

1 The evolutionary origins of primate scleral coloration

2 Alex S. Mearing^{1*}, Judith M. Burkart², Jacob Dunn^{1,3,4}, Sally E. Street⁵ & Kathelijne Koops^{1,2}

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4 ¹Department of Archaeology, Fitzwilliam Street, University of Cambridge, Cambridge, CB2 1QH,
5 United Kingdom

6 ²Department of Anthropology, University of Zurich, Zurich, 8057, Switzerland

7 ³School of Life Sciences, Anglia Ruskin University, Cambridge, CB1 1PT, United Kingdom

8 ⁴Department of Cognitive Biology, University of Vienna, Vienna, 1090, Austria

9 ⁵Department of Anthropology, University of Durham, Durham, DH1 3LE, United Kingdom

10 *Corresponding author: A.S. Mearing (alexmearing@live.co.uk)

11

12 **Abstract**

13 Primate gaze following behaviors are of great interest to evolutionary scientists studying social
14 cognition. The ability of an organism to determine a conspecific's likely intentions from their gaze
15 direction may confer an advantage to individuals in a social group. This advantage could be
16 cooperative and/or competitive. Humans are unusual in possessing depigmented sclerae
17 whereas most other extant primates, including the closely related chimpanzee, possess dark
18 scleral pigment. The origins of divergent scleral morphologies are currently unclear, though
19 human white sclerae are often assumed to underlie our hyper-cooperative behaviors. Here, we
20 use phylogenetic generalized least squares (PGLS) analyses with previously generated species-
21 level scores of proactive prosociality, social tolerance (both n=15 primate species), and
22 conspecific lethal aggression (n=108 primate species) to provide the first quantitative,
23 comparative test of three complementary hypotheses. The cooperative eye [M. Tomasello, B.
24 Hare, H. Lehmann, J. Call, *J. Hum. Evol.* 52, 314–320 (2007)] and self-domestication [B. Hare,
25 *Annu. Rev. Psychol.* 68, 155-186 (2017)] explanations predict white sclerae to be associated with
26 cooperative, rather than competitive, environments. The gaze camouflage hypothesis [H.
27 Kobayashi, S. Kohshima, *J. Hum. Evol.* 40, 419-435 (2001)] predicts that dark scleral pigment
28 functions as gaze direction camouflage in competitive social environments. We show that white
29 sclerae in primates are associated with increased cooperative behaviors whereas dark sclerae
30 are associated with reduced cooperative behaviors and increased intra-specific lethal aggression.
31 Our results lend support to all three hypotheses of scleral evolution, suggesting that primate
32 scleral morphologies evolve in relation to variation in social environment.

33 **Main Text**

34

35 **Introduction**

36

37 The primate order contains a remarkable amount of variation in external ocular morphology
38 (**Figure 1**), including differences in scleral volume, width-height ratios and pigment profiles (1-7).
39 The former two measurements have been linked in phylogenetic comparative analyses to social
40 (i.e., group size and neocortex ratio), ecological (i.e., habitat use) and life history (i.e., body mass)
41 drivers (3). However, to our knowledge, no comparative quantitative study has yet examined the
42 relationship between ocular pigment and social behavior across primate species. Humans are
43 often considered to possess unique ocular configurations (1-3, 6-7). We possess especially large
44 width to height ratios, especially large scleral volumes (1-4) and white, depigmented sclerae (1-2,
45 5-7). Contrastingly, most non-human primate species (hereafter 'primates'), including the closely
46 related chimpanzee, instead synthesize dark scleral pigment (1-2, 6-7). Interestingly, the equally
47 closely related bonobo possesses sclerae of an intermediate average brightness between
48 humans and chimpanzees (5).

49

50 The 'cooperative eye hypothesis' (6), suggests that the human depigmented sclera functions to
51 facilitate hyper-cooperative behaviors (2, 6, 8) through, for example, the establishment of joint
52 attentional states. That is, the ability of two or more individuals to jointly focus on one object or
53 concept (6). A cooperation experiment, for example, found that participants who could view their
54 partner's gaze were better able to communicate referential meaning (about both the current and
55 required location of objects) than where their gazes were obscured (9). A white background may
56 signal iridal direction more conspicuously and in a manner that is more difficult to conceal than
57 would a dark background (6, 10). Other primates can also follow conspecific gaze direction (11-
58 14), but it is not yet clear whether they can follow gaze with a similar aptitude as humans. Only
59 humans, for example, prioritize the use of eye direction over head direction when following a
60 conspecific's gaze (7). Humans can also determine conspecific iridal direction from a distance of
61 up to 15 meters, though this may be partially mediated by the eyebrows (15). The cooperative
62 eye hypothesis proposes that both the unusually depigmented human sclera and the potentially
63 unusual sophistication of human gaze following could be associated with directional selection for
64 cooperation.

