Predictors of orbital convergence in primates: A test of the snake detection hypothesis of primate evolution

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ABSTRACT

Traditional explanations for the evolution of high orbital convergence and stereoscopic vision in primates have focused on how stereopsis might have aided early primates in foraging or locomoting in an arboreal environment. It has recently been suggested that predation risk by constricting snakes was the selective force that favored the evolution of orbital convergence in early primates, and that later exposure to venomous snakes favored further degrees of convergence in anthropoid primates. Our study tests this snake detection hypothesis (SDH) by examining whether orbital convergence among extant primates is indeed associated with the shared evolutionary history with snakes or the risk that snakes pose for a given species. We predicted that orbital convergence would be higher in species that: 1) have a longer history of sympatry with venomous snakes, 2) are likely to encounter snakes more frequently, 3) are less able to detect or deter snakes due to group size effects, and 4) are more likely to be preyed upon by snakes. Results based on phylogenetically independent contrasts do not support the SDH. Orbital convergence shows no relationship to the shared history with venomous snakes, likelihood of encountering snakes, or group size. Moreover, those species less likely to be targeted as prey by snakes show significantly higher values of orbital convergence. Although an improved ability to detect camouflaged snakes, along with other cryptic stimuli, is likely a consequence of increased orbital convergence, this was unlikely to have been the primary selective force favoring the evolution of stereoscopic vision in primates.

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Introduction

Primates are notable among mammals in terms of possessing a visual system characterized by highly convergent (i.e., forward-facing) orbits and an associated expansion of visual brain structures (Allman, 1977; Barton, 2004; Heesy, 2005, 2008). An increase in orbital convergence leads to a large degree of binocularity (i.e., overlap of the visual fields of each eye), allowing for stereoscopic vision (Heesy, 2004). Stereopsis in turn enhances the ability to perceive depth, primarily at close range (~1 m: see Cartmill, 1974; Ross, 2000; Heesy, 2009), and effectively allows individuals to distinguish camouflaged objects from their background (see Pettigrew, 1978; Heesy, 2009). Adaptive explanations for these

visual features have been subject to considerable debate for the last several decades (reviewed in Ross and Martin, 2007), with various authors arguing that stereoscopic vision was favored in early primates because of the advantages it provided in nocturnal visual predation (Cartmill, 1992), acrobatic locomotion in an arboreal environment (Martin, 1990; Crompton, 1995), or feeding on small fruits in low-light conditions (Sussman, 1991).

More recently, it has been suggested that orbital convergence was favored in early primates because of the advantages stereoscopic vision provided in detecting camouflaged constricting snakes, which may have been among the first predators of primates (reviewed in Isbell, 2006, 2009). Further, Isbell (2006, 2009) argues that variation in aspects of the visual system among extant primates, including variation in orbital convergence, can be explained by the differential risk they have faced from venomous snakes, primarily of the viperid and elapid families, in their evolutionary history. Specifically, Isbell (2006, 2009) points out that Malagasy strepsirhines, having never faced venomous snakes, have relatively low degrees of orbital convergence. In contrast,

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catarrhines have the most convergent orbits among primates and have likely shared their evolutionary history with venomous snakes since at least the early Eocene. This snake detection hypothesis (SDH) (Isbell, 2006, 2009) further explains aspects of the visual system of platyrrhines, including a degree of orbital convergence intermediate between that of lemurs and catarrhines, as a result of the fact that they may have been freed from the selective pressures of venomous snakes from the period when they first arrived in South America until the probable later arrival of lancehead vipers (*Bothrops* and *Bothrocophias* spp.) on the continent in the middle to late Miocene.

However, beyond the non-statistical comparisons of measures of orbital convergence between some of the primate clades (Isbell, 2006, 2009), there have been no tests of whether or not orbital convergence among primates indeed varies with the shared history between venomous snakes and primates as the SDH posits. In addition to the differences in degrees of orbital convergence between the major primate clades, there is also considerable variation within clades in this regard (Ross, 1995; Heesy, 2005). If both the high degree of orbital convergence in primates relative to other mammals and the differences in convergence between the major primate clades is due to the selective pressures imposed by snakes, then it should also be expected that variation in the risk posed by snakes will explain some of this within clade variation. Beyond whether or not a given species is sympatric with venomous snakes, several additional factors should affect the risk of snake attack a particular primate species faces (summarized in Table 1): the population density of snakes in the habitat, the frequency in which snakes are likely to be encountered, the likelihood of detecting or deterring the snake before a successful attack is made, and the degree to which the species is likely to be targeted by snakes as a potential prey and successfully attacked.

First, snake density will affect risk for primates because a greater number of snakes present per unit area in the habitat will increase the probability and frequency of snake encounters (Hutchinson and Waser, 2007). We used rainfall, temperature, and latitude as proxies for snake densities based on previous research showing a strong relationship between these ecological variables and factors related to species richness and population density, including those of snakes and other reptiles (e.g., Rogers, 1976; Schall and Pianka, 1978; Greene, 1997; Reed, 2003; Araújo et al., 2006; Terribile and Diniz-Filho, 2009; Terribile et al., 2009). Further, like other ectotherms, temperature plays a large role in the overall biology of snakes, being positively related to activity levels (Hailey and Davies, 1986), attack speed (Greenwald, 1974), digestion rate (Skoczylas, 1970), and metabolic rate (Dorcas et al., 2004), all factors which are likely to influence the risk they pose to primates. In addition, these climate variables are directly related to habitat quality and structure, which are well-connected to animal abundances (i.e., densities; Brown, 1995). In turn, prey densities are known to be an important factor driving snake growth rates (Forsman and Lindell, 1991). This should further influence the degree of risk that snake predation poses on primates.

