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1   **Developmental transitions in body color in chacma baboon infants:**

2   **implications to estimate age and developmental pace**

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22   **ABSTRACT**

23   **Objectives:** In many primates, one of the most noticeable morphological developmental traits

24   is the transition from natal fur and skin color to adult coloration. Studying the chronology and

25   average age at such color transitions can be an easy and non-invasive method to (i) estimate the

26 age of infants whose dates of birth were not observed, and (ii) detect inter-individual differences

27 in the pace of development for infants with known birth dates.

28 **Materials and Methods**: Using a combination of photographs and field observations from 73

29 infant chacma baboons (*Papio ursinus*) of known ages, we (1) scored the skin color of six

30 different body parts from pink to grey, as well as the color of the fur from black to grey, (2)

31 validated our method of age estimation using photographic and field observations on an

32 independent subset of 22 infants with known date of birth, and (3) investigated ecological,

33 social and individual determinants of age-related variation in skin and fur color.

34 **Results**: Our results show that transitions in skin color can be used to age infant chacma

35 baboons less than seven months old with accuracy (median number of days between actual and

36 estimated age = 10, range=0-86). We also reveal that food availability during the mother's

37 pregnancy, but not during lactation, affects infant color-for-age and therefore acts as a predictor

38 of developmental pace.

39 **Discussion:** This study highlights the potential of monitoring within- and between-infant

40 variation in color to estimate age when age is unknown, and developmental pace when age is

41 known.

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43 *Keywords: ageing method, primate, inter-individual variation, food availability*

44

45 **INTRODUCTION**

46 The relationship between age and physical maturation has been a major topic of interest in

47 behavioral and evolutionary ecology. Across species, different developmental paces shed light

48 on between-species life-history variations (Sibly, Grady, Venditti, & Brown, 2014). For

49 example, primates, including humans, have longer periods of lactation, associated with slower

50 postnatal growth and smaller litter size compared to other mammals of similar sizes (Dufour &

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51   Sauther, 2002). Across populations and individuals of a same species, variation in infant

52   developmental pace can have important fitness consequences on later survival and future

53   reproduction (Lindström, 1999) as well as on maternal reproductive success, via a trade-off

54   balancing investment in current versus future progeny (Lee, Majluf, & Gordon, 1991;

55   Maestripieri, 2002; Trivers, 1972).

56   Developmental pace may vary in relation to various environmental, social, maternal and

57   individual traits. Specifically, and as for all mammals, the quantity and quality of milk represent

58   a primary influence on infant growth trajectory (Lee, 1996). For example, a positive impact of

59   exclusive breastfeeding in the first 3-5 months of life on growth rates is observed among

60   children in Bangladesh (Arifeen, Black, Caul, Antelman, & Baqui, 2001). In non-human

61   primates, food availability between conception and weaning is an important source of variation

62   in developmental pace, which is likely mediated by maternal condition for young infants who

63   do not yet feed independently (Lee, 1996). As a result, the seasonal timing of birth, as well as

64   maternal traits that may affect the nutritional status of mothers, may affect growth and

65   development (Lee, 1996; Lummaa, 2003; Vandeleest & Capitanio, 2012). For example, in

66   hierarchical societies, dominant females often have a better access to food, which may lead to

67   higher reproductive rates and faster offspring development (Clutton-Brock & Huchard, 2013;

68   Stockley & Bro-Jørgensen, 2011). Individual traits, like infant sex, may also impact the

69   developmental pace of sexually dimorphic primates (Lonsdorf, 2017). Finally, selective

70   pressures such as predation risk (Coslovsky & Richner, 2011; Fontaine & Martin, 2006),

71   infanticide risk (Bădescu et al., 2016) or group size (Borries, Larney, Lu, Ossi, & Koenig, 2008)

72   may further impact developmental trajectories, depending on the species considered.

73   In more than 30% of primate species, one of the most noticeable and widespread

74   morphological developmental traits is the transition from natal fur and skin color to adult

75   coloration (Ross & Regan, 2000; Treves, 1997). Neonatal fur coloration may have evolved to

76   promote allomaternal care, infant attraction and protection by other group members, or in

77   response to infanticide risk (Ross & Regan, 2000; Treves, 1997). Even if the ultimate function

78   of neonatal fur color remains unclear (Hrdy, 1976; Treves, 1997), careful monitoring of such

79   developmental transitions at the individual level could have at least two important applications.

80   First, if the age at which such transitions occur does not vary excessively across individuals, it

81   can be an easy and non-invasive method to estimate individual ages in transitional infants for

82   whom the date of birth is unknown (Altmann & Altmann, 1981). Such a method relies on the

83   detailed description of age-related changes in body coloration for a cohort of infants of known

84   ages. This approach, which can be applied using observational data only, has significant

85   advantages over many other common methods, such as body weight or dental eruption patterns,

86   which rely on invasive measurements (Hohn, 2009; Morris, 1972).

87   Second, for infants of known ages, inter-individual differences in the age of color

88   transitions may reflect broader individual variation in developmental pace, if they correlate with

89   physical growth or other indicators of behavioral development, such as social, feeding and

90   locomotor development, or the temporal dynamics of the mother-offspring relationship

91   (Barthold, Fichtel, & Kappeler, 2009; Treves, 1997). Few studies have investigated such

92   correlations. Across species, the loss of natal pelage of 138 primate species is partially

93   correlated with the temporal dynamics of mother-offspring spatial proximity, i.e. this color

94   change begins around the period when the infant spends a considerable amount of time (25%)

95   out of the mother's arm-reach (Treves, 1997). Within species, the transition from natal to adult

96   fur coincides with advanced physical independence, such as independent locomotion and

97   feeding on solid food as is the case in red-fronted lemurs (*Eulemur fulvus rufus*) (Barthold et

98   al., 2009). In such cases, recording infant color changes at particular ages may represent one

99   easy way to quantify individual differences in developmental pace, and an early-life indicator

100   of weaning age, which is a crucial life history trait affecting maternal fitness.

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101   Baboons are among the most studied of the non-human primates, but our ability to

102   estimate infant age and our understanding of the determinants of infant developmental pace in

103   this species are still limited. Little work has been done to estimate infant age based on color

104   transitions since two seminal papers on yellow baboons (*Papio cynocephalus*) forty years ago

105   (Altmann & Altmann 1981; Rasmussen 1979) - although a short preliminary study has also

106   been published on chacma baboons (*Papio ursinus*) (Whitehead, Henzi, & Piper, 1990). These

107   studies report that the fur and skin of infants of both species show different coloration compared

108   to adults. When they are born, the fur is black and the exposed skin on the face, ears, hands,

109   and feet are pink, and they gradually acquire the physical traits of adults, grey skin and dark

110   grey fur for chacma baboons (yellow fur for yellow baboons) in their first year of life. This

111   transition may operate following a specific chronology, with some parts of the body turning

112   grey before others (Altmann & Altmann, 1981). However, those studies have only described

113   the chronology of the color transitions, while the accuracy of a method based on such transitions

114   to estimate infant ages has never been assessed.

