1   Predictors of orbital convergence in primates: A test of the snake

2   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 which 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, but 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, 1986; 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, catarrhines have the most convergent orbits among primates and have

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68 likely shared their evolutionary history with venomous snakes since at least the early Eocene.

69 This snake detection hypothesis (SDH) (Isbell, 2006, 2009) further explains aspects of the visual

70 system of platyrrhines, including a degree of orbital convergence intermediate between that of

71 lemurs and catarrhines, as a result of the fact that they may have been freed from the selective

72 pressures of venomous snakes from the period when they first arrived in South America until the

73 probable later arrival of lancehead vipers (*Bothrops* and *Bothrocophias* spp.) on the continent in

74 the middle to late Miocene.

75   However, beyond the non-statistical comparisons of measures of orbital convergence

76 between some of the primate clades (Isbell, 2006, 2009), there have been no tests of whether or

77 not orbital convergence among primates indeed varies with the shared history between venomous

78 snakes and primates as the SDH posits. In addition to the differences in degrees of orbital

79 convergence between the major primate clades, there is also considerable variation within clades

80 in this regard (Ross, 1995; Heesy, 2005). If both the high degree of orbital convergence in

81 primates relative to other mammals and the differences in convergence between the major

82 primate clades is due to the selective pressures imposed by snakes, then it should also be

83 expected that variation in the risk posed by snakes will explain some of this within-clade

84 variation. Beyond whether or not a given species is sympatric with venomous snakes, several

85 additional factors should affect the risk of snake attack a particular primate species faces

86 (summarized in Table 1): the population density of snakes in the habitat, the frequency in which

87 snakes are likely to be encountered, the likelihood of detecting or deterring the snake before a

88 successful attack is made, and the degree to which the species is likely to be targeted by snakes

89 as a potential prey and successfully attacked.

90   First, snake density will affect risk for primates because a greater number of snakes

91   present per unit area in the habitat will increase the probability and frequency of snake

92   encounters (Hutchinson and Waser, 2007). We used rainfall, temperature, and latitude as proxies

93   for snake densities based on previous research showing a strong relationship between these

94   ecological variables and factors related to species richness and population density, including

95   those of snakes and other reptiles (e.g., Rogers, 1976; Schall and Pianka, 1978; Greene, 1997;

96   Reed, 2003; Araújo et al., 2006; Terribile and Diniz-Filho, 2009; Terribile et al., 2009). Further,

97   like other ectotherms, temperature plays a large role in the overall biology of snakes, being

98   positively related to activity levels (Hailey and Davies, 1986), attack speed (Greenwald, 1974),

99   digestion rate (Skoczylas, 1970), and metabolic rate (Dorcas et al., 2004), all factors which are

100   likely to influence the risk they pose to primates. In addition, these climate variables are directly

101   related to habitat quality and structure, which are well-connected to animal abundances (i.e.

102   densities; Brown, 1995). In turn, prey densities are known to be an important factor driving

103   snake growth rates (Forsman and Lindell, 1991). This should further influence the degree of risk

104   that snake predation poses on primates.

105   Second, patterns of movement should also affect the frequency with which primates will

106   encounter snakes, with average speed with which they move through their habitat being

107   especially important in this regard (Hutchinson and Waser, 2007). Therefore, species that have a

108   longer daily path length should encounter snakes more frequently than those species that move a

109   shorter distance per day. Daily path length is likely to be especially important in determining the

110   frequency of encounters with those snake species that employ a largely sit-and-wait/ambush

111   strategy and rely on camouflage to avoid detection by prey and/or predators (i.e., most viperids

112   and constrictors: Shine, 1980; Greene, 1997; Beaupre and Montgomery, 2007).

113   Third, the ability to detect snakes before an attack may increase with group size. This

114   may occur as the result of early detection (e.g., van Schaik et al., 1983) and warning (e.g.,

115   Wheeler, 2008). Similarly, larger groups might be better able to deter an attacking snake through

116   mobbing behavior (e.g., Tello et al., 2002; Perry et al., 2003; Erberle and Kappeler, 2008).

117   Finally, whether or not a primate species is potential prey for snakes will affect risk of

118   attack because prey should be more likely to be attacked when encountered than would non-prey.