Second, patterns of movement should also affect the frequency with which primates will encounter snakes, with average speed in which primates move through their habitat being especially important in this regard (Hutchinson and Waser, 2007). Therefore, species that have a longer daily path length should encounter snakes more frequently than those species that move a shorter distance per day. Daily path length is likely to be especially important in determining the frequency of encounters with those snake species that employ a largely sit-and-wait/ambush strategy and rely on camouflage to avoid detection by prey and/or predators (i.e., most viperids and constrictors: Shine, 1980; Greene, 1997; Beaupre and Montgomery, 2007).

Third, the ability to detect snakes before an attack may increase with group size. This may occur as the result of early detection (e.g., van Schaik et al., 1983) and warning (e.g., Wheeler, 2008). Similarly, larger groups might be better able to deter an attacking snake through mobbing behavior (e.g., Tello et al., 2002; Perry et al., 2003; Erberle and Kappeler, 2008).

Finally, whether or not a primate species is potential prey for snakes will affect risk of attack because prey should be more likely to be attacked when encountered than would non-prey. The most important factors in determining whether or not a given animal species is likely to be targeted as potential prey by snakes are body size and shape, with snakes being unable to consume animals that are too large in terms of mass or girth due to the fact that snakes consume their prey whole (Greene, 1997). Given that primates vary little in their overall body shape (Fleagle, 1999), primate body mass is likely the most important factor affecting whether or not a given snake species preys on a given species of primate. The available evidence indicates that nearly all, except perhaps the very largest catarrhines and Malagasy lemurs, are likely to be vulnerable to predation by constrictors to some degree (e.g., Greene, 1997; Luiselli and Angelici, 1998; Shine et al., 1998; Rivas, 2000; Burney, 2002; Miller and Treves, 2011). In contrast, venomous snakes pose a serious threat to all primates (except in Madagascar, where venomous snakes are absent) given that individuals that knowingly or unknowingly approach too closely may be bitten defensively, and such bites are frequently fatal (e.g., Chippaux, 1998; Foerster, 2008; see Isbell, 2006, 2009 for a review of all known similar cases involving non-human primates). However, the prey of venomous snakes rarely exceed 0.5 kg (e.g., Luiselli et al., 2000; Shine and Sun, 2003; Luiselli and Akani, 2003; Hartmann et al., 2005; see also Greene, 1997), indicating that only the very smallest primates are likely to be targeted as prey by venomous snakes. Gaboon vipers (*Bitis gabonica*), the heaviest extant venomous snake, may sometimes prey on slightly larger mammals (Greene, 1997), and there has been one observation of an attempted

Table 1
Factors proposed to be associated with risk of attack by snakes, the proxies for these factors included in the current analysis, and the predicted relationship between the proxies and risk of snake attack.

Factor	Proxy[a]	Degree of risk	
		Low	High
Evolutionary history with venomous snakes	Biogeographic region	Madagascar	Neotropics[b], Africa/Asia
Snake density	Environmental variables	High latitude, low rainfall/temp	Low latitude, high rainfall/temp
Frequency of encounter	DPL[c]	Short DPL	Long DPL
Detect/deter before successful attack	Group size	Large groups	Small groups
Potential as prey	Body mass	Large mass	Small mass

[a] See text for justification of the proxy variables.
[b] Neotropics predicted to be intermediate between Madagascar and Africa/Asia (see text).
[c] DPL = daily path length.

predation on a ∼3 kg juvenile cercopithecine monkey (Foerster, 2008, pers. comm.). In this latter case, the primate was too large for the predator to ingest (Foerster, 2008), and systematic research indicates that the typical prey of these large vipers are considerably smaller (Luiselli and Akani, 2003).

Body size may be of further importance in affecting how vulnerable a given species is to being detected by snakes, but because snakes use a variety of methods to detect prey (Hartline, 1971; de Cock Buning, 1984; Schwenk, 1995), it is not clear how this would be related to susceptibility to predation. For instance, snakes can detect prey via heat sensing (de Cock Buning, 1984), possibly making small primates more vulnerable to detection due to their faster metabolic rate and surface-to-volume ratio (Fleagle, 1999). In contrast, a large primate, which presumably would produce more vibrations, may be more detectable because snakes can also detect prey through vibrations on the ground (Hartline, 1971).

This study tests whether the ability to detect snakes has been an important selective force in the evolution of orbital convergence in primates by examining whether, independent of phylogeny, orbital convergence among extant primates is associated with the extent of the shared evolutionary history with snakes and whether those extant primates that are more vulnerable to attacks by snakes have more convergent orbits than those that are less vulnerable. Specifically, if the SDH is correct, it is predicted that orbital convergence will be highest in biogeographic areas with the longest shared evolutionary history between primates and venomous snakes. Further, orbital convergence should be higher in those species that live in low latitude, warm, and high rainfall habitats, are characterized by small group sizes, have longer daily path lengths, and are smaller in body size (Table 1) because these factors should increase the risk of snake attack faced by individuals of a particular species. In addition, Isbell (2006, 2009) hypothesized that more enhanced color vision should be related to additional increases in orbital convergence to compensate for a decreased ability to distinguish camouflaged objects (see also Morgan et al., 1992). Therefore, there should be a significant relationship between color vision phenotype and orbital convergence if the SDH holds true.

Methods

Data sources

All data used in this study were obtained from the published literature, supplemented in a few cases with data from unpublished sources (see Table 2). Orbital convergence values were taken from Ross (1995) (61 species) and Heesy (2005) (70 species). These two datasets were not combined because the methods used by Ross produced lower values for species also measured by Heesy (matched pairs *t*-test, $p < 0.01$). Consequently, we conducted all analyses twice, once with each data set.