65

66 Alternatively, the 'self-domestication hypothesis' posits that white sclerae may be pigment-related
67 by-products associated with the human self-domestication process (7). Selection for tolerance
68 and against aggression is predicted to result in the reduction in number and migration velocity of
69 neural crest cells in early embryogenesis. This alteration may be responsible for domestication-
70 syndrome - a range of behavioral and morphological traits that co-emerge with docility (16).

71 Pigment-producing melanocytes are derived from neural crest cells, so the reduction of
72 melanocytes in a pale sclera (7) is potentially explicable as a correlated by-product of selection
73 for social tolerance rather than as an explicitly functional adaptation.

74

75 The hypotheses describe above focus on the evolution of the human ocular morphology and the
76 supposed uniqueness of human white sclerae. However, gaze cues are used widely in the
77 primate order (e.g., gaze following or aversion; 11-14, 17). The 'gaze camouflage hypothesis',
78 proposes that dark scleral pigment in primates may function as gaze direction camouflage from
79 competitive conspecifics and predators (2). The ability to observe a conspecific's gaze direction
80 and, using that information and context, to learn about the emotional and/or intentional state of
81 others may be a useful skill for organisms living within a social group (18-19). However, the act of
82 observing another's gaze direction may produce a source of information conflict. For instance,
83 although it may be useful to third-party onlookers to receive social information (intentionally
84 signaled or otherwise) as to one's emotional and/or intentional states, it is not necessarily
85 advantageous to the individual themselves to be sharing such information indiscriminately since
86 this could be adversely utilized by competitors. For example, an experiment has been reported in
87 which the location of food is revealed to a chimpanzee (witness), with another chimpanzee
88 (witness-of-witness) unable to see the food's location but able to observe the witness. The
89 witness, potentially aware of having been observed, repeatedly misled the witness-of-witness by
90 leading him to empty containers (20). Similarly, chimpanzees have been observed to avert their
91 gaze from a high value food item if they, alone, are knowledgeable about its location and are in
92 the presence of a dominant conspecific (17). These examples illustrate that communicating one's
93 visual direction conspicuously and/or indiscriminately may not always be an optimal social
94 strategy.

95

96 Here, we utilize the remarkable diversity of primate ocular morphologies to provide the first
97 quantitative, comparative investigation of the role of sociality in primate scleral color evolution.
98 We compare scleral brightness with three behavioral measures: 'proactive prosociality', 'social
99 tolerance', and 'conspecific lethal violence'. Prosociality refers to any behavior which benefits
100 another organism but where the originator does not benefit themselves (21). Prosociality can be
101 reactive, e.g., in response to help-calls or subtle coercion (22), or proactive, that is, unsolicited
102 (21). In humans, our heightened prosociality is considered to have facilitated the emergence of
103 interdependent groups (23) as well as cumulative culture and technology (8). A previous report
104 found the degree of allomaternal care to best predict observed patterns of proactive prosociality
105 in primates, suggesting that increased prosocial tendencies may emerge with cooperative
106 breeding systems (8). Social tolerance, that is, the tolerance towards groupmates and their

107 interests, is not prosocial, but equally is also non-competitive. Meanwhile, competitive behaviors
108 such as lethal violence are often similarly adaptive social strategies (24) as they may relate to
109 territory or resource control (25) and can be flexible and coalitionary in format (26). These three
110 measures enable the examination of the evolutionary role of scleral pigment across different
111 social environment. Proactive prosociality is indicative of highly cooperative environments, social
112 tolerance represents a behavior of intermediate social value and, by contrast, conspecific lethal
113 violence is indicative of highly competitive social environments.

114

115 Under the gaze camouflage hypothesis, we therefore predict heightened conspecific lethal
116 aggression to predict darker sclerae, and for dark sclerae to be likewise associated with low
117 values of proactive prosociality and social tolerance. Both the cooperative eye hypothesis
118 (directional selection) and the self-domestication hypothesis (correlated by-product) predict white
119 sclerae to be associated with heightened proactive prosociality, although the self-domestication
120 hypothesis explains the presence of prosociality as a correlated by-product of selection for social
121 tolerance (8, 27-28). Hence, an association between scleral brightness and proactive prosociality,
122 but not social tolerance, could be taken as evidence against the self-domestication hypothesis.

