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# 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.

## 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.