We examined nine predictor variables that characterize the shared evolutionary history with venomous snakes or are likely to influence visual system morphology and/or current risk of mortality posed by snakes. For each primate species, we obtained data for: 1) biogeographic region, 2) daily path length, 3) color vision type, 4) female body mass, 5) activity period, 6) absolute value of the latitudinal midpoint of the geographic range, 7) mean temperature, 8) mean rainfall, and 9) mean group size. In many cases, the predictor variables are averages across a number of study sites, while climate data are the mean value across the entire geographic range of the species. Such averages were deemed to be appropriate because the orbital convergence values are also species means. Biogeographic region was treated as an ordinal variable related to the duration of time primates have been sympatric with

venomous snakes: 1) Madagascar, 2) the Neotropics, 3) Africa and Asia (see Isbell, 2006, 2009). We coded activity period as an ordinal variable: 1) nocturnal, 2) cathemeral, 3) diurnal. We did not make any specific predictions regarding how this should affect orbital convergence based on the SDH, but included this variable because the average light conditions during a species' active period is important in shaping the visual system (e.g., Kirk, 2006). We coded color vision type as an ordinal variable: 1) monochromatic, 2) dichromatic, 3) polymorphic dichromatic-trichromatic, and 4) fully trichromatic. Color vision data were obtained from Bradley and Mundy (2008), Tan and Li (1999), and Surridge et al. (2003), except for *Avahi laniger* and *Eulemur coronatus*. The color vision phenotype of these two species is uncertain, so we ran the analyses testing all possible options. We found that whether these two species were scored as monochromatic, polymorphic, or fully trichromatic had a negligible impact on our results. For the statistics presented below, these species were scored as dichromatic, the presumed color vision type of most, particularly nocturnal, lemur species (Tan and Li, 1999). Finally, female mass was chosen over male mass because female primates tend to be smaller than their male counterparts and should therefore better represent the threat of snake predation a given species faces. Additional justification of the predictor variables can be found in the Introduction.

Statistical analyses

First, we log transformed the dependent variables as well as female mass, latitude, rainfall, temperature, and group size prior to analysis to better meet the assumptions of parametric tests (Sokal and Rohlf, 1995). Next, we calculated phylogenetically independent contrasts for each variable to account for the non-independence of data due to evolutionary history (Felsenstein, 1985). To calculate contrasts, we used the PDAP module (Midford et al., 2007) in Mesquite (Maddison and Maddison, 2007) and the primate phylogeny presented in Bininda-Emonds et al. (2007). We set all branch lengths equal to one, as this branch length designation best met the important assumption of independent contrasts analyses that there is no relationship between the absolute values of the standardized contrasts and branch lengths (Garland et al., 1992).

We used two types of analyses to determine the best predictors of orbital convergence across primates. First, we conducted a linear multiple regression including all predictor variables. We examined the residuals from this analysis to identify potential outliers, which were defined as samples with studentized residuals greater than three or less than minus three, and/or Cook's distances near or greater than one (Quinn and Keough, 2002). Because outliers can produce spurious results and mask true biological patterns (e.g., Nunn and Barton, 2001; Kamilar, 2009a), we removed them from the initial dataset and re-ran the regression.

We also used the outlier-free dataset to determine the best combination of variables predicting orbital convergence without overfitting the model. This is typically accomplished with step-wise regression models, yet several authors have showed that these analyses are prone to spurious results due to the order in which variables are entered into the model (Quinn and Keough, 2002; Burnham and Anderson, 2003). Instead, we implemented an information theoretic approach, which has been increasingly popular in biology and physical anthropology (Towner and Luttbeg, 2007; Kamilar and Paciulli, 2008; Kamilar et al., 2010). We used Akaike's Information Criterion, with correction for small sample size (i.e., <40 samples per predictor variable) (AICc) to determine the best models and variables that explain variation in primate visual systems (Burnham and Anderson, 2003). AICc provides a measure of the likelihood of a model given a particular dataset,

Table 2
The ecological, social, and morphological data used in the analysis. Doyle and Bearder 1977; Harcourt and Nash 1986; Wright, 1986; White, 1991; Meyers, 1993; Smith and Jungers, 1997; Müller and Thalmann, 2002; Nunn and van Schaik, 2002; Carbone et al., 2005; Irwin, 2006; Kamilar, 2006; Ossi and Kamilar, 2006; Pontzer, 2006; Campbell et al., 2007; Tan et al., 2007; Jones et al., 2009; Veracini, 2009 (Data sources).