123

124 **Results**

125

126 **Proactive Prosociality**

127

128 Log (Scleral brightness) was significantly positively associated with sqrt (proactive prosociality)
129 scores across the 15 primate species. Where lambda was taken at its maximum likelihood
130 ($\lambda_{ML}=0$), a statistically significant relationship was observed ($p= < 0.001$, $R^2=0.711$,
131 estimate=0.085, $t=5.66$; **Figure 2**). Similarly, where lambda was assumed to equal 1, a highly
132 conservative comparison, the statistically significant relationship was still observed ($p= < 0.001$,
133 $R^2=0.723$, estimate=0.083, $t=5.83$).

134

135 **Social Tolerance**

136 Scleral brightness was significantly positively associated with social tolerance scores across the
137 15 primate species. Where lambda equals its maximum likelihood ($\lambda_{ML}=0$), a significant
138 relationship was observed ($p=0.047$, $R^2=0.269$, estimate=90.58, $t=2.19$; **Figure 3**). Likewise,
139 where weighted by lambda=1, the positive association between scleral brightness and social
140 tolerance is still statistically significant ($p=0.03$, $R^2=0.314$, estimate=95.57, $t=2.44$).

141

142 **Conspecific Lethal Violence**

143 A significant negative association was observed across the 108 primate species between log
144 (scleral brightness) and sqrt (conspecific lethal violence). Where lambda was taken at its

145 maximum likelihood ($\lambda_{ML}=0.698$), a statistically significant observation was observed ($p < 0.001$,
146 $R^2=0.118$, estimate=-0.088, $t=-3.77$; **Figure 4**). Similarly, where lambda was assumed to equal 1,
147 a statistically significantly relationship was still observed ($p < 0.001$, $R^2=0.306$, estimate=-0.144,
148 $t=-6.84$).

149

150 **Discussion**

151

152 Our findings provide broad support for all three hypotheses tested: the gaze camouflage,
153 cooperative eye and self-domestication hypotheses. We show that scleral pigmentation varies
154 with differences in social behaviors between species of extant primates. Proactive prosociality, an
155 experimentally derived measure of the degree to which individuals were willing to help their
156 groupmates with no possibility of directly benefitting themselves, was associated with significantly
157 increased scleral brightness (white sclerae being depigmented). Social tolerance, a measure of
158 the evenness of the distribution of food items in the same species, was also associated with
159 increased scleral brightness, though based on p-values and coefficients of determination (R^2)
160 appears to be a weaker predictor than proactive prosociality. Scleral brightness was significantly
161 negatively associated with the percentage of deaths attributable to conspecific lethal aggression.

162

163 The presence of scleral pigmentation is likely to be a functional adaptation, rather than a product
164 of random drift, due to the metabolic cost incurred in synthesizing dark pigment (2, 7). That the
165 extent of conspecific lethal violence negatively predicts scleral brightness (i.e., predicts darker,
166 more pigmented sclerae), may indicate that scleral pigment functions as a mechanism of gaze
167 camouflage to conspecifics and/or predators (2). Chimpanzees, who are considered more
168 reactively aggressive and less cooperative than humans and bonobos (7, 27), and who likewise
169 possess significantly darker sclerae (5), have been shown to use visual concealment (29) and
170 gaze aversion (17) when engaged in food competition. The presence of pigment could confer an
171 advantage in terms of concealing gaze direction from groupmates and/or predators (though the
172 latter was not tested here) in a competitive context (2). The fact that we have observed this
173 relationship across the primate order is consistent with the conclusion that gaze following
174 behaviors are widespread beyond the immediate hominid family (12).

175

176 Similarly, the presence of increased scleral brightness could also be adaptive – a position
177 consistent with the cooperative eye hypothesis. Our results indicate that increased scleral
178 brightness is associated with increased cooperative behaviors and reduced lethal violence. This
179 finding is consistent with several previous studies. For example, a previous report found the
180 degree of allomaternal care to best predict variation in proactive prosociality, arguing that this
181 behavior may emerge with cooperative breeding systems (8). Additionally, alloparental care

182 frequencies have been linked to neural control of facial musculature in primates (30), suggesting
183 that the proper conveyance of non-verbal signals is of increased importance in cooperative
184 breeding species. Furthermore, common marmosets (*Callithrix jacchus*), but not capuchin (*Cebus*
185 *apella*) or tonkean monkeys (*Macaca tonkeana*), have been shown to share direct gaze when
186 working on cooperative tasks that may be ambiguous (31-32). Of interest, these studies are also
187 consistent with our finding that the four brightest species' sclerae across our sample are found
188 among humans and cooperative breeders: common marmosets (*Callithrix jacchus*), Goeldi's
189 marmosets (*Callimico goeldii*), humans and cotton-top tamarins (*Saguinus oedipus*). This finding
190 is contrary to a commonly held belief that white sclerae are a uniquely human morphology (1-2, 6-
191 7).