119   The most important factors in determining whether or not a given animal species is likely to be

120   targeted as potential prey by snakes are body size and shape, with snakes being unable to

121   consume animals that are too large in terms of mass or girth due to the fact that snakes consume

122   their prey whole (Greene, 1997). Given that primates vary little in their overall body shape

123   (Fleagle, 1999), primate body mass is likely the most important factor affecting whether or not a

124   given snake species preys on a given species of primate. The available evidence indicates that

125   nearly all, except perhaps the very largest catarrhines and Malagasy lemurs, are likely to be

126   vulnerable to predation by constrictors to some degree (e.g., Greene, 1997; Luiselli and Angelici,

127   1998; Shine et al., 1998; Rivas, 2000; Burney, 2002; Miller and Treves, 2011). In contrast,

128   venomous snakes pose a serious threat to all primates (except in Madagascar, where venomous

129   snakes are absent) given that individuals that knowingly or unknowingly approach too closely

130   may be bitten defensively, and such bites are frequently fatal (e.g., Chippaux, 1998; Foerster,

131   2008; see Isbell, 2006, 2009 for a review of all known similar cases involving non-human

132   primates). However, the prey of venomous snakes rarely exceed 0.5 kg (e.g., Luiselli et al., 2000;

133   Shine and Sun, 2003; Luiselli and Akani, 2003; Hartmann et al., 2005; see also Greene, 1997),

134   indicating that only the very smallest primates are likely to be targeted as prey by venomous

135   snakes. Gaboon vipers (*Bitis gabonica*), the heaviest extant venomous snake, may sometimes

136   prey on slightly larger mammals (Greene, 1997), and there has been one observation of an

137   attempted predation on a ~ 3 kg juvenile cercopithecine monkey (Foerster, 2008; Foerster, pers.

138   comm.). In this latter case, the primate was too large for the predator to ingest (Foerster, 2008),

139   and systematic research indicates that the typical prey of these large vipers are considerably

140   smaller (Luiselli and Akani, 2003).

141   Body size may be of further importance in affecting how vulnerable a given species is to

142   being detected by snakes, but because snakes use a variety of methods to detect prey (Hartline,

143   1971; de Cock Buning 1984; Schwenk, 1995), it is not clear how this would be related to which

144   primates are more susceptible to predation. For instance, snakes can detect prey via heat sensing

145   (de Cock Buning, 1984), possibly making small primates more vulnerable to detection due to

146   their faster metabolic rate and surface to volume ratio (Fleagle, 1999). In contrast, a large

147   primate, which presumably would produce more vibrations, may be more detectable because

148   snakes can also detect prey through vibrations on the ground (Hartline, 1971).

149   This study tests whether the ability to detect snakes has been an important selective force

150   in the evolution of orbital convergence in primates by examining whether, independent of

151   phylogeny, orbital convergence among extant primates is associated with the extent of the shared

152   evolutionary history with snakes and whether those extant primates that are more vulnerable to

153   attacks by snakes have more convergent orbits than those that are less vulnerable. Specifically, if

154   the SDH is correct, it is predicted that orbital convergence will be highest in biogeographic areas

155   with the longest shared evolutionary history between primates and venomous snakes. Further,

156   orbital convergence should be higher in those species that live in low latitude, warm, and high

157   rainfall habitats, are characterized by small group sizes, have longer daily path lengths, and are

158   smaller in body size (Table 1) because these factors should increase the risk of snake attack faced

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159 by individuals of a particular species. In addition, Isbell (2006, 2009) hypothesized that more

160 enhanced color vision should be related to additional increases in orbital convergence to

161 compensate for a decreased ability to distinguish camouflaged objects (see also Morgan et al.,

162 1992). Therefore, there should be a significant relationship between color vision phenotype and

163 orbital convergence if the SDH holds true.

164

165 **Methods**

166 *Data sources*

167   All data used in this study were obtained from the published literature, supplemented in a

168 few cases with data from unpublished sources (see Table 2). Orbital convergence values were

169 taken from Ross (1995) (61 species) and Heesy (2005) (70 species). These two data sets were not

170 combined because the methods used by Ross produced lower values for species also measured

171 by Heesy (matched pairs t-test, p<0.01). Consequently, we conducted all analyses twice, once

172 with each data set.

