noted before [Martin, 1986; Pettigrew, 1986b]. However, to my knowledge no one has previously argued that orbit orientation in megachiropterans is related to the flying locomotion employed by this group. Although it is beyond the limits of this study, I would suggest that orbit convergence in megachiropterans has evolved for reasons other than those argued for non-flying mammals as discussed in the introduction, but instead for reasons similar to those for binocularity in birds. Martin [1999; Martin and Katzir, 1999] has argued that binocularity in birds, which is limited compared to mammals, has evolved to take advantage of optic flow fields, the patterns of retinal image motion that provide information on locomotor heading, velocity, and time to impact relative to objects or environmental substrates [e.g., Lee and Reddish, 1981; Lee, 1994]. Megachiropterans face similar problems during aerial locomotion, and the visual sys-

tems of both megachiropterans and some birds might have evolved to provide similar navigation cues, and should be investigated further.

The data presented in this study support the nocturnal visual predator scenario as the most explanatory for increased orbital convergence associated with the origin of primates. The general observation that most non-primate eutherian mammals with high (strepsirhine-like) orbit convergence live in light-limited environments and are predatory is entirely consistent with the nocturnal visual predation hypothesis of primate origins [Cartmill, 1972, 1974, 1992; Allman, 1977; Pettigrew, 1978, 1986a]. The observation that the earliest fossil primates for which complete or nearly complete cranial material are available exhibit orbit convergence values most similar to strepsirhine primates strongly supports this view [e.g., Cartmill, 1974; Ross, 1995; Ni et al., 2004].

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