192

193 Alternatively, it may be that white sclera simply represent the absence of pigment which is
194 synthesized only for use in competitive environments or, alternatively, could be by-products
195 associated with self-domestication processes (7, 28). The self-domestication hypothesis predicts
196 that selection for social tolerance, and against aggression, may generate prosocial behavior as a
197 correlated by-product (27-28). Therefore, our finding that social tolerance, in addition to proactive
198 prosociality, significantly predicts scleral brightness is consistent with the self-domestication
199 perspective. However, we therefore cannot differentiate between self-domestication and
200 cooperative eye explanations at this time. Furthermore, these may not be mutually exclusive
201 perspectives. It could be, as an example, that white sclerae originated as a correlated by-product
202 of self-domestication processes but subsequently became the subject of directional selection,
203 thereby increasing fitness, as neural bases for social cue recognition have developed around this
204 morphology (see 33).

205

206 These results provide a potential function and/or origin of divergent scleral morphologies and
207 affirm that differences in scleral morphology are associated with differences in species' social
208 behavior. Recently, an investigation using relative measures (i.e., producing a ratio of the
209 brightness contrast between the iris and sclera) found humans, bonobos and chimpanzees to
210 have comparable, not distinct, gaze conspicuousness, despite their different scleral morphologies
211 (5). This methodology, however, produces contrast ratios which may not be appropriate for large
212 scale comparisons and which do not account for the physical properties of visible light that may
213 bias the naturalistic perception of shade (34). Our results refute these findings and show that
214 differences in primate scleral colorations are explicable with divergent social behaviors, indicating
215 that the naturalistic perception of shade cannot be adequately captured with relative
216 methodologies alone (34).

217

218 The sample sizes for the behavioral measures proactive prosociality and social tolerance may be
219 considered small (both $n=15$). However, both represent the high amount of labor, hours and
220 logistics required to experimentally extract these data (8). These behavioral data enable a deeper
221 analysis than the use of common sociality proxies such as social group size. For example, many
222 species, such as humans, chimpanzees and bonobos, live in large social groups (3) but differ
223 widely in the social behaviors that are associated with ocular morphologies (7; 27). The use of
224 such species-level behavioral proxies are therefore more appropriate, though the smaller sample
225 size (and the use of different species within datasets) does exclude the possibility of multiple
226 regression techniques. Likewise, the use of conspecific lethal violence data (35) acts as a useful
227 indicator of a species' aggressiveness. That said, the original compilation method did not
228 separate between inter- and intra-group aggression, infanticide or maternal abandonment,
229 behaviors that likely have different neural and functional bases (27) and which may exert different
230 influences on scleral morphology. This may explain the weaker model fit in the conspecific lethal
231 violence regression.

232

233 A limitation relates to the lighting properties of online photographs. Quantitative analyses of color
234 from digital photographs often require photographs to be taken in controlled settings and/or with
235 the use of a color standard for calibration (36). This is not possible when analyzing existing,
236 uncalibrated photographs, however, this is less relevant when exclusively analyzing brightness
237 rather than the additional hue and saturation values that comprise the full perception of color
238 (rather than shade alone) from digital sources (34, 37). Although the ambient brightness of the
239 photo represents a minor source of unaccounted variation, this is mitigated by the use of multiple
240 distinct photos per species (minimum 6) with the majority of photos (97.6%) containing both eyes
241 per individual for further average calculations. In this respect, we follow a previously established
242 data collection methodology (5, 37). Furthermore, this approach, rather than a laboratory-based
243 analysis, relates more closely to the naturalistic perception of ocular morphologies by onlookers
244 since primates will continue to interact with conspecifics across a range of locations and times
245 with different ambient shades. Hence, this enables more ecologically valid testing of the function
246 of sclerae in relation to social interactions and allows us to examine a much larger dataset than
247 would otherwise be possible.

248

249 In sum, we provide the first quantitative comparative analysis of the relationship between
250 primate ocular pigment and social behavior. Human white eyes have long been a mystery by
251 comparison to the dark scleral phenotypes observed among primates. Here, we show that pale
252 scleral color is associated with cooperation whereas dark scleral color is associated with reduced
253 cooperation and increased lethal aggression in extant primates. This refutes the recent notion

254 that gaze conspicuousness be considered comparable, not distinct, between humans and *Pan*
255 and lends support to the cooperative eye, self-domestication and gaze camouflage hypotheses of
256 eye-behavior co-evolution.