Species	Female mass (kg)	DPL (km)	Group size	Rain (mm)	Temp (C)	Latitude	AP	CV	OC (Ross)	OC (Heesy)	Region	Clade
Alouatta belzebul	5.52	0.761	8	164.4	24.9	-6.8	D	T	71.5	73.7	NT	H
Alouatta caraya	4.33	0.478	14.6	116.6	22.9	-20.34	D	T		76.5	NT	H
Alouatta palliata	5.7	0.39	13.1	185.3	23.7	6.95	D	T	76.5		NT	H
Alouatta seniculus	5.6	0.55	7.9	182.3	25.1	0.68	D	T	67.6		NT	H
Aotus nigriceps	1.04	0.708	4.1	180.7	25.2	-7.72	N	M		62.8	NT	H
Aotus trivirgatus	0.736	0.252	2.5	178.6	24.8	4.15	N	M		67.5	NT	H
Ateles belzebuth	5.4	2.3	14.5	227.0	25.8	-0.44	D	P		75.0	NT	H
Ateles geoffroyi	6.3	1.68	42	153.9	24.3	12.38	D	P	77.8	80.8	NT	H
Ateles paniscus	7.8	2.7	20	157.7	25.6	2.06	D	P		79.9	NT	H
Avahi laniger	1.1	0.46	2	176.9	19.7	-19.63	N	?	49.8	54.7	MD	S
Brachyteles arachnoides	11.1	0.96	19.6	132.7	21.2	-22.66	D	P	74.6	82.4	NT	H
Cacajao calvus	2.88	3.75	39	211.9	25.5	-5.73	D	P	70.7		NT	H
Callicebus moloch	0.9	0.62	4.5	174.0	24.6	-7.7	D	P		85.4	NT	H
Callicebus personatus	1.38	0.69	6	107.4	21.2	-19.25	D	P		82.3	NT	H
Callimico goeldii	0.6	2	6.85	209.2	26.0	-5.33	D	P	63.9	69.9	NT	H
Callithrix argentata	0.36	1.04	9.5	171.9	25.4	-3.09	D	P	57.5	61.9	NT	H
Callithrix humeralifera	0.3	1.12	8.5	163.7	25.9	-5.36	D	P		64.5	NT	H
Callithrix jacchus	0.3	0.75	8.55	99.4	25.0	-6.58	D	P		63.5	NT	H
Cebuella pygmaea	0.122	0.29	5.5	208.5	25.6	-5.96	D	P	60.1	66.7	NT	H
Cebus albifrons	2.54	1.85	25	193.0	25.3	-0.82	D	P		77.9	NT	H
Cebus apella	2.53	2	7.9	154.2	24.1	-10.77	D	P	75.1	74.8	NT	H
Cebus capucinus	2.60	2	18.15	216.6	24.1	8.74	D	P	68.5	72.8	NT	H
Cercocebus agilis	5.43	1.29	20.35	54.0	27.4	-2.1	D	T		87.7	AF	H
Cercocebus torquatus	5.50	2.333	26.85	175.6	25.2	4.2	D	T	70.1		AF	H
Cercopithecus ascanius	3.39	1.59	15	131.0	23.7	-2.71	D	T	80.2		AF	H
Cercopithecus campbelli	2.70	1.692	9	226.7	25.3	8.53	D	T	71.0		AF	H
Cercopithecus mitis	5.69	1.33	20.7	109.1	22.1	-1.9	D	T	73.4		AF	H
Cheirogaleus medius	0.18	0.865	1	85.1	24.0	-19.03	N	D	47.0	66.9	MD	S
Chiropotes satanas	2.75	2.5	15.5	165.5	24.1	1.97	D	P	71.5		NT	H
Chlorocebus aethiops	3.73	1.38	17.5	70.9	21.7	12.6	D	T	74.6	91.0	AF	H
Colobus guereza	9.73	0.54	7.6	108.9	23.2	5.15	D	T	72.4	79.2	AF	H
Daubentonia madagascarensis	2.61	2.95	1	149.1	21.7	-18.79	N	D	53.2	56.4	MD	S
Erythrocebus patas	5.88	3.43	31.3	73.4	26.4	7.97	D	T	74.4	91.3	AF	H
Eulemur coronatus	1.77	0.912	9.5	105.1	23.8	-13.06	C	?		51.7	MD	S
Eulemur fulvus	2.43	0.14	12	156.1	21.4	-16.64	C	P	52.7	56.0	MD	S
Eulemur mongoz	1.67	0.61	2.93	125.9	26.2	-16.11	C	D		57.8	MD	S
Eulemur rubriventer	2.00	0.444	3	178.1	19.4	-18.45	C	P		61.1	MD	S