115   More is known about developmental pace in baboons, but few studies have focused on

116   the specific pace of developmental transitions in coloration. High levels of individual variation

117   can be seen across various indicators of development including changes in fur and skin color,

118   as well as in growth rate and behavioral development, with some infants maturing faster than

119   others (Altmann 1980; Altmann and Alberts 2005; Altmann and Altmann 1981; Johnson 2003).

120   Food availability in the environment is a major factor influencing individual variation in growth

121   rate (Altmann & Alberts, 2005). The timing of the birth in the annual cycle could thus impact

122   infant developmental pace, as seasonal variation in food availability largely occur across

123   tropical Africa (Feng, Porporato, & Rodriguez-Iturbe, 2013). Moreover, maternal traits are also

124   known to affect baboon infant development: yellow baboon infants of dominant females have

125   faster growth rates and reach sexual maturity earlier than those of subordinates (Alberts &

126 Altmann, 1995; Altmann & Alberts, 2005; Charpentier, Tung, Altmann, & Alberts, 2008). In

127 this same population, offspring of multiparous females are larger for their age than offspring of

128 primiparous females (Altmann & Alberts, 2005). Overall, while the determinants of individual

129 variation in growth trajectories have already been explored, less is known about color

130 transitions in baboons. Examining such variation may contribute to a better understanding of

131 processes affecting growth and physical maturation, and changes in the color of certain body

132 parts could be used as indicators of developmental pace in baboon species.

133 Using the skin and fur coloration of wild infant chacma baboons, we first characterize

134 in detail the temporal sequence of physical maturation from natal to adult-like coloration to

135 compare the chronology of these coloration transitions with other baboon populations and

136 species. Second, we assess the accuracy of the developed method by using these dates of

137 coloration transitions to estimate the ages of infants, and comparing age estimates with their

138 known birth dates. We then examine the main determinants of individual variation in body color

139 transitions for a cohort of infants of known ages, focusing on the influence of ecological factors

140 (food availability during pregnancy and early lactation, timing of infant birth in the annual

141 cycle), maternal traits (rank and parity) and individual traits (sex) on the age at transitions.

142

Material and Methods

1   Study site

145 Data were taken by different field observers each year between 2005 and 2019 from three

146 habituated groups of chacma baboons (J and L since 2005, and M, a fission of group J, since

147 2016) living in Tsaobis Nature Park (22°23S, 15°44'50E). Chacma baboons at the Tsaobis

148 Baboon Project live in a semi-arid region of Namibia, on the edge of the Namib Desert. Annual

149 rainfall is low and variable which leads to relatively low, and highly unpredictable food

150 availability (Cowlishaw & Davies, 1997). Nonetheless, rainfall occurs most years, and peaks

151   between January and April, resulting in an annual food peak of variable intensity and duration

152   from February to May. The groups were followed daily on foot from dawn to dusk, allowing

153   observers to collect a variety of demographic, life-history, behavioral and group spatial data.

154   Each group member was known individually through ear notches and identifying marks, and

155   each new birth in a group was recorded. Reproductive states of adult females were recorded

156   every day in the field, and they were classified as: (i) pregnant, where pregnancy was

157   determined *post hoc* following infant birth, and encompassed the six months between the

158   conceptive cycle and the birth; (ii) lactating, for the period from infant birth until the resumption

159   of cycling; and (iii) cycling, including both swollen females (i.e., sexually receptive with a

160   perineal swelling) and non-swollen females between two swelling phases. Groups were not

161   followed year-round, and each year a field season of variable length was conducted

162   (median=126 days, range: 57-240 days).

163

164   *2   Ecological and individual traits*

165   To investigate the determinants of individual variation in physical development, we considered

166   both ecological and individual traits. We estimated food availability with the normalized

167   difference vegetation index (NDVI). This measure has previously been used as a proxy of food

168   availability in our population (Baniel, Cowlishaw, & Huchard, 2018) and other baboon

169   populations (Zinner, Peí Aez, & Torkler, 2001). We extracted the mean NDVI per 16-day

170   period on a 500 m resolution from 2004 until 2019 on the NASA website (MOD13A1 product)

171   (Didan, Barreto Munoz, Solano, & Huete, 2015) within the home ranges of the three habituated

172   groups. Using the GPS locations recorded every 30 minutes by the observers during daily group

173   follows, between 2005 and 2019, we computed 100% isopleth home ranges for our three groups

174   separately using kernel density estimates ('kernelUD' function, h set to 'href') implemented in

175   the adehabitatHR package (Calenge, 2006). We then computed a daily NDVI value for each

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176   group on its given home range using a linear interpolation between two known NDVI values of

177   16 days-intervals.

178   The social rank of adult females was established each year for each group separately using

179   *ad libitum* and focal observations of dyadic agonistic interactions (supplants, displacements,

180   threats, chases and physical attacks). We computed a linear hierarchy among adult females

181   using Matman 1.1.4 (Noldus Information Technology, 2013), and then calculated a relative

182   rank for each female controlling for group sizes. This relative rank was computed using the

183   formula $(N-r)/(N-1)$, where N was the number of adult females in the group in a given year, and

184   r was the absolute rank of the female (ranging from 1 to N, 1 being the most dominant).

185   Although adult females' ranks are relatively stable through time, individuals' relative ranks

186   change as females enter and leave the hierarchy through maturation and death, respectively.

187   Each female was assigned one relative rank per year, ranging from 0 (for the lowest ranking

188   female) to 1 (for the highest-ranking), as hierarchy is inherited and stable for female baboons.

189   For analyses of infant development, we considered the mother's rank during the year her infant

190   was born.

191   The mother's parity was assigned using long-term life-history data. Females were

192   considered primiparous between the birth of their first and second infant, and multiparous after

193   the birth of their second infant.