173   We examined nine predictor variables that characterize the shared evolutionary history

174 with venomous snakes or are likely to influence visual system morphology and/or current risk of

175 mortality posed by snakes. For each primate species, we obtained data for: 1) biogeographic

176 region, 2) daily path length, 3) color vision type, 4) female body mass, 5) activity period, 6)

177 absolute value of the latitudinal midpoint of the geographic range, 7) mean temperature, 8) mean

178 rainfall, and 9) group size. In many cases, the predictor variables are averages across a number of

179 study sites, while climate data are the mean value across the entire geographic range of the

180 species. Such averages were deemed to be appropriate because the orbital convergence values

181 are also species means. Biogeographic region was treated as an ordinal variable related to the

182   duration of time primates have been sympatric with venomous snakes: 1) Madagascar, 2) the

183   Neotropics, 3) Africa and Asia (see Isbell, 2006, 2009). We coded activity period as an ordinal

184   variable: 1) nocturnal, 2) cathemeral, 3) diurnal. We did not make any specific predictions

185   regarding how this should affect orbital convergence based on the SDH, but included this

186   variable because the average light conditions during a species' active period is important in

187   shaping the visual system (e.g., Kirk, 2006). We coded color vision type as an ordinal variable:

188   1) monochromatic; 2) dichromatic; 3) polymorphic dichromatic-trichromatic; and 4) fully

189   trichromatic. Color vision data were obtained from Bradley and Mundy (2008), Tan and Li

190   (1999), and Surridge et al. (2003), except for *Avahi laniger* and *Eulemur coronatus.* The color

191   vision phenotype of these two species is uncertain, so we ran the analyses testing all possible

192   options. We found that whether these two species were scored as monochromatic, polymorphic,

193   or fully trichromatic had a negligible impact on our results. For the statistics presented below,

194   these species were scored as dichromatic, the presumed color vision type of most, particularly

195   nocturnal, lemur species (Tan and Li 1999). Finally, female mass was chosen over male mass

196   because female primates tend to be smaller than their male counterparts and should therefore

197   better represent the threat of snake predation a given species faces. Additional justification of the

198   predictor variables can be found in the Introduction.

199

200   *Statistical analyses*

201   First, we log transformed the dependent variables as well as female mass, latitude,

202   rainfall, temperature, and group size prior to analysis to better meet the assumptions of

203   parametric tests (Sokal and Rohlf, 1995). Next, we calculated phylogenetically independent

204   contrasts for each variable to account for the non-independence of data due to evolutionary

205 history (Felsenstein, 1985). To calculate contrasts, we used the PDAP module (Midford et al.,

206 2007) in Mesquite (Maddison and Maddison, 2007) and the primate phylogeny presented in

207 Bininda-Emonds et al. (2007). We set all branch lengths equal to one, as this branch length

208 designation best met the important assumption of independent contrasts analyses that there is no

209 relationship between the absolute values of the standardized contrasts and branch lengths

210 (Garland. et al., 1992).

211 We used two types of analyses to determine the best predictors of orbital convergence

212 across primates. First, we conducted a linear multiple regression including all predictor variables.

213 We examined the residuals from this analysis to identify potential outliers, which were defined

214 as samples with studentized residuals greater than 3 or less than -3, and/or Cook's distances near

215 or greater than 1 (Quinn and Keough, 2002). Because outliers can produce spurious results and

216 mask true biological patterns (e.g., Nunn and Barton, 2001; Kamilar, 2009), we removed them

217 from the initial dataset and re-ran the regression.

218 We also used the outlier-free dataset to determine the best combination of variables

219 predicting orbital convergence without overfitting the model. This is typically accomplished with

220 step-wise regression models, yet several authors have showed that these analyses are prone to

221 spurious results due to the order in which variables are entered into the model (Quinn and

222 Keough, 2002; Burnham and Anderson 2003). Instead, we implemented an information theoretic

223 approach, which has been increasingly popular in biology and physical anthropology (Towner

224 and Luttbeg, 2007; Kamilar and Paciulli, 2008; Kamilar et al. 2010). We used Akaike's

225 Information Criterion, with correction for small sample size (i.e., <40 samples per predictor

226 variable) (AICc) to determine the best models and variables that explain variation in primate

227 visual systems (Burnham and Anderson, 2003). AICc provides a measure of the likelihood of a

228   model given a particular dataset, while minimizing the model's assumptions (i.e., number of

229   predictor variables). Models within two AICc values of the "best" model are treated as equally

230   good at explaining the dependent dataset (Burnham and Anderson, 2003).