257

258 **Materials and Methods**

259

260 We obtained species-level scores of proactive prosociality and social tolerance across 15 extant
261 primate species from (8). Full methodological details can be found with the original paper. In brief,
262 the authors used a group service apparatus (38) to measure proactive prosociality and social
263 tolerance. Captive primates were habituated to the apparatus and taught the function of an
264 accessible lever which moved a board containing food into reach. Food was placed on the board
265 in two positions - one where the individual pulling the lever could reach the food themselves and
266 another where the individual pulling the lever could not reach the food themselves, but could
267 make the food accessible to their group-mates. The resultant data are comparable between
268 groups and species due to the standardization of this procedure. Proactive prosociality measured
269 how many items of food an individual made available to their groupmates that they themselves
270 could not access. Social tolerance was quantified where the board was in a fixed position with the
271 food accessible and repeatedly replenished (35 times) as it was eaten. The authors then
272 measured the evenness of the distribution of food items within the group to produce social
273 tolerance scores. Lastly, conspecific lethal aggression was scored as the percentage of deaths
274 per species (study populations are taken to be representative of each species) that were
275 attributable to conspecific lethal aggression obtained from published data for 108 extant primate
276 species (35).

277

278 We collected primate facial images from an online google image search completed in February
279 2021 and which used the common species name and the word “face” as key words. Some
280 chimpanzee and bonobo images were collected from a previous study (5) and the Royal Burgers’
281 Zoo, Netherlands. Human images are public domain and were collected from the Pexels.com
282 database using the key words “man”, “woman”, “face” and “eyes”. We then analyzed scleral
283 brightness using ImageJ 1.x (39). Images were selected from this search to ensure the resolution
284 of the external eye was of sufficient quality, that the eyes were unobscured by other objects and
285 that there was no apparent photo manipulation present. Images were converted to greyscale
286 such that the value of each pixel varied from 0 (black) to 255 (white) with intermediate scores
287 being corresponding shades of grey. We then extracted scleral brightness values following
288 existing techniques (5, 37). We collected values from within a rectangular selection area placed
289 on the visible sclera for each eye per photo. A minimum of six photos were collected per species,
290 although it is not known whether these represent six distinct individuals in all cases. We then

291 calculated the median pixel value per selection area (due to the potential for outliers such as poor
292 lighting, camera quality or light reflections) and the mean value per individual (i.e., mean of both
293 eyes/selection areas), and subsequently the mean scleral brightness value per species. Of the
294 944 total facial photos, 21 (2.2%) presented with a cranial angle from which only 1 eye was
295 clearly visible. In these few cases, the one accessible eye was taken to be representative of the
296 scleral brightness of that individual. Species which were documented by (35), but for which
297 insufficient number or quality of facial photos was available from online materials or which were
298 not uniquely represented in the GenBank taxonomy were not included in analyses but are listed
299 (see supplementary **Table S1**).

300

301 Phylogenetic generalized least squares analysis (PGLS) was completed in R version 4.0.3. (40)
302 using the 'caper' package version 1.0.1. (41). A consensus phylogeny with branch lengths
303 proportional to time (i.e., a chronogram) was generated and pruned for use from 10ktrees.com
304 version 3 (42) and used the GenBank taxonomy (43). Variables were log transformed where
305 residuals were non-normally distributed or to improve linearity. Where a variable contained zero-
306 values, it was instead square root transformed as, unlike with log transformations, this does not
307 require the input of an arbitrary constant which influences goodness-of-fit (44). Diagnostic plots
308 including Q-Q, density and fitted and residual value plots were generated and inspected using the
309 'plot.pgls' function in the 'caper' package (41). Residual normality was further established using
310 Shapiro-Wilk tests on model residuals. The significance value (i.e., alpha) is placed at 0.05. We
311 estimated phylogenetic signal in PGLS analyses using Pagel's λ , which indicates the degree to
312 which the co-variance in model residuals is proportional to shared evolutionary history between
313 species, assuming a Brownian motion model of evolutionary change over time (45-46). λ varies
314 from 0 to 1, where 0 indicates that species are independent of one another and 1 the maximum
315 level of phylogenetic signal, i.e., that co-variances are directly proportional to shared evolutionary
316 history (45-46). Estimates of the maximum likelihood of lambda were subject to wide confidence
317 intervals, a limitation increasingly common with reduced sample sizes (47) (likelihood profiles with
318 confidence intervals are given in supplementary materials; **figures S1-S3**). For this reason, and
319 to present a full picture of results, two result statements are provided per statistical test: one
320 where lambda is assumed to equal its maximum likelihood (λ_{ML}) and one where lambda is taken
321 to equal 1 (the strictest phylogenetic control). The latter approach is highly conservative as higher
322 phylogenetic control typically reduces the significance of independent variables (48).