194

195   *3   Infant color scoring*

196   Infant coloration was scored using photographs and direct field observations. An observation,

197   which could be either from a photograph or from the field, was a set of scores of different body

198   parts on a given day for a given infant baboon. We used photographs opportunistically taken

199   by field observers between 2005 and 2018 of infant baboons aged between 0-19 months old

200   (N=255 pictures of 109 infants in total, median=2 pictures per individual, range: 1-11 pictures

201 per individual). We discarded photographs when luminosity or quality were too poor to give a

202 color score. In addition, in 2018 and 2019, infant baboons were scored every two weeks using

203 direct field observations, until they finally turned completely grey. We obtained 158 field

204 observations on 28 infants in this way, i.e. with no photograph (median=5.5 observations per

205 individual, range: 1-10 observations per individual). Infant baboons were scored on

206 photographs by one observer (Author 2), and in the field by one observer (Author 1). We

207 determined the inter-individual consistency of scores by scoring independently the same set of

208 60 pictures, and compared score similarity with the intra-class correlation coefficient for each

209 body part (Koo & Li, 2016). To do so, we computed intra-class coefficient looking at the

210 absolute agreement of a single-fixed rater with a two-way mixed models, using the ICC function

211 of the 'psych' package in R (Revelle, 2020). The scoring reliability was excellent for each body

212 part (mean ± SD, ICC = 0.92 ± 0.06, see also Table S1 of the Supporting Information). Thus,

213 in total, we scored coloration for 134 infants between 2005 and 2019.

214   In addition to determining the color of the fur covering the whole body, we scored the skin

215 color of the following body parts: ears, eye contours, hands and feet, muzzle, muzzle tip, and

216 ischial callosities (see Figure 1 for locations of these body parts). For each body part, we

217 attributed a score between 1 and 5 following previous work (Altmann & Altmann, 1981;

218 Rasmussen, 1979), such that 1 is fully pink, 2 is distinctively pinker than grey, 3 is a mixture

219 of pink and grey, 4 is distinctively greyer than pink, and 5 is fully grey (Figure 2). For the fur,

220 1 is fully black, 3 is a mixture of black to grey, and 5 is fully grey; we did not use scores 2 and

221 4 because the color transition for the fur is less obvious than for other body parts (Figure 2).

222 We scored all the body parts that were visible in each photograph. The data that support the

223 findings   of   this   study   are   openly   available   in   Mendeley   data:

224 http://dx.doi.org/10.17632/65vk9tck25.1.

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226 ### *4   Accuracy of age estimations based on fur and skin coloration*

227 To describe the physical transition in fur and skin coloration and further test whether it is a

228 reliable method to estimate the age of an infant, we focused on scores from a sample of 73

229 infants of known age, that is, whose date of birth was known with a maximum uncertainty of

230 10 days. These dates of birth were determined from having been present on either the day of

231 birth (51 infants, hereafter called Sample 1) or the day of conception (22 infants, called Sample

232 2). The conception day was identified as the exact day of deturgescence of the sexual swelling

233 in the conceptive cycle, which was the cycle followed by a pregnancy and by no other cycle.

234 We then estimated the dates of birth of these 22 infants by adding 190 days to the conception

235 date, based on the fact that the mean gestation length is 190 days at Tsaobis with little variability

236 (range: 181-200 days, SD = 5, N = 13 pregnancies where both conception and birth were

237 observed). We considered only baboons aged less than 8 months, as older baboons, from 8 to

238 19 months old, were all fully grey. We thus restricted our dataset to this Cohort 1, comprising

239 242 observations from 73 infants: 148 photographs on 59 infants and 94 field observations on

240 16 infants (including 2 infants that were both photographed and observed in the field in 2018).

241 Specifically, we obtained 238 scores for ears, 201 for eye contours, 238 for fur, 203 for hands

242 and feet, 239 for muzzle, 91 for muzzle tip and 143 for ischial callosities.

243   To determine the body parts that showed the most reliable timing in color transition to

244 predict ages, we computed a correlation matrix using the Spearman's rank correlation

245 coefficient between infant age (in months) and color scores for each body part of individuals in

246 Cohort 1. We also examined pairwise correlation coefficients between the different coloration

247 scores to determine whether some body parts provided redundant information because they

248 changed color at the same age. It is important to note that the dataset used to generate these

249 correlations is pseudoreplicated to some extent given that some individuals contribute multiple

250 observations. These correlation coefficients are nevertheless useful to compare values across

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251 body parts, but should be interpreted with caution to evaluate the statistical significance of any

252 single correlation.

253   To determine the accuracy of coloration scoring as an estimate of infants' ages, we

254 computed the difference between the actual known age and the estimated age of another,

255 independent subset of 70 observations on 22 infants. To do so, we divided our Cohort 1 in two

256 sub-samples, namely Sample 1, including 172 observations of 51 infants with precisely known

257 dates of birth (less than 10 days of uncertainty), and Sample 2, including 70 observations on 22

258 infants (with exactly 10 days of uncertainty on their date of birth, since it had been inferred

259 from conception date). We use Sample 1 as the reference for age estimation at color transitions,

260 and Sample 2 to validate our method on a fully independent sample.

261   With Sample 1, we first conducted a principal component analysis (PCA) taking into

262 account the color scores of the seven body parts considered, using the function 'PCA' of the

263 'FactoMineR' package (Husson, Josse, Le, & Maintainer, 2020). We had a considerable

264 number of missing values in our dataset as it was generally impossible to score all body parts

265 from a single picture. To conduct a PCA with missing values, we performed imputations to

266 complete the dataset using the 'imputPCA' function of the 'missMDA' package (Josse &

267 Husson, 2016), which uses an iterative algorithm taking into account similarities between

268 observations, as well as relationships between the scores of different body parts. The first

269 dimension of the PCA (PC1) explained 86.6% of the variance of the color scores (versus 8.8%

270 for the second dimension), and was the only PC retained for downstream analyses. We then

271 investigated the relationship between PC1 and infant age (in days). To do so, we compared

272 several linear models, all with PC1 as response variable, and containing as fixed effects a

273 polynomial function of age modelled with variable degrees (from 1 to 8). We selected the best

274 model of this subset as the one minimizing the Akaike Information Criterium (AIC), and a

275 polynomial function of age of degree 4 was retained in our model.

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276   Next, we followed four steps to quantify the accuracy of age estimation from Sample 2.

277   First, we estimated the missing values of the Sample 2 dataset on color scores using the method

278   described above ('missMDA' package) (Josse & Husson, 2016). Second, we predicted the

279   values of PC1 using the color scores of the seven body parts, using the 'predict.PCA' function

280   of the 'FactoMineR' package, that took into account the PC1 values computed from Sample 1

281   (Husson et al., 2020). Third, we used the linear model (that was computed on Sample 1) to

282   calculate one age estimate for each of these predicted values of PC1, i.e. for each observation

283   of Sample 2. More precisely, we used the 'uniroot' function in R to solve the equation of 4

284   degrees linking each PC1 value with infant age. Fourth, we computed the absolute difference,

285   in days, between the actual known age (± five days of uncertainty) and this estimated age to

286   quantify the accuracy of our method of age estimation.