Galago senegalensis	0.25	2.1	3.5	80.1	25.0	1.95	N	D		46.3	AF	S
Gorilla gorilla	101.39	0.7	6	152.9	24.2	0.88	D	T	80.4	107.7	AF	H
Hapalemur griseus	1.20	0.43	3.1	177.3	19.7	-19.45	D	D	56.1	60.2	MD	S
Hylobates agilis	5.67	1.22	4.2	239.8	25.4	0.16	D	T		80.7	AS	H
Hylobates hoolock	6.50	1.1	3.2	153.6	17.5	23.44	D	T		75.1	AS	H
Hylobates lar	5.05	1.49	3.2	172.7	23.0	13.68	D	T	73.5	79.8	AS	H
Hylobates moloch	5.70	1.4	2.15	211.9	23.8	-7	D	T		73.9	AS	H
Hylobates muelleri	5.70	0.9	3.2	266.5	24.0	1.13	D	T	77.6		AS	H
Hylobates syndactylus	9.55	0.86	3.8	226.7	24.2	0.14	D	T	74.8		AS	H
Indri indri	7.92	0.25	3.1	187.1	20.0	-17.23	D	P	56.7	61.7	MD	S
Lagothrix lagotricha	6.08	1	33	226.6	25.8	0.02	D	P	75.3	78.5	NT	H
Lemur catta	2.47	0.95	16.45	62.9	23.0	-23.05	D	P	51.3	60.5	MD	S
Leontopithecus rosalia	0.56	1.44	4.5	128.3	20.7	-22.1	D	P	62.1	69.1	NT	H
Lophocebus albigena	6.73	1.27	16	141.7	23.8	0.22	D	T	75.5	87.8	AF	H
Loris tardigradus	0.12	1.35	1	147.3	25.2	6.75	N	D	54.4	61.6	AS	S
Macaca nemestrina	6.13	2	22.6	245.0	24.7	3.04	D	T	75.0		AS	H
Macaca nigra	6.21	6	35	230.8	22.5	1.01	D	T	80.8		AS	H
Macaca sylvanus	11.00	1.72	43	45.9	14.8	34.21	D	T	71.0		AS	H
Mandrillus sphinx	11.92	3	13.9	161.2	24.4	-0.76	D	T	75.2		AF	H
Miopithecus talapoin	1.09	2.32	64	104.3	23.2	-7.68	D	T	73.3	80.6	AF	H
Nasalis larvatus	9.46	0.71	11.25	257.1	25.0	1.42	D	T	69.8		AS	H
Otolemur crassicaudatus	1.11	1.25	3.5	87.1	22.0	-14.71	N	M	57.3	55.0	AF	S
Pan troglodytes	37.62	3.05	50	149.7	24.2	2.2	D	T	80.6	80.0	AF	H
Papio anubis	13.30	3.8	43	98.2	24.3	8.04	D	T	81.8	84.0	AF	H
Papio hamadryas	14.03	8.6	36.9	45.9	21.6	12.72	D	T	85.4		AF	H
Phaner furcifer	0.43	3.7	1	176.3	22.3	-15.35	N	D	37.5	42.2	MD	S
Pithecia pithecia	1.58	1.88	3	157.0	25.4	2.92	D	P	65.8	66.4	NT	H
Pongo pygmaeus	37.12	0.5	1	258.7	23.8	1.33	D	T	82.0	83.3	AS	H
Presbytis melalophos	6.60	0.88	14	278.5	24.7	-3.33	D	T		90.2	AS	H
Procolobus badius	6.16	0.58	34	161.5	26.1	9.69	D	T	74.5	84.8	AF	H
Procolobus verus	4.20	1.21	8.5	186.9	25.3	7	D	T	81.7		AF	H
Propithecus diadema	5.50	0.987	6	183.8	19.8	-17	D	P		62.6	MD	S
Propithecus tattersalli	3.50	0.788	4.1	104.5	25.2	-13.08	D	P		56.7	MD	S
Propithecus verreauxi	3.66	0.85	6.3	58.1	23.5	-22.63	D	P	57.1	62.2	MD	S
Rhinopithecus roxellana	11.60	2.1	65	73.4	9.0	32.32	D	T	85.0	86.1	AS	H
Saguinus fuscicollis	0.37	1.32	6	196.8	25.4	-5.28	D	P	58.8	67.8	NT	H
Saguinus nigricollis	0.41	1	6.3	256.2	26.1	-3.04	D	P		68.1	NT	H
Saguinus oedipus	0.40	1.37	7.05	120.3	26.3	9.22	D	P		74.0	NT	H
Saimiri boliviensis	0.75	2.1	54	171.5	24.3	-11.05	D	P		81.7	NT	H

Table 2 (*continued*)

Saimiri oerstedii	0.58	3.35	25.1	228.0	26.6	8.77	D	P		72.4	NT	H
Saimiri sciureus	0.61	1.5	34.85	186.9	25.3	-0.64	D	P	66.8	69.9	NT	H
Semnopithecus entellus	10.53	1.083	19	78.8	25.4	23.49	D	T	79.9	88.2	AS	H
Tarsius bancanus	0.10	1.8	1	256.4	24.7	0.56	N	P	46.3	52.5	AS	H
Tarsius spectrum	0.11	0.448	3	229.4	215.5	-1.97	N	P	54.1	59.0	AS	H
Tarsius syrichta	0.12	1.118	1	183.1	24.1	9.07	N	P	46.7	53.4	AS	H
Theropithecus gelada	12.24	2.5	10	92.5	17.3	10.95	D	T	82.4	89.5	AF	H
Trachypithecus cristatus	6.57	0.44	27.4	242.9	25.0	0.54	D	T	78.3	72.9	AS	H
Trachypithecus johnii	11.20	0.5	10	128.0	25.7	10.75	D	T	75.0	86.4	AS	H
Varecia variegata	3.58	2.305	2.8	188.6	19.9	-19.18	D	P	49.2		MD	S
Varecia v. rubra	3.64	1.74	6	176.3	22.3	-15.44	D	P		54.6	MD	S
Varecia v. variegata	3.52	1.13	2.8	188.6	19.9	-19.18	D	P		58.3	MD	S

Abbreviations: DPL = daily path length; Rain = mean monthly rainfall; Temp = mean monthly temperature; Latitude = Latitudinal midpoint of geographic range; AP = activity pattern; C = cathemeral; D = diurnal; N = nocturnal; CV = color vision type; D = dichromatic; M = monochromatic; P = polymorphic; T = trichromatic; OC = orbital convergence; Region = biogeographic region; AF = Africa; AS = Asia; MD = Madagascar; NT = Neotropics; H = Haplorrhini; S = Strepsirhini.

Data sources (color coded): Doyle and Bearder 1977; White, 1991; Meyer, 1993; Smith and Jungers, 1997; Harcourt and Nash 1986; Wright, 1986; Müller and Thalmann, 2002; Nunn and van Schaik, 2002; Carbone et al., 2005; Irwin, 2006; Kamilar, 2006; Ossi and Kamilar, 2006; Pontzer, 2006; Campbell et al., 2007; Tan et al., 2007; Jones et al., 2009; Veracini, 2009.

while minimizing the model's assumptions (i.e., number of predictor variables). Models within two AICc values of the "best" model are treated as equally good at explaining the dependent dataset (Burnham and Anderson, 2003).

In addition, we calculated the AICc weight for each model, which is a measure of the relative likelihood of each model being the best. We also calculated the sum of AICc weights for each independent variable to assess their relative importance for predicting the dependent variable (Burnham and Anderson, 2003). For example, if female body mass exhibited a score of 0.942, it would be about three times as likely to be an important variable compared to rainfall with a value of 0.296. This value is on a scale from zero to one, and is based on the frequency of the predictor variable being entered into each possible model weighted by the model's ability to explain the dependent variable.

The regression and AICc analyses were performed with Statistica and included a zero intercept, which is a requirement of analyses using independent contrasts data (Garland et al., 1992).