231   In addition, we calculated the AICc weight for each model, which is a measure of the

232   relative likelihood of each model being the best. We also calculated the sum of AICc weights for

233   each independent variable to assess their relative importance for predicting the dependent

234   variable (Burnham and Anderson, 2003). For example, if female body mass exhibited a score of

235   0.942, it would be about three times as likely to be an important variable compared to the rainfall

236   with a value of 0.296. This value is on a scale from 0 to 1, and is based on the frequency of the

237   predictor variable being entered into each possible model weighted by the model's ability to

238   explain the dependent variable.

239   The regression and AICc analyses were performed with Statistica and included a zero

240   intercept, which is a requirement of analyses using independent contrasts data (Garland et al.,

241   1992).

242   Finally, we used G*Power (Faul et al., 2009) to determine the detectable effect size of

243   our analyses using our two datasets. Given our sample size, the number of predictor variables,

244   and the two-tailed nature of our analyses, the test found that the Heesy dataset can detect an

245   effect size of 0.20 and the Ross dataset an effect size of 0.25. Consequently, our analyses should

246   be able to detect relatively small effect sizes.

247

248   **Results**

249   Our initial multiple regressions predicting orbital convergence produced significant

250   models using both datasets, yet they also contained an outlier contrast: *Cheirogaleus medius* vs.

251 *Phaner furcifer*. Our outlier-free analyses similarly produced statistically significant models

252 (Heesy dataset: r^2=0.313, p=0.005; Ross dataset: r^2=0.290, p=0.032) (Table 3). Using the full-

253 model multiple regressions we found that orbital convergence was best predicted by female mass

254 using the Heesy (Beta= 0.319, p=0.008) and Ross datasets (Beta= 0.261, p=0.063) (Table 3).

255 Larger species exhibited greater orbital convergence compared to small ones, independent of

256 other factors. Daily path length approached statistical significance using the Heesy dataset, with

257 species that travel shorter distances per day tending to have more convergent orbits than those

258 that travel greater distances (Beta= -0.208, p=0.079). Similarly, diurnal species tended to have

259 more convergent orbits compared to nocturnal species (p=0.092). The remaining variables,

260 including the extent of the shared history with venomous snakes, were weak predictors of orbital

261 convergence.

262 The information theoretic approach produced fairly similar results. We found nine

263 equivalently good models explaining orbital convergence using the Heesy data and 19 best

264 models using the Ross dataset (Tables 4 and 5). Female body mass was the only variable

265 appearing in all of the best models using the Heesy dataset and was found in 15 of the 16 best

266 models using the Ross dataset. Female mass exhibited the highest sum of AICc weight for each

267 dataset (Figure 1). Daily path length and color vision phenotype displayed moderately high

268 values using the Heesy dataset only. In addition, activity period exhibited a moderately high sum

269 of AICc weight for the Ross dataset only.

270

271 **Discussion**

272 The results of the current analysis do not support the hypothesis that predatory and

273 defensive attacks by snakes have been the primary selective force favoring the evolution of

274 stereoscopic vision through increasing orbital convergence in primates. Indeed, the basic premise

275 of the hypothesis, that those primates with a longer shared history with venomous snakes have

276 more convergent orbits (Isbell, 2006, 2009), was not supported. This is likely due in part to the

277 strong relationship between phylogeny and biogeography among primates, with many of the

278 major subclades being limited to particular biogeographic areas (Fleagle and Reed, 1996;

279 Kamilar, 2009), indicating that the relationship between biogeography and orbital convergence

280 may be better explained as phylogenetic differences than ecological differences between the

281 regions. Indeed, the African and Asian strepsirhines (galagos and lorises, respectively), which

282 are more closely related to Malagasy lemurs than to sympatric catarrhines, have orbital

283 convergence values which overlap completely with those of lemurs but are lower than those of

284 all catarrhines (Ross, 1995; Heesy, 2005; Table 2). The low degree of orbital convergence in

285 lorisiformes, despite having a shared evolutionary history with venomous snakes that is likely

286 identical to that of the catarrhines, seems to falsify the SDH (see also Wheeler, 2010).

287   The relationship between biogeography, exposure to venomous snakes, and the evolution

288 of stereoscopic vision is further confounded by the uncertainty of the shared evolutionary history

289 of some primates and venomous snakes (Wheeler, 2010). While the evidence is strong that the

290 African and Asian primates have had greater exposure to venomous snakes than have those in

291 Madagascar (reviewed in Isbell, 2006, 2009), it is difficult to ascertain the degree to which

292 platyrrhines have been exposed to venomous snakes during their evolutionary history.