287   In order to investigate the effect of the number of body parts that were scored on the

288   accuracy of our age estimates, as well as which body part was the most informative in this

289   context, we repeated this process with a variable number of body parts. From the seven body

290   parts initially considered, we first removed the fur scores from Samples 1 and 2, as the scores

291   of this body part had the lowest correlation with PC1. We then repeated this process by

292   progressively removing one body part at a time, based on the relative values of the correlation

293   between PC1 and the raw scores of that body part, removing first those parts for which scores

294   were least correlated to PC1. Chronologically, we first removed fur, followed by hands and

295   feet, ischial callosities, muzzle and eye contours. Our last round of analyses contained only

296   scores from ears and muzzle tip.

297   We also tested whether the 5-level scale for color scores produced more accurate age

298   estimations than a simpler 3-level scale with the following levels: (1) pink (score 1 in our 5-

299   level scale), (2) transitional (pooling scores 2, 3, 4 in our 5-level scale), (3) grey (score 5 in our

300   5-level scale). Using only one score instead of three for transitional colors can facilitate data

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301 collection in the field, and be less subjective across observers. We then repeated the same

302 processes described for Samples 1 and 2, to quantify the accuracy of the age estimation under

303 a 3-level scale of color scores for different number of body parts considered.

304   We also tested the effect of the number of observations per individual on the accuracy of

305 age estimates. In Sample 2, there were 70 observations from 22 infants (range = 1-8, median=2

306 observations per infant). For all infants with more than one observation, we computed one

307 estimated birth date by averaging the different birth date estimates from each observation. We

308 then computed the difference, in days, between the actual and estimated birth dates as an

309 indicator of estimation accuracy to compare the accuracy of age estimates obtained from a

310 variable number observations of a given infant.

311   Moreover, we investigated the potential effects of the actual age of an infant on the accuracy

312 of age estimations per observation, to test whether the accuracy of our age estimates may

313 decrease for older juveniles. To do so, we ran a linear mixed model, with the accuracy of age

314 estimates per observation (i.e. the absolute number of days between actual age and estimated

315 age) as a response variable, the actual age as the only fixed effect, and infant identity as the

316 only random effect (to control for repeated observations). For this analysis, we used all

317 observations available from Sample 1, for all 7 body parts scored on a 5-level scale.

318   Finally, we were interested in quantifying the effects of observation types, i.e. field or

319 photographic observations, on the accuracy of age estimation per observation. To do so, we ran

320 a linear mixed model, with the accuracy of age estimates per observation as a response variable,

321 the observation type as the only fixed effect, and infant identity as the only random effect (to

322 control for repeated observations). For this analysis, we used all observations available from

323 Sample 1, for all 7 body parts scored on a 5-level scale to estimate ages of Sample 2 (Sample 2

324 contained 38 field observations from 5 infants and 32 photographic observations from 17

325 infants).

13

326

5   *Determinants of individual variation in the pace of color changes*

328   To identify the main determinants of developmental pace, we used 242 observations from the

329   full sample of 73 infants with known ages (Cohort 1), and ran general additive mixed models

330   (GAMMs). We first computed a weighted mean color score for each observation, where the

331   score of each body part was given a different weight depending on its correlation with infant

332   age (see above). More precisely, we attributed less weight to body parts that were less correlated

333   with age by dividing their color score by their correlation coefficient, on the basis that the

334   developmental pace of these body parts was less variable across individuals for a given age,

335   and so presumably less affected by environmental and individual factors. We thus obtained a

336   general score of color development across all body parts for a given observation. Our response

337   variable was the weighted mean color score per observation (continuous variable).

338   GAMMs allow to fit non-linear relationships between the response variable and one or

339   more fixed effect(s), using thin plate splines (Wood, 2003). We first determined the best model

340   describing the age effect on mean color scores, with the identity of infant set as random effect

341   to take into account the lack of independence between multiple observations of a same

342   individual. To do so, we compared GAMMs containing either (1) a simple, continuous effect

343   of age; (2) age modelled as a polynomial of degree 2; (3) a polynomial of degree 3; or (4) age

344   modelled using a thin plate regression spline. We selected the best model as the one minimizing

345   the Akaike Information Criterium (AIC). We found that the age modelled using a thin plate

346   regression spline was retained in all our models (See Table S2 in the Supporting Information

347   for model selection on the weighted mean color score response variable for an example). We

348   then ran our global GAMMs, with age modelled with a spline, infant identity as random effect,

349   and including the following additional fixed effects:

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350   *- Food availability during infant growth.* We expected infants whose gestation and birth

351   occurred during periods of high food availability to develop faster for their age (Altmann &

352   Alberts, 2005; Johnson, 2003). To test which time period of infant development (prenatal

353   versus postnatal) was most sensitive to variations in food availability, we investigated the

354   effects of both food availability during pregnancy (approximated by the mean NDVI daily

355   values between conception and birth date for a given infant) and early lactation (approximated

356   by the mean NDVI daily values between birth and observation date for a given infant). As these

357   two indicators of food availability were highly correlated (Pearson correlation = 0.39,

358   confidence interval: [0.28; 0.49], t=6.58, P-value$<10^{-4}$), leading to collinearity, we included

359   them separately in two different models.

360   *- Date of birth.* We expected infants born at particular times of the year to develop more

361   quickly. The NDVI is only a partial proxy of food availability, and other components of

362   seasonal variation that are not necessarily captured by NDVI (such as temperature, photoperiod,

363   or particular plant phenologies) may further affect developmental pace. As a given date in the

364   annual cycle is a circular variable (at least when considering environmental seasonality), we

365   used a sine fixed effect expressed as follows to introduce the infant's date of birth, converted

366   in radians, into our multivariate linear model: $\sin{(Infant's\ date\ of\ birth + \varphi)}$

367   Where φ is the phase value. We changed the phase value φ (to 0, $\pi/6$, $\pi/3$, $\pi/2$, $2*\pi/3$, $5*\pi/6$) to

368   account for potential phase shifts across the year, i.e. to consider all the months of the year as

369   possible birth months maximizing faster development. For example, a positive effect of the sine

370   phase of $\pi/6$ would maximize February, and a negative effect will maximize August. We ran

371   sequentially six different multivariate models (GAMMs with the six different phase values)

372   containing all other fixed effects, and we selected the best phase as the one minimizing the AIC

373   (which is $\pi/3$ for the weighted mean color score model).

15

374   -   *Mother's dominance rank*. We expected infants from dominant females to develop more

375   quickly, following studies on other aspects of baboon developmental pace (Altmann & Alberts,

376   2005; Cheney et al., 2004; S. Johnson, 2003).