Finally, we used G*Power (Faul et al., 2009) to determine the detectable effect size of our analyses using our two datasets. Given our sample size, the number of predictor variables, and the two-tailed nature of our analyses, the test found that the Heesy dataset can detect an effect size of 0.20 and the Ross dataset an effect size of 0.25. Consequently, our analyses should be able to detect relatively small effect sizes.

Results

Our initial multiple regressions predicting orbital convergence produced significant models using both datasets, yet they also contained an outlier contrast: *Cheirogaleus medius* versus *Phaner furcifer*. Our outlier-free analyses similarly produced statistically significant models (Heesy dataset: $r^2 = 0.313$, $p = 0.005$; Ross

dataset: $r^2 = 0.290$, $p = 0.032$) (Table 3). Using the full model multiple regressions, we found that orbital convergence was best predicted by female mass using the Heesy (Beta = 0.319, $p = 0.008$) and Ross datasets (Beta = 0.261, $p = 0.063$) (Table 3). Larger species exhibited greater orbital convergence compared with small ones, independent of other factors. Daily path length approached statistical significance using the Heesy dataset, with species that travel shorter distances per day tending to have more convergent orbits than those that travel greater distances (Beta = −0.208, $p = 0.079$). Similarly, diurnal species in the Ross dataset tended to have more convergent orbits compared with nocturnal species ($p = 0.092$). The remaining variables, including the extent of the shared history with venomous snakes, were weak predictors of orbital convergence.

The information theoretic approach produced fairly similar results. We found nine equivalently good models explaining orbital convergence using the Heesy data and 19 best models using the

Table 3
Full model multiple regressions predicting orbital convergence in primates using phylogenetically independent contrasts.

Predictors	Heesy dataset		Ross dataset	
	Std. Beta	p	Std. Beta	P
Daily path length	−0.208	0.079	−0.013	0.921
Color vision	0.171	0.268	0.048	0.738
Female mass	0.319	0.008	0.261	0.063
Group size	−0.001	0.992	−0.090	0.503
Activity period	0.147	0.364	0.266	0.092
Biogeographic region	0.069	0.536	0.110	0.373
Mean rainfall	−0.023	0.859	−0.181	0.245
Mean temperature	0.083	0.494	0.157	0.228
Latitude	0.163	0.194	0.102	0.475
Full model results	$r^2 = 0.313$, $p = 0.005$, df = 9,59		$r^2 = 0.290$, $p = 0.032$, df = 9,50	

*Results presented without outlier contrasts.

Table 4
Best models predicting orbital convergence using Akaike's Information Criterion with correction for small sample size. The analyses are based on phylogenetically independent contrasts generated from the Heesy (2005) dataset.

Model		Independent Variables				df	AICc	Δ AICc	AICc Weight	Log-Likelihood Ratio Chi^2
1	Mass	DPL	Latitude	CV		4	−184.919	0	0.048	11.608
2	Mass	DPL	CV			3	−184.593	0.326	0.041	9.026
3	Mass	DPL	AP			3	−183.704	1.215	0.026	8.137
4	Mass	DPL	Latitude	AP		4	−183.268	1.652	0.021	9.956
5	Mass	DPL	AP	CV		4	−183.233	1.686	0.021	9.922
6	Mass	DPL	Rainfall	CV		4	−183.199	1.72	0.020	9.888
7	Mass	DPL	Latitude	AP	CV	5	−183.158	1.762	0.020	12.174
8	Mass	DPL	Latitude	Region	CV	5	−182.977	1.942	0.018	11.993
9	Mass	CV				2	−182.929	1.99	0.018	5.175

All models within two AICc values from the best model are considered equivalently good models. Only the best models are provided here.
DPL = daily path length; CV = color vision phenotype; AP = activity pattern; region = biogeograpic region.

Ross dataset (Tables 4 and 5). Female body mass was the only variable appearing in all of the best models using the Heesy dataset and was found in 15 of the 16 best models using the Ross dataset. Female mass exhibited the highest sum of AICc weight for each dataset (Fig. 1). Daily path length and color vision phenotype displayed moderately high values using the Heesy dataset only. In addition, activity period exhibited a moderately high sum of AICc weight for the Ross dataset only.

Discussion

The results of the current analysis do not support the hypothesis that predatory and defensive attacks by snakes have been the primary selective force favoring the evolution of stereoscopic vision through increasing orbital convergence in primates. Indeed, the basic premise of the hypothesis, that those primates with a longer shared history with venomous snakes have more convergent orbits (Isbell, 2006, 2009), was not supported. This is likely due in part to the strong relationship between phylogeny and biogeography among primates, with many of the major sub-clades being limited to particular biogeographic areas (Fleagle and Reed, 1996; Kamilar, 2009b), indicating that the relationship between biogeography and orbital convergence may be better explained as phylogenetic differences than ecological differences between the regions. Indeed, the African and Asian strepsirhines (galagos and lorises, respectively), which are more closely related to Malagasy lemurs than to sympatric catarrhines, have orbital convergence values that overlap completely with those of lemurs but are lower than those of all catarrhines (Ross, 1995; Heesy, 2005; Table 2). The low degree of orbital convergence in lorisiformes, despite having a shared evolutionary history with venomous snakes that is likely identical to that of the catarrhines, seems to falsify the SDH (see also Wheeler, 2010).