293 Specifically, although the molecular evidence most parsimoniously places the last common

294 ancestor (LCA) of lancehead vipers in South America at 23 - 10 mya (Wüster et al., 2002, 2008),

295 the age of the LCA is best viewed as a minimum estimate for arrival, as stem members of this

296 clade could have been present in South America prior to the diversification of the crown clade,

297   as has been argued, for example, in New World monkeys (Hodgson et al., 2009). While the

298   evidence thus favors the idea that some degree of early platyrrhine evolution occurred in the

299   absence of venomous snakes, it is difficult to draw firm conclusions regarding whether or not

300   this is the case or how long that period might have been. Even more challenging is determining

301   whether the observed variation in the visual systems of crown platyrrhines, relative to

302   catarrhines, can be attributed to the fact that the former radiated in the absence of venomous

303   snakes (Isbell, 2006, 2009), as this radiation began only 23 to 17 mya (Schrago, 2007; Hodgson

304   et al., 2009).

305   In addition to the lack of a significant effect of biogeography on orbital convergence,

306   there was also no relationship between orbital convergence and the degree of risk that snakes

307   pose to extant primates; indeed, the trends were in the opposite direction than predicted by the

308   SDH in several cases. For example, both the multiple regressions and the AICc analyses

309   indicated that mean female body mass, together with activity period, were the most important

310   variables in predicting orbital convergence, although in the opposite direction than predicted:

311   species less likely to be targeted as prey by snakes (i.e., larger species) are characterized by *more*

312   convergent orbits. Similarly, although daily path length was not a significant predictor of orbital

313   convergence in either of the two datasets (but was the second most important variable in seven of

314   the eight AICc models conducted with the Heesy dataset), this variable showed a negative

315   relationship with orbital convergence independent of other factors, including phylogeny; thus,

316   those species that are likely to encounter snakes more frequently tend to have less convergent

317   orbits. Likewise, the relationship between orbital convergence and the likelihood of detecting or

318   deterring snakes before an attack (based on group size) was weak in both data sets. Finally,

319   support for the hypothesis that more enhanced color vision should be associated with further

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320 increases in orbital convergence to compensate for a decreased ability to distinguish

321 camouflaged objects (Isbell, 2006; 2009) was weak, being of secondary importance in the Heesy

322 dataset but only minor importance in the Ross dataset.

323   The variables which were consistently the most important predictors of orbital

324 convergence were body size and activity pattern. Although body size was predicted to have a

325 significant effect if orbital convergence evolved to make detecting snakes more efficient, the

326 effect was in the opposite direction than predicted because those primates more likely to be

327 targeted as prey by snakes (i.e., smaller species) were found to have less convergent orbits. The

328 relationship between orbital convergence and both body size and activity pattern is most likely

329 related to a negative allometric relationship between relative orbit size and orbital convergence

330 (Ross, 1995; see also Cartmill, 1972). A decrease in relative orbit size is argued to have evolved

331 in early anthropoids as the result of their evolution of diurnal habits from a nocturnal ancestor

332 (Ross 1995, 1996, 2000), a phenomenon which would be expected if that nocturnal ancestor had

333 also been a visual predator (Ross, 1996, 2000; Kirk, 2006), and to have decreased further as

334 anthropoids grew larger due to orbit size scaling with negative allometry against body size

335 (Martin, 1990; see also Ross, 1995, 1996). An allometric relationship between relative orbit size

336 and convergence may explain the observed differences in convergence between the major

337 primate clades: all catarrhines are diurnal and are on average larger than platyrrhines, which in

338 turn are on average larger than (extant) strepsirhines (Smith and Jungers, 1997), many of which

339 are nocturnal and thus have relatively large orbits (Kirk, 2006).

340   Simple allometry, however, cannot explain all the variation in orbital convergence within

341 or between clades: extant diurnal strepsirhines have less convergent orbits than similar-sized

342 diurnal anthropoids despite similarity in their relative orbit size (see Figure 1 in Kirk, 2006;

343 lorisids and some tarsiers have more convergent orbits than expected given their relatively large

344 eyes (a fact that could be used to argue in support either the nocturnal visual predation

345 hypothesis or the SDH: Ross, 1995; see also Nekaris, 2005); and papionins, apes, and

346 callitrichines (the latter likely being among the extant primates that are most vulnerable to

347 predation by snakes; Miller and Treves, 2011) have less convergent orbits than expected given

