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

3
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21

22 **Abstract**

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

41

42 **Keywords:** binocularity, stereopsis, camouflage, predation, primate origins, anthropoid origins

43

44

45 **Introduction**

46 Primates are notable among mammals in terms of possessing a visual system characterized by
47 highly convergent (i.e., forward-facing) orbits and an associated expansion of visual brain
48 structures (Allman, 1977; Barton, 2004; Heesy, 2005, 2008). An increase in orbital convergence
49 leads to a large degree of binocularity (i.e., overlap of the visual fields of each eye), allowing for
50 stereoscopic vision (Heesy, 2004). Stereopsis in turn enhances the ability to perceive depth, but
51 primarily at close range (~ 1 m: see Cartmill, 1974; Ross, 2000; Heesy, 2009), and effectively
52 allows individuals to distinguish camouflaged objects from their background (see Pettigrew,
53 1986; Heesy, 2009). Adaptive explanations for these visual features have been subject to
54 considerable debate for the last several decades (reviewed in Ross and Martin, 2007), with
55 various authors arguing that stereoscopic vision was favored in early primates because of the
56 advantages it provided in nocturnal visual predation (Cartmill, 1992), acrobatic locomotion in an
57 arboreal environment (Martin, 1990; Crompton, 1995), or feeding on small fruits in low-light
58 conditions (Sussman, 1991).

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

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

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 (Schrage, 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

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

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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407

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648

649 **Figure captions**

650 **Fig. 1.** The importance of all independent variables for predicting orbital convergence based on
651 AICc weights. The sum of AICc weights for each independent variable is produced by summing
652 the Akaike weights across all models where the variable occurs. It is a relative measure of the
653 importance of each variable for predicting orbital convergence.