377   - *Mother's parity*. We expected infants from primiparous mothers to develop more

378   slowly, following studies on other aspects of baboon developmental pace (Altmann & Alberts,

379   2005).

380   - *Infant sex*. We did not expect any sex difference in the pace of early morphological

381   development, following studies on other aspects of baboon developmental pace (Altmann &

382   Alberts, 2005; Altmann & Altmann, 1981; Johnson & Kapsalis, 1995). Nevertheless, we

383   included this variable to control for potential unexpected sex differences.

384   - *Group identity,* to control for possible differences between social groups.

385   We further considered each body part separately (seven models) to test whether the same

386   determinants affected all body parts or only some of them, and to evaluate which body parts

387   were most sensitive to ecological, individual and maternal traits. Here, our response variables

388   were the scores of one given body part, and were coded as ordinal, with five categories for each

389   body part (except for the fur, with only three categories). We ran all the GAMMs using the

390   'gam' function of the 'mgcv' package (Wood, 2003), in R version 3.5.0 (R Core Team, 2018).

391   Ordinal response variables for each body part were specified with the family 'ocat' of the

392   'mgcv' package (Wood, 2003). We computed parameter estimates for each fixed effect, with

393   Wald statistic tests (X^2) and P-values associated. For smooth effects, we computed the effective

394   degrees of freedom, with the Wald statistic test and the P-value. We considered an effect to be

395   significant when its P-value was < 0.05. We were also interested in quantifying the importance

396   of inter-individual variation in developmental pace, and so tested the significance of the random

397   intercept, looking similarly at its P-value. For each model, we also checked graphically the

398   normality of the residuals' distribution and the accuracy of the number of knots used for the

399 age thin plate spine (this parameter constrains the 'wiggliness' of the smooth, i.e. the number

400 of bow points in the fitted curve) (Wood, 2003) using the 'gam.check' function of the 'mgcv'

401 package (Wood, 2019). Graphical representations were made using the 'mgcViz' package

402 (Fasiolo, Nedellec, Goude, & Wood, 2018).

403

RESULTS

405 **1   Characterization of fur and skin color changes in chacma baboon infants**

406 All results associated with the characterization of fur and skin color changes in relation to age

407 are summarized in Figure 3. All baboons were fully grey (i.e., at all body parts) after 8 months

408 of age, with similar fur and skin coloration as adults. The fur, muzzle or hands and feet were

409 the first body parts to turn grey, on average between 1 and 2 months of age. Hands and feet, as

410 well as the muzzle, started to transition around 1 month old until becoming fully grey at approx.

411 4 months of age. Ears started to turn grey after 2 months and were totally grey by 5 months.

412 The last body parts to change color were the eye contours, the ischial callosities, and the tip of

413 the muzzle, which started to transition at approx. 3 months of age, and finished after 5 months.

414 The qualitative chronology of the transition was apparent in the correlation matrix (Table 1):

415 hands and feet scores were highly correlated with muzzle scores, and eye contours scores were

416 highly correlated with muzzle tip scores. Nonetheless, the order in which body parts change

417 color was not always consistent across individuals. For some infants, we observed ears turning

418 grey before muzzles and hands, or ischial callosities turning grey before the muzzle tip and ears.

419 Overall, a chacma baboon infant with entirely pink skin and black fur was almost always

420 younger than 2 months old, as at least the hands and feet started to turn grey after this age. An

421 infant with entirely grey skin and fur was at least 4 months old, as no infant was observed with

422 a grey tip of the muzzle before this age. Finally, a transitional infant was aged between 1 and 6

423 months old.

424

2   Accuracy of age estimates based on color scores

426 The color scores were strongly correlated with the known ages of infants for all body parts,

427 though correlation coefficients were slightly lower for the fur and the ischial callosities (Table

428 1). This means that the scores of these two body parts produce less precise age estimates,

429 probably due to higher inter-individual variation in the age of transition of these parts compared

430 to others. For example, a 3-month-old baboon could exhibit the full range of colors for ischial

431 callosities, from fully pink to fully grey; and a 1-month-old baboon could exhibit a fully black

432 or a fully grey fur (Figure 3).

433   In order to test the accuracy of infant body coloration as a method of age estimation, we

434 computed a composite score (using PCA) from 172 observations of all body parts from 51

435 infants of known ages (births observed, Sample 1), and then predicted this composite score to

436 estimate ages on an independent sample of 70 observations from 22 infants of known ages

437 (Sample 2). We obtained a median difference of 12 days between the actual age and the

438 estimated age using 70 observations, 7 body parts and a 5-level scale of color scores (Table 2).

439 We also investigated the effects of the number of body parts considered, and the number of

440 levels of the color scale. Decreasing the number of body parts considered only slightly

441 decreased the accuracy of age estimates (Table 2), and the same conclusion applied for using a

442 3-level color scale instead of a 5-level one – though using a 3-level scale in combination with

443 few body parts decreased accuracy more substantially (Table 2). Our best age estimations per

444 observation were computed when considering the skin across all 6 body parts but excluding the

445 fur, and using a 5-level color scale (absolute number of days of between actual and estimated

446 ages: median = 10.7, range = 0.1–86.4). We also investigated the effect of the number of

447 observations per infant on the accuracy of age estimates: the more observations, the more

448 accurate were the estimates (Figure S1, Supporting Information). Finally, the accuracy of age

449   estimates significantly decreased with age ($X^2 = 10.0$, P-value $= 1.54 \times 10^{-3}$) (Figure S2,

450   Supporting Information), and were lower for photographic compared to field observations

451   (Figure S3, Supporting information), albeit the latter effect did not reach significance ($X^2 =$

452   3.63, P-value =0.06).

453

454   **3   Determinants of individual variations in the pace of color changes**

455   Finally, we investigated the determinants of inter-individual variations in age-related color

456   scores, looking at ecological (food availability during pregnancy or during early-lactation, birth

457   timing), maternal (parity, rank) and individual (sex) predictors using GAMMs controlling for

458   age with a spline regression (Figure 4). The model explained 93% of the variation in the

459   weighted mean color scores. We detected significant inter-individual differences in mean color

460   scores (Table 3), and in most body parts (except for the muzzle tips, for which we had fewer

461   infants scored compared to other parts, see Table S3 in Supporting Information). Our index of

462   food availability during pregnancy influenced the weighted mean color score (controlled for

463   age): infants turned grey earlier considering all their body parts together when food during

464   pregnancy was abundant (Table 3, Figure 5). In contrast food availability during lactation did

465   not (Table S4, Supporting Information). We did not detect any effect of maternal (rank and

466   parity) nor individual (birth date and sex) traits on variation in infant mean color scores

467   controlled for age (Table 3). Looking at individual variation in color transitions for each body

468   part separately, we found a positive effect of food availability during pregnancy on the score of

469   ischial callosities only (Table S3, Supporting Information). We also found a positive effect of

470   the timing of birth on the scores of muzzle tips (maximizing scores for infants born in

471   December-January) but not for other body parts (Table S3, Supporting Information). We did

472   not detect any effect of food availability during lactation, maternal traits, i.e. maternal rank and

473   parity, on variation in infant color for any body part (Table S3, Supporting Information).