323

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325

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440 Figures and Tables

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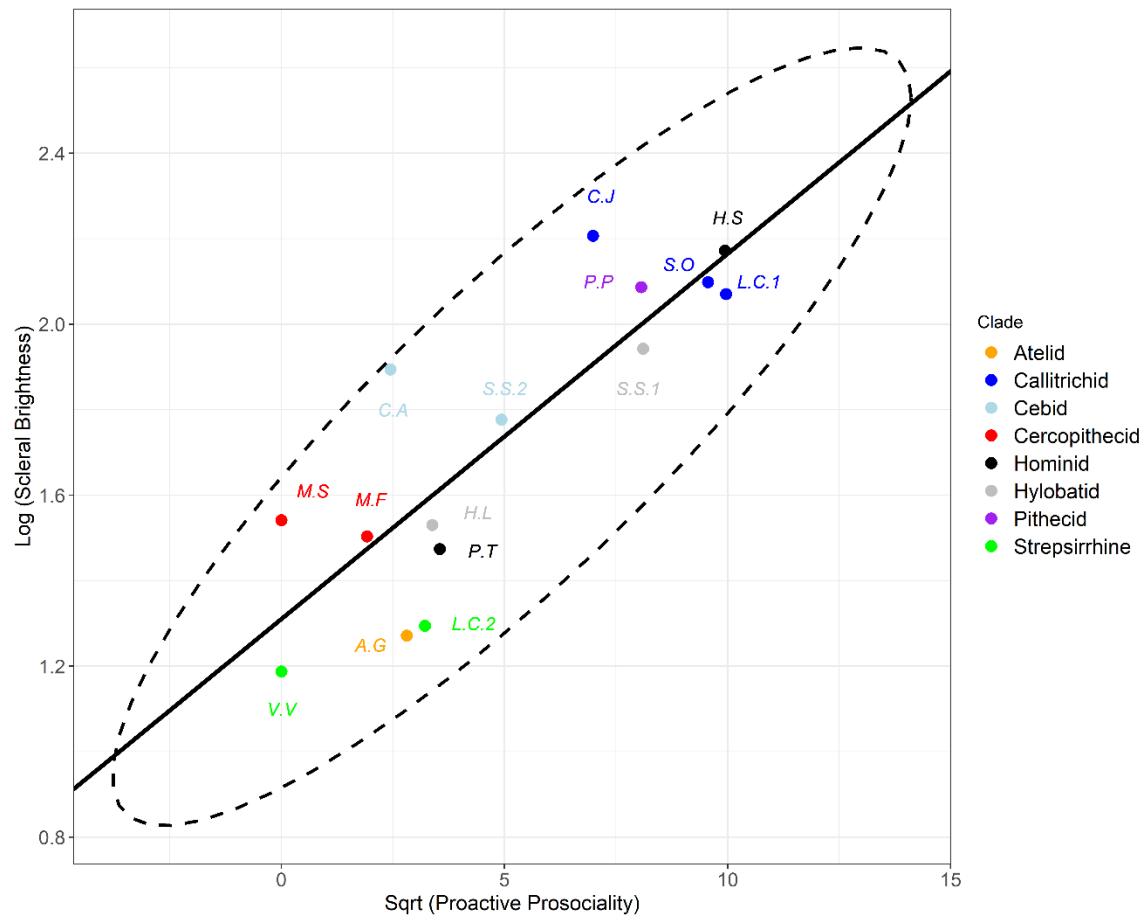