348 their relatively small orbits (Ross, 1995). Indeed, while the relationship between orbit size and

349 convergence is strong for primates as a whole and a number of primate sub-clades, the

350 relationship between these variables is non-significant among platyrrhines and is weak (but still

351 statistically significant) in catarrhine primates (Ross, 1995). These deviations from the general

352 trend are important because they demonstrate that allometry would not necessarily completely

353 limit the ability to evolve increased stereopsis if snakes were indeed an important selective force

354 in the evolution of the primate visual system. It is also important to note that the current analysis

355 included factors related to relative orbit size (i.e., body size and activity pattern; Kirk, 2006), but

356 even with these variables considered, neither historical biogeography nor the current risk posed

357 by snakes explained further variation in orbital convergence in primates.

358   With a lack of support for the SDH in the current analysis, the nocturnal visual predation

359 hypothesis remains the best supported hypothesis for the evolution of orbital convergence

360 (Heesy, 2008; 2009). While the current analysis falsifies the SDH's premise that the degree of

361 orbital convergence in extant primates is driven by their shared evolutionary history with

362 venomous snakes, one could still argue that a lack of support for the additional predictions does

363 not necessarily refute the SDH's explanation for orbital convergence, because snakes could be

364 responsible for the differences seen between the major primate clades without orbital

365 convergence tracking changes in the risk posed by snakes. However, there is no reason to suspect

366 that the selective pressures posited by the SDH to have acted on these more ancient nodes should

367 not have continued to exert pressure, although to various degrees on different taxa, depending on

368 the degree of threat that snakes have posed. If snakes have indeed been the major factor driving

369 the evolution of primate visual system diversity as proposed by Isbell (2006, 2009), then

370 distantly related taxa facing similarities in the threat posed by snakes should be expected to

371 independently evolve more convergent orbits. Indeed, such evolutionary convergences due to

372 similar ecological pressures are common in primate evolution (see Lockwood and Fleagle,

373 1999). That the observed trends in the current analysis were in many cases opposite to the

374 direction predicted indicates that snakes are exerting little, if any, selective pressures on orbital

375 convergence in extant taxa. The fact that those species least likely to be targeted as prey by

376 snakes (i.e., larger species) have significantly higher degrees of orbital convergence is perhaps

377 the strongest indication that some factor other than selective pressures posed by snakes is

378 responsible for the observed trends.

379 The current results may also be confounded by the fact that microhabitat use by both

380 snakes and primates will affect the rate in which the species encounter one another, but

381 limitations in the availability of such data do not allow for an analysis including these variables.

382 However, because the limited studies available indicate that venomous snake communities

383 include species that occupy a range of microhabitats within a given habitat, ranging from

384 terrestrial to the emergent canopy (e.g., Fitzgerald et al., 2002; see also Luiselli et al., 2005), it

385 seems likely that such a variable would have only a minimal effect on the results.

386 Although the current analysis does not indicate that the likelihood of either encountering

387 snakes or being targeted by snakes as prey has been the principal force underlying the evolution

388 of increased orbital convergence in primates, it seems very likely that an increased ability to

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389   detect snakes (as well as any other camouflaged object) visually is a likely consequence of an

390   increase in stereoscopic vision. Beyond the evolution of stereoscopy, the SDH also provides

391   potential explanations for the evolution of other aspects of the primate visual system, including a

392   number of neuroanatomical features (Isbell 2006, 2009), which may or may not stand up to

393   further scrutiny (Heesy, 2010), but which are nonetheless worthy of rigorous testing. Indeed, it

394   seems indisputable that snakes have exerted some, possibly strong, selective pressures on

395   primates, as evidenced by the fact that non-human primates typically perceive venomous snakes

396   as dangerous (e.g., Boinski, 1988; Range and Fischer, 2004; Ramakrishnan et al., 2005; Ouattara

397   et al., 2009), even among populations devoid of snake species that prey on primates (e.g., Barros

398   et al., 2002; Wheeler, 2008). Likewise, the high number of fatalities from snake bites in some

399   human populations (although normally in anthropogenically-altered areas; e.g., Chippaux, 1998;

400   Alirol et al., 2010) evinces the threat that venomous snakes can pose to even non-prey species.

401   Future field, captive, and comparative studies will likely yield additional insights into the

402   possible effect of snakes and other predators on the evolution of primate diversity.

403

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Figure captions

Fig. 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.