The relationship between biogeography, exposure to venomous snakes, and the evolution of stereoscopic vision is further confounded by the uncertainty of the shared evolutionary history of some primates and venomous snakes (Wheeler, 2010). While the evidence is strong that the African and Asian primates have had greater exposure to venomous snakes than have those in Madagascar (reviewed in Isbell, 2006, 2009), it is difficult to ascertain the degree to which platyrrhines have been exposed to venomous snakes during their evolutionary history. Specifically, although the molecular evidence most parsimoniously places the last common ancestor (LCA) of lancehead vipers in South America at 23−10 Ma (Wüster et al., 2002, 2008), the age of the LCA is best viewed as a minimum estimate for arrival, as stem members of this clade could have been present in South America prior to the diversification of the crown clade, as has been argued, for example, in New World monkeys (Hodgson et al., 2009). While the evidence thus favors the idea that some degree of early platyrrhine evolution occurred in the absence of venomous snakes, it is difficult to draw firm conclusions regarding whether or not this is the case or how long that period might have been. Even more challenging is determining whether the observed variation in the visual systems of crown platyrrhines, relative to catarrhines, can be attributed to the fact that the former radiated in the absence of venomous snakes (Isbell, 2006, 2009), as this radiation began only 23 − 17 Ma (Hodgson et al., 2009).

Table 5
Best models predicting orbital convergence using Akaike's Information Criterion with correction for small sample size. The analyses are based on phylogenetically independent contrasts generated from the Ross (1995) dataset.

Model		Independent Variables				df	AICc	Δ AICc	AICc Weight	Log-Likelihood Ratio Chi^2
1	Mass	AP				2	−165.573	0.000	0.026	3.963
2	Mass	Rainfall	AP			3	−165.566	0.007	0.026	6.144
3	Mass	Rainfall	Temp	AP		4	−164.970	0.603	0.020	7.803
4	Mass	Latitude	AP			3	−164.929	0.644	0.019	5.507
5	Mass	AP	Region			3	−164.446	1.127	0.015	5.023
6	Mass	Rainfall	AP	Region		4	−164.345	1.228	0.014	7.178
7	Mass	Temp	AP			3	−164.320	1.254	0.014	4.897
8	Rainfall	AP				2	−164.267	1.307	0.014	2.657
9	Mass	Temp	Latitude	AP		4	−164.218	1.355	0.013	7.051
10	Mass	Rainfall				2	−164.075	1.499	0.012	2.464
11	Mass	Latitude	AP	Region		4	−163.972	1.601	0.012	6.805
12	Mass					1	−163.732	1.841	0.011	0.000
13	Mass	GS	Rainfall	AP		4	−163.679	1.894	0.010	6.512
14	Mass	Rainfall	Latitude	AP		4	−163.661	1.912	0.010	6.494
15	Mass	DPL	Rainfall	AP		4	−163.615	1.958	0.010	6.448
16	Mass	Rainfall	CV			3	−163.609	1.964	0.010	4.186

All models within two AICc values from the best model are considered equivalently good models. Only the best models are provided here.
DPL = daily path length; CV = color vision phenotype; AP = activity pattern; GS = group size; region = biogeograpic region.
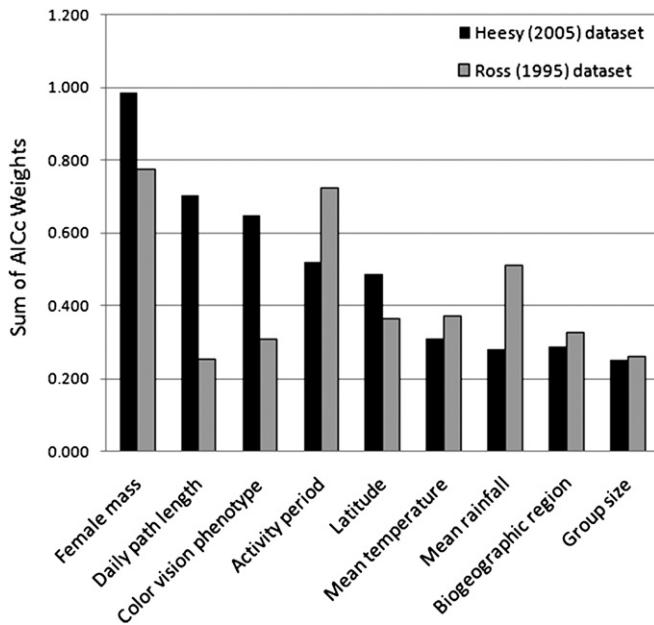
Figure 1. The importance of all independent variables for predicting orbital convergence based on AICc weights. The sum of AICc weights for each independent variable is produced by summing the Akaike weights across all models where the variable occurs. It is a relative measure of the importance of each variable for predicting orbital convergence.

In addition to the lack of a significant effect of biogeography on orbital convergence, there was also no relationship between orbital convergence and the degree of risk that snakes pose to extant primates; indeed, the trends were in the opposite direction than predicted by the SDH in several cases. For example, both the multiple regressions and the AICc analyses indicated that mean female body mass, together with activity period, were the most important variables in predicting orbital convergence, although in the opposite direction than predicted: species less likely to be targeted as prey by snakes (i.e., larger species) are characterized by more convergent orbits. Similarly, although daily path length was not a significant predictor of orbital convergence in either of the two datasets (but was the second most important variable in seven of the eight AICc models conducted with the Heesy dataset), this variable showed a negative relationship with orbital convergence independent of other factors, including phylogeny. Thus, those species that are likely to encounter snakes more frequently tend to have less convergent orbits. Likewise, the relationship between orbital convergence and the likelihood of detecting or deterring snakes before an attack (based on group size) was weak in both datasets. Finally, support for the hypothesis that more enhanced color vision should be associated with further increases in orbital convergence to compensate for a decreased ability to distinguish camouflaged objects (Isbell, 2006, 2009) was weak, being of secondary importance in the Heesy dataset but only minor importance in the Ross dataset.