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444 **Figure 1.** Ocular diversity in the primate order. All photos under creative commons license unless
445 otherwise specified. *H. lar* credit to user: MatthiasKabel
446 (https://commons.wikimedia.org/wiki/Hylobatidae#/media/File:Hylobates_lar_pair_of_white_and_black_02.jpg). *T. obscurus* credit to Lip Kee Yap
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448 Michael Gäbler ([https://en.m.wikipedia.org/wiki/File:Saguinus_oedipus_\(Linnaeus,_1758\).jpg](https://en.m.wikipedia.org/wiki/File:Saguinus_oedipus_(Linnaeus,_1758).jpg)). *P.*
449 *pithecia* credit to Hans Hillewaert
450 (https://en.wikipedia.org/wiki/Pitheciidae#/media/File:Pithecia_pithecia.jpg). *H. sapiens* photo is in
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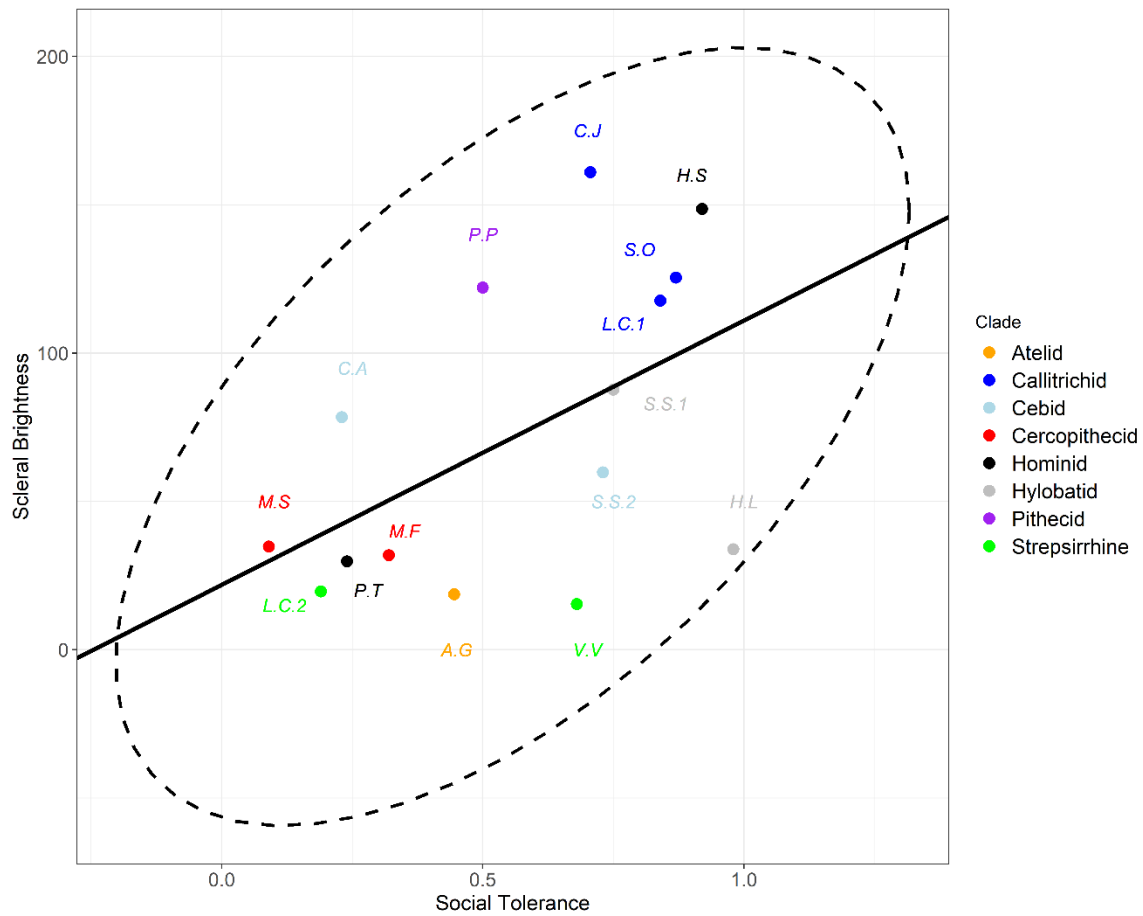
452 *the public domain, credit to Fernanda Latronica (<https://www.pexels.com/photo/close-up->*
453 *photography-of-bearded-man-713520/)*. *P. troglodytes* photo provided by the Royal Burgers' Zoo,
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455 (https://commons.wikimedia.org/wiki/File:Bonobos_11yr_male_3yr_male_grin_Twycross.jpg)
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Figure 2. PGLS regression plot comparing log (scleral brightness) with sqrt (proactive prosociality) with in $n=15$ primate species. Confidence ellipse computed to 95% confidence. CJ = *Callithrix jacchus*; HS = *Homo sapiens*; SO = *Saguinus oedipus*; LC1 = *Leontopithecus chrysomelas*; PP = *Pithecia pithecia*; SS1 = *Symphalangus syndactylus*; SS2 = *Saimiri sciureus*; CA = *Cebus apella*; MS = *Macaca silenus*; MF = *Macaca fuscata*; HL = *Hylobates lar*; PT = *Pan troglodytes*; LC2 = *Lemur catta*; AG = *Ateles geoffroyi*; VV = *Varecia variegata*.