474

DISCUSSION

476 Our purpose in this study was twofold: (1) to assess how well infant chacma baboons with

477 unknown ages can be aged on the basis of their skin and fur color, and (2) to explore potential

478 environmental, maternal, and individual predictors of variation in the pace of infant color

479 development for infants with known ages. The age estimates obtained using infant color scores

480 were generally accurate (median number of days between actual age and estimate age per

481 observations = 10, range=0-86 days). All the tools required for estimating ages in a chacma

482 baboon population are provided in this paper. Figures 1 and 2 can be used to score baboon

483 coloration directly in the field (or using photographs), and the methods section details how the

484 first dimension of a composite score (using PCA), derived from these color scores, can be

485 computed to estimate ages. Various recommendations can be made to improve the accuracy of

486 age estimates:

487   1. Use the color scores from all body parts except fur, as age estimates were most accurate

488   with this configuration. However, decreasing the number of body parts considered does

489   not decrease the accuracy of age estimations dramatically. For example, considering

490   only two body parts (ears and muzzle tip) instead of six reduces the accuracy of age

491   estimations by only 4.5 days. Nonetheless, such a result may vary across primate

492   species, and one should establish the relevant body parts to be considered in different

493   species.

494   2. Score the same individual repeatedly, as an infant with 8 observations had a birth date

495   estimation error of 5 days in average, compared to more than 30 days for infants with

496   only a single observation. Ideally, infants should be scored as early as possible (as

497   accuracy decreases as infants age) and regularly until it turns fully grey.

498   3. Prioritize field observations. Photographic evidence can be less accurate because color

499   scores may be influenced by fluctuating light conditions. If necessary, photographic

500   approaches should exploit multiple high-resolution photographs of the same individual

501   on a given day at different times and angles to control for light variation.

502   4. Consider using a 3-level color scale, which is slightly less accurate than a 5-level scale

503   but also more practical, and may maximize inter-observer reliability. However, such

504   choice depends on the trade-off between the accuracy targeted and the conditions of

505   data collection (e.g., single versus multiple observers).

506   In addition, this study opens the possibility of a similar application for machine learning where

507   an algorithm could predict the age of an infant based on pictures, as long as a large set of high-

508   quality pictures (see recommendation #3) of known-age individuals is available to initialize the

509   algorithm. This relatively recent method is based on mathematical and statistical approaches

510   through which computers can 'learn' from data to then make predictions. Such methods have

511   been used in a wide range of field applications, and are becoming increasingly common (Al-

512   Jarrah, Yoo, Muhaidat, Karagiannidis, & Taha, 2015).

513   Changes in the pigmentation of infants' ears and muzzles at Tsaobis follow a similar pattern

514   to that observed in another population of wild chacma baboon living in Mkuzi Game Reserve

515   (South Africa), with an onset of grey coloration appearing around 1-2 months, and the full

516   transition completed around 4-6 months of age (Whitehead et al., 1990). Our detailed

517   characterization of the age at which fur and skin turn grey indicates that infant chacma baboons'

518   coloration develops faster than yellow baboons (Altmann & Altmann, 1981; Rasmussen, 1979).

519   Whilst chacma baboon infants have all turned grey by 8 months of age, most yellow baboon

520   infants are still in the transition phase at this age, and only exhibit adult color around 12 to 14

521   months of age, depending on the population (Altmann & Altmann, 1981; Rasmussen, 1979). In

522   addition, in contrast to yellow baboons, the order in which body parts change color was not

523   always consistent across individuals in this study. Discrepancies observed in the age and

524   chronology of transition between baboon species highlight that such patterns are species-

525   specific, and that the methodology presented here should be developed and validated separately

526   for each species.

527   Inter-individual variation in the rate of maturation was high for each body part considered

528   in this study, as found in yellow baboons (Altmann & Altmann, 1981; Rasmussen, 1979).

529   Specifically, the change in fur color was a less accurate indicator of age, as fur turned grey

530   relatively early and showed marked individual variation. Failure to derive accurate age

531   estimates remains non-negligible (we had a maximum of 86 days difference between actual and

532   estimated age when relying on 6 body parts), due to the existence of outlier individuals with

533   very fast or slow development. This suggests that, whilst this method of age estimation is not

534   perfect, infant coloration can provide a simple and non-invasive proxy to detect individual

535   variation in developmental pace on a semi-quantitative scale. Nevertheless, despite their utility

536   for tracking other developmental factors (Barthold et al., 2009; Treves, 1997), studies linking

537   age-related changes in color to other indicators of developmental pace are very rare in baboons.

538   Only one study on Amboseli yellow baboons recorded that late changes in paracallosal skin

539   color can be seen as a first sign of developmental abnormality, being followed by delayed

540   maturation, locomotor disability and finally death (Altmann & Altmann, 1981).

541   Regarding the determinants of individual variations in color-for-age considering all body

542   parts together, we found that higher food availability during pregnancy, but not during early-

543   lactation, accelerated the transition towards adult coloration. In line with this, infant yellow

544   baboons from a food-enhanced group grew more rapidly than individuals from wild-foraging

545   groups (Altmann & Alberts, 2005). Similarly, in Phayre's leaf monkeys (*Trachypithecus*

546   *phayrea*) infants in larger groups transitioned from natal to adult fur color later, suggesting that

547   food competition affects infant color maturation and development (Borries et al., 2008). Here,

22

548we distinguished pre-natal from post-natal food availability, and our results emphasize the

549importance of maternal condition during pregnancy for infant post-natal color development. In

550capital breeders like baboons or humans, females can store energy to use it later, and conception

551likelihood generally peaks during periods of high food availability to increase the success of

552their reproductive attempt (Brockman & van Schaik, 2005). Numerous human studies similarly

553show that maternal nutritional status during pregnancy has a significant impact on infant birth

554weight, early-life development, health and survival (Emery Thompson, 2013; Martorell &

555Gonzalez-Cossio, 1987). This study, by highlighting the effect of prenatal food availability on

556inter-individual variations in color-for-age, suggests that similar effects could occur in baboons,

557and that color-for-age may thus be a reliable indicator of other developmental dimensions.