The variables that were consistently the most important predictors of orbital convergence were body size and activity pattern. Although body size was predicted to have a significant effect if orbital convergence evolved to make detecting snakes more efficient, the effect was in the opposite direction than predicted because those primates more likely to be targeted as prey by snakes (i.e., smaller species) were found to have less convergent orbits. The relationship between orbital convergence and both body size and activity pattern is most likely related to a negative allometric relationship between relative orbit size and orbital

convergence (Ross, 1995; see also Cartmill, 1972). A decrease in relative orbit size is argued to have evolved in early anthropoids as the result of their evolution of diurnal habits from a nocturnal ancestor (Ross, 1995, 1996, 2000), a phenomenon that would be expected if that nocturnal ancestor had also been a visual predator (Ross, 1996, 2000; Kirk, 2006), and to have decreased further as anthropoids grew larger due to orbit size scaling with negative allometry against body size (Martin, 1990; see also Ross, 1995, 1996). An allometric relationship between relative orbit size and convergence may explain the observed differences in convergence among the major primate clades. All catarrhines are diurnal and are on average larger than platyrrhines, which in turn are on average larger than (extant) strepsirhines (Smith and Jungers, 1997), many of which are nocturnal and thus have relatively large orbits (Kirk, 2006).

Simple allometry, however, cannot explain all of the variation in orbital convergence within or between clades. Extant diurnal strepsirhines have less convergent orbits than similar-sized diurnal anthropoids despite similarity in their relative orbit size (see Fig. 1 in Kirk, 2006). Lorisids and some tarsiers have more convergent orbits than expected given their relatively large eyes (a fact that could be used to argue in support for either the nocturnal visual predation hypothesis or the SDH: Ross, 1995; see also Nekaris, 2005), and papionins, apes, and callitrichines (the latter likely being among the extant primates that are most vulnerable to predation by snakes; Miller and Treves, 2011) have less convergent orbits than expected given their relatively small orbits (Ross, 1995). Indeed, while the relationship between orbit size and convergence is strong for primates as a whole and a number of primate subclades, the relationship between these variables is non-significant among platyrrhines and is weak (but still statistically significant) in catarrhine primates (Ross, 1995). These deviations from the general trend are important because they demonstrate that allometry would not necessarily completely limit the ability to evolve increased stereopsis if snakes were indeed an important selective force in the evolution of the primate visual system. It is also important to note that the current analysis included factors related to relative orbit size (i.e., body size and activity pattern; Kirk, 2006), but even with these variables considered, neither historical biogeography nor the current risk posed by snakes explained further variation in orbital convergence in primates.

With a lack of support for the SDH in the current analysis, the nocturnal visual predation hypothesis remains the best supported hypothesis for the evolution of orbital convergence (Heesy, 2008, 2009). While the current analysis falsifies the SDH's premise that the degree of orbital convergence in extant primates is driven by their shared evolutionary history with venomous snakes, one could still argue that a lack of support for the additional predictions does not necessarily refute the SDH's explanation for orbital convergence, because snakes could be responsible for the differences seen between the major primate clades without orbital convergence tracking changes in the risk posed by snakes. However, there is no reason to suspect that the selective pressures posited by the SDH to have acted on these more ancient nodes should not have continued to exert pressure, although to various degrees on different taxa, depending on the degree of threat that snakes have posed. If snakes have indeed been the major factor driving the evolution of primate visual system diversity as proposed by Isbell (2006, 2009), then distantly related taxa facing similarities in the threat posed by snakes should be expected to independently evolve more convergent orbits. Indeed, such evolutionary convergences due to similar ecological pressures are common in primate evolution (see Lockwood and Fleagle, 1999). That the observed trends in the current analysis were in many cases opposite to the direction predicted indicates that snakes are exerting little, if any, selective

pressures on orbital convergence in extant taxa. The fact that those species least likely to be targeted as prey by snakes (i.e., larger species) have significantly higher degrees of orbital convergence is perhaps the strongest indication that some factor other than selective pressures posed by snakes is responsible for the observed trends.

The current results may also be confounded by the fact that microhabitat use by both snakes and primates will affect the rate in which the species encounter one another, but limitations in the availability of such data do not allow for an analysis including these variables. However, because the limited studies available indicate that venomous snake communities include species that occupy a range of microhabitats within a given habitat, ranging from terrestrial to the emergent canopy (e.g., Fitzgerald et al., 2002; see also Luiselli et al., 2005), it seems likely that such a variable would have only a minimal effect on the results.

Conclusions

Although the current analysis does not indicate that the likelihood of either encountering snakes or being targeted by snakes as prey has been the principal force underlying the evolution of increased orbital convergence in primates, it seems very likely that an increased ability to detect snakes (as well as any other camouflaged object) visually is a likely consequence of an increase in stereoscopic vision. Beyond the evolution of stereoscopy, the SDH also provides potential explanations for the evolution of other aspects of the primate visual system, including a number of neuroanatomical features (Isbell, 2006, 2009), which may or may not stand up to further scrutiny (Heesy, 2010), but which are nonetheless worthy of rigorous testing. Indeed, it seems indisputable that snakes have exerted some, possibly strong, selective pressures on primates, as evidenced by the fact that non-human primates typically perceive venomous snakes as dangerous (e.g., Boinski, 1988; Range and Fischer, 2004; Ramakrishnan et al., 2005; Ouattara et al., 2009), even among populations devoid of snake species that prey on primates (e.g., Barros et al., 2002; Wheeler, 2008). Likewise, the high number of fatalities from snake bites in some human populations (although normally in anthropogenically-altered areas; e.g., Chippaux, 1998; Alirol et al., 2010) evinces the threat that venomous snakes can pose to even non-prey species. Future field, captive, and comparative studies will likely yield additional insights into the possible effect of snakes and other predators on the evolution of primate diversity.

Acknowledgments

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