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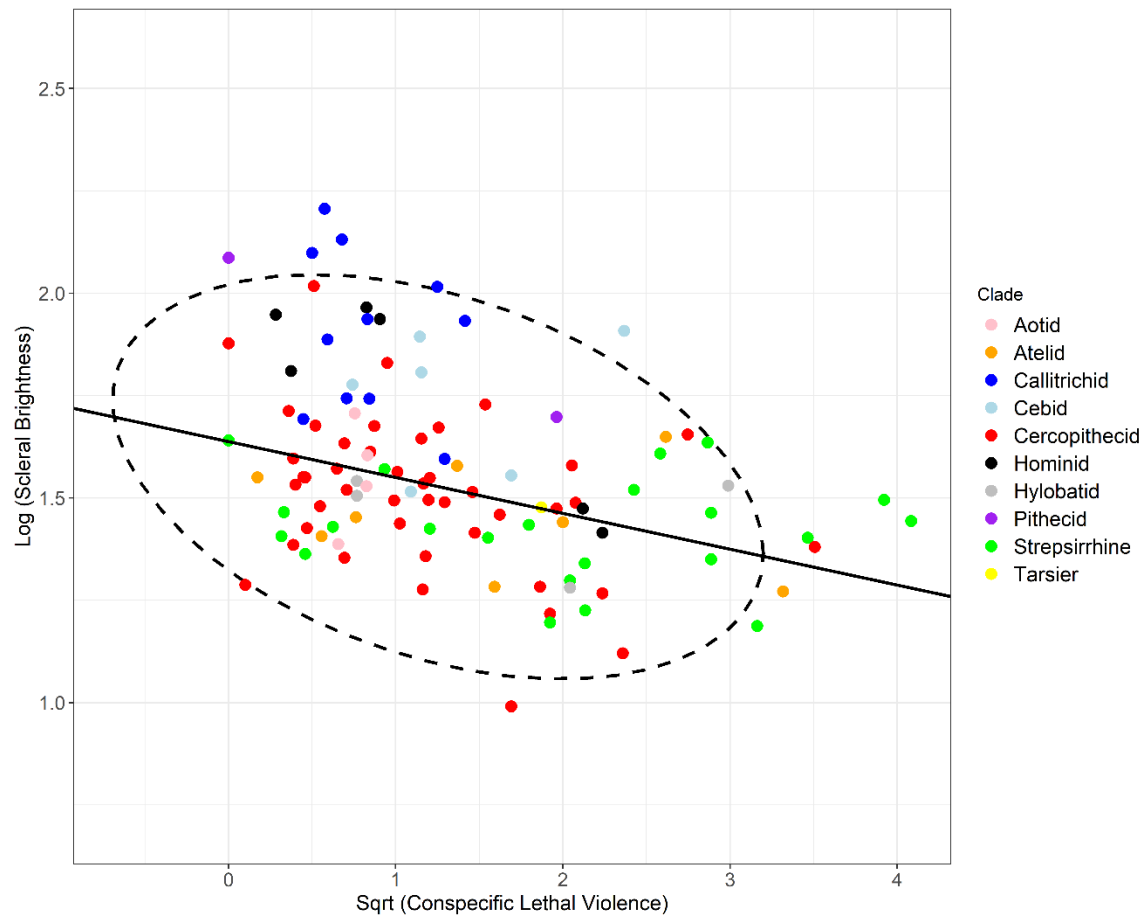
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Figure 3. PGLS regression plot comparing scleral brightness with social tolerance scores in $n=15$ primate species. Confidence ellipse computed to 95% confidence. C.J = *Callithrix jacchus*; H.S = *Homo sapiens*; S.O = *Saguinus oedipus*; LC1 = *Leontopithecus chrysomelas*; PP = *Pithecia pithecia*; SS1 = *Symphalangus syndactylus*; SS2 = *Saimiri sciureus*; CA = *Cebus apella*; MS = *Macaca silenus*; MF = *Macaca fuscata*; HL = *Hylobates lar*; PT = *Pan troglodytes*; LC2 = *Lemur catta*; AG = *Ateles geoffroyi*; VV = *Varecia variegata*.

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Figure 4. PGLS regression plot comparing *log (scleral brightness)* with *sqrt (conspecific lethal violence)*. That is, the percentage of deaths due to conspecific lethal violence in $n=108$ primate species. Confidence ellipse computed to 95% confidence indicating bivariate outliers.