558Studies on various primates including baboons have also shown that the infants of dominant

559females exhibit faster development in terms of growth rate and age at weaning (Altmann &

560Alberts, 2005; Fedigan, 1983; Pusey, 2012). Yet, surprisingly, maternal rank did not affect

561individual variation in infant color in this study. Given that color scores reflect inter-individual

562variation in maternal nutritional condition (see above), it is possible that rank does not capture

563such differences at Tsaobis, perhaps because most food resources are not monopolizable, or

564because subordinate females adopt foraging and social strategies that help to mitigate the costs

565of their low rank (Marshall, Carter, Ashford, Rowcliffe, & Cowlishaw, 2015; Sick et al., 2014).

566Interestingly, looking at the color development of each body part separately, we found that

567the only body part affected by prenatal food availability was the ischial callosities. This suggests

568that the color scoring of different body parts could be used for different purposes; for example,

569ischial callosities are a better indicator of developmental pace than of age. Further investigations

570of the determinants of color changes at specific body parts showed that infants born in

571December-January have greyer muzzle tips for their age than others. However, the muzzle tip

572was scored on the lowest number of infants (N = 16), and such a small sample size questions

573   the robustness of this result that was not replicated using other body parts. Using a larger dataset

574   will be necessary to reach conclusive results.

575   Our study of the determinants of inter-individual variation of color-for-age is preliminary

576   for several reasons. First, we were not able to explore the impact of other factors that are known

577   to influence infant color transitions, like variation in social dynamics and infanticide risk

578   (Bădescu et al., 2016) that are probably of considerable evolutionary significance for young

579   chacma baboons (Cheney et al., 2004; Palombit, 2003). Second, further studies are needed to

580   explore the correlation between age-related changes in coloration and developmental

581   milestones like weaning age for chacma baboons. Testing whether color development co-varies

582   with other dimensions of development would indicate if it could be used as a reliable indicator

583   of developmental pace that may ultimately be connected to fitness. In line with this suggestion,

584   the transition from natal to adult fur coloration of wild ursine colobus (*Colobus vellerosus*)

585   infants has been used as a proxy of developmental pace to show that high infanticide risk

586   accelerates infant development (Bădescu et al., 2016). Finally, examining the potential effects

587   of infant coloration on protective behavior from other group members, and on the level of

588   alloparenting care received wherever it is relevant (Brent, Teichroeb, & Sicotte, 2008; Ross &

589   Regan, 2000) could be an interesting perspective to test other hypotheses proposed to account

590   for the evolution of natal coat in primates.

591   Our study demonstrates that monitoring the skin color transition of infant baboons is a non-

592   invasive and accurate method to estimate age up to 8 months old, with a median accuracy of 10

593   days, which can decrease further if the same individual is scored repeatedly. Our study

594   additionally highlights inter-individual variability in the ages of color transitions. This suggests

595   that scoring the change in infants' body coloration can also be used to detect individual variation

596   of developmental pace, and certain body parts are more variable than others for a given age,

597   and thus represent promising candidates in this respect. In this context, food availability during

598　prenatal life affected infant color-for-age in our population, suggesting that maternal nutritional

599　condition during pregnancy plays a central role in infant color development. Further research

600　is necessary to determine whether such scores correlate with broader aspects of development

601　(morphological, behavioral, and physiological), and which body parts are most useful.

602

DATA AVAILABILITY STATEMENT

603

604　The data that support the findings of this study are openly available in Mendeley data:

605　http://dx.doi.org/10.17632/65vk9tck25.1

606

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FIGURE LEGENDS

Figure 1: Picture of an infant chacma baboon showing the different body parts scored in this study.

 Figure 2: Pictures showing examples of color scores for different body parts. The first column refers to score 1, i.e. pink skin for each body part, and black fur. The second column refers to score 2, i.e., body parts that are pinker than grey (this score did not exist for fur). The third column refers to score 3, i.e., body parts that are just as pink as grey (and for fur, just as black as grey). The fourth column refers to score 4, i.e., body parts that are greyer than pink (this score did not exist for fur). The last column refers to the score 5, i.e. grey for all body parts as well as for fur.

Figure 3: Color scores (from 1 to 5) of the different body parts of an infant according to its age (in months), using 242 observations on 73 infants with known birth date (Cohort 1). Month 0 indicates an infant less than 1 month old, Month 1 indicates an infant aged between 1 and 2 months old, etc. Each boxplot color represents a body part (see legend for details, ISC refers to ischial callosities). The median value for each boxplot is represented by a diamond, and outlier points are indicated by dark red dots.

Figure 4: Weighted mean color score according to infant age (in days). Each dot represents the age component smooth function of the weighted mean color score according to individual age. The red curve shows the fitted smooth effect, and the 95% upper and lower confidence intervals are represented by the dashed blue curves.

Figure 5: Effect of food availability during pregnancy on infant weighted mean color scores, controlled for infant age, identity and all other fixed effects included in our GAMM. Each dot represents an observation (raw values). The red curve shows the fitted linear effect of food availability, and the dashed blue curves represent the 95% upper and lower confidence intervals.

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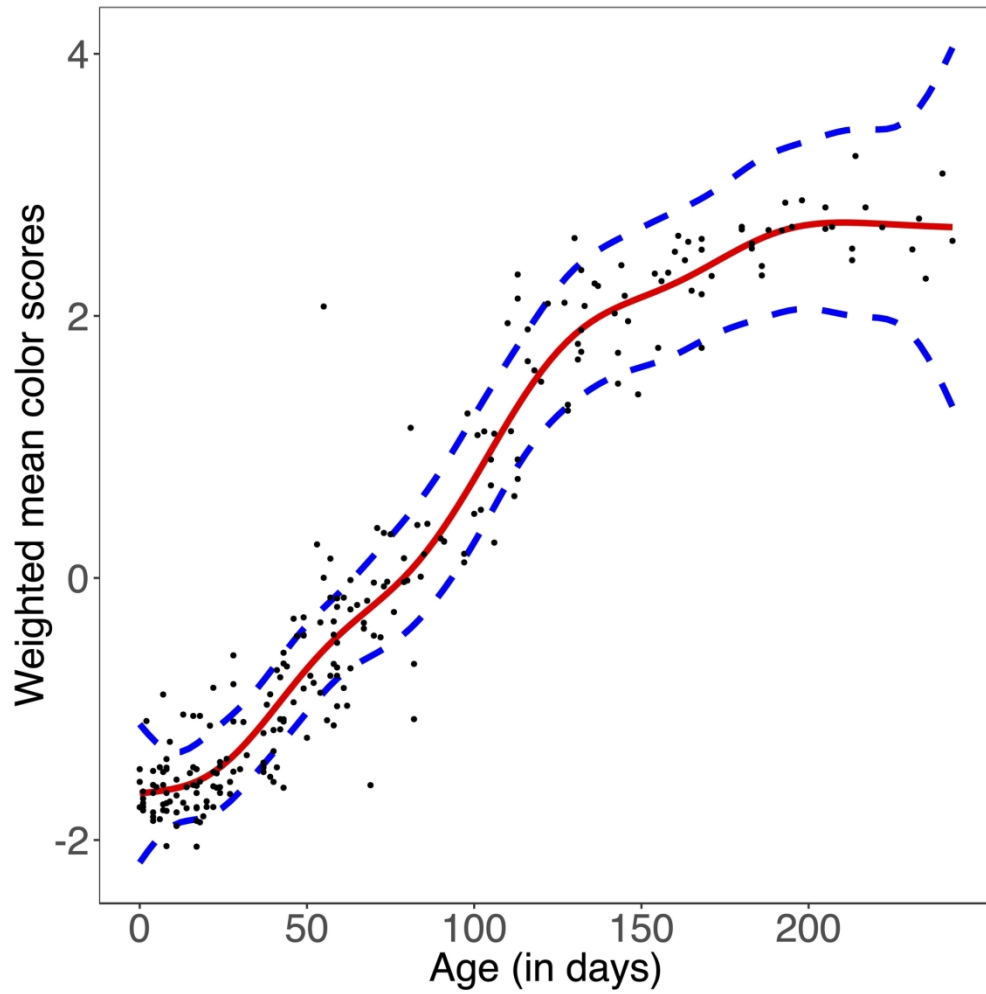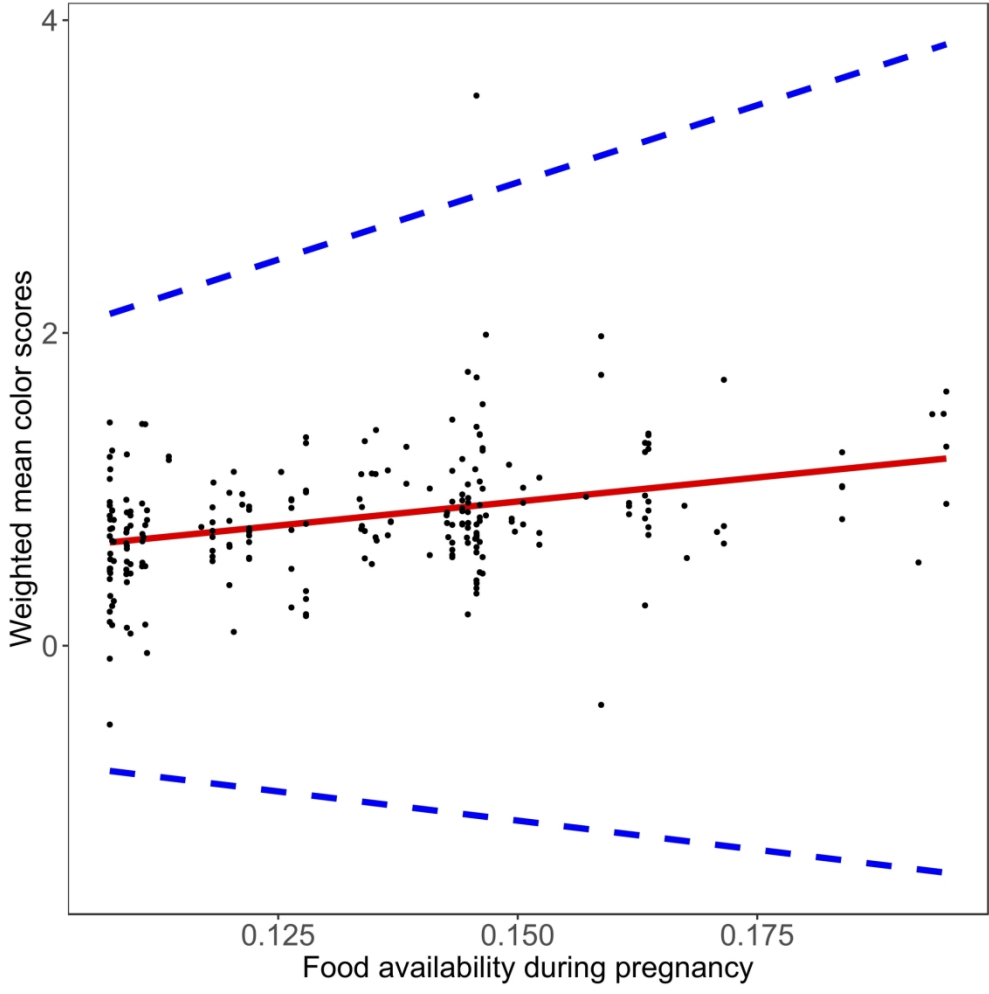43
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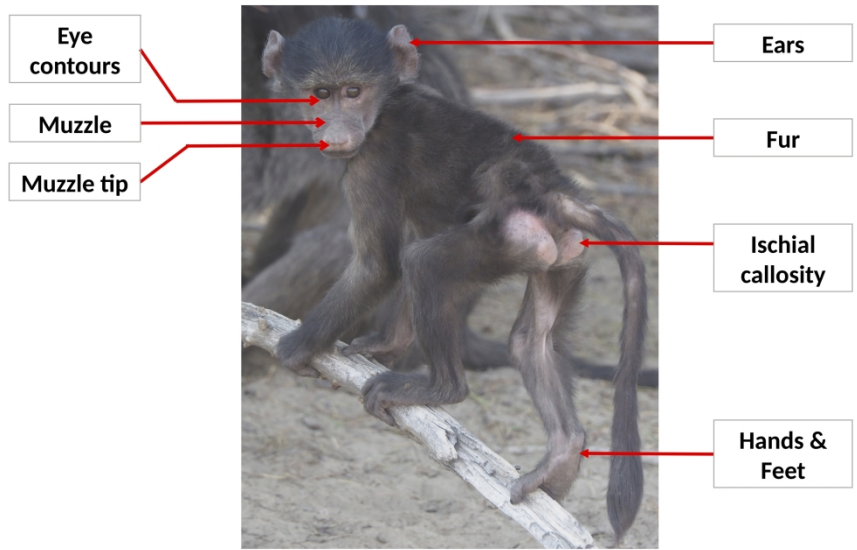
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