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1 **Developmental transitions in body color in chacma baboon infants:**
2 **implications to estimate age and developmental pace**

3 Jules Dezeure¹, Julie Dagorrette¹, Alice Baniel², Alecia J. Carter³, Guy Cowlshaw⁴, Harry H.
4 Marshall⁵, Claudia Martina^{3,4,6}, Cassandra Raby^{4,7}, Elise Huchard¹

5 ¹Institute of Evolutionary Biology of Montpellier (ISEM), Université de Montpellier, CNRS,
6 IRD, EPHE, Montpellier, France.

7 ²Department of Anthropology, Stony Brook University, Stony Brook, NY, USA

8 ³Department of Anthropology, University College London, London, UK

9 ⁴Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY

10 ⁵Centre for Research in Ecology, Evolution and Behaviour, Department of Life Sciences,
11 University of Roehampton, London, SW15 4JD, UK

12 ⁶Department of Behavioural Biology, University of Vienna, Althanstrasse 14, 1090, Austria

13 ⁷Institute of Integrative Biology, University of Liverpool, Biosciences Building, Liverpool,
14 L69 7ZB, UK

15
16 **Corresponding author:**

17 Jules Dezeure, Institute of Evolution Science of Montpellier, UMR 5554, University of
18 Montpellier, CNRS, IRD, EPHE, Place Eugène Bataillon, Cc 065, 34095 Montpellier Cedex
19 05, France.

20 Email: jules.dezeure@etu.umontpellier.fr

21
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.

42

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 &

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.

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

143 **Material and Methods**

144 *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 (Cowlshaw & 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, Cowlshaw, & 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

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 \pm SD, ICC = 0.92 \pm 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>.

225

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

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 Criterion (AIC), and a
275 polynomial function of age of degree 4 was retained in our model.

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 (\pm 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

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).

326

327 *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 Criterion (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:

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], $t=6.58$, $P\text{-value}<10^{-4}$), 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:

$$367 \quad \sin(\text{Infant's date of birth} + \varphi)$$

368 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
369 account for potential phase shifts across the year, i.e. to consider all the months of the year as
370 possible birth months maximizing faster development. For example, a positive effect of the sine
371 phase of $\pi/6$ would maximize February, and a negative effect will maximize August. We ran
372 sequentially six different multivariate models (GAMMs with the six different phase values)
373 containing all other fixed effects, and we selected the best phase as the one minimizing the AIC
374 (which is $\pi/3$ for the weighted mean color score model).

375 - *Mother's dominance rank*. We expected infants from dominant females to develop more
376 quickly, following studies on other aspects of baboon developmental pace (Altmann & Alberts,
377 2005; Cheney et al., 2004; S. Johnson, 2003).

378 - *Mother's parity*. We expected infants from primiparous mothers to develop more
379 slowly, following studies on other aspects of baboon developmental pace (Altmann & Alberts,
380 2005).

381 - *Infant sex*. We did not expect any sex difference in the pace of early morphological
382 development, following studies on other aspects of baboon developmental pace (Altmann &
383 Alberts, 2005; Altmann & Altmann, 1981; Johnson & Kapsalis, 1995). Nevertheless, we
384 included this variable to control for potential unexpected sex differences.

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

386 We further considered each body part separately (seven models) to test whether the same
387 determinants affected all body parts or only some of them, and to evaluate which body parts
388 were most sensitive to ecological, individual and maternal traits. Here, our response variables
389 were the scores of one given body part, and were coded as ordinal, with five categories for each
390 body part (except for the fur, with only three categories). We ran all the GAMMs using the
391 'gam' function of the 'mgcv' package (Wood, 2003), in R version 3.5.0 (R Core Team, 2018).
392 Ordinal response variables for each body part were specified with the family 'ocat' of the
393 'mgcv' package (Wood, 2003). We computed parameter estimates for each fixed effect, with
394 Wald statistic tests (X^2) and P-values associated. For smooth effects, we computed the effective
395 degrees of freedom, with the Wald statistic test and the P-value. We considered an effect to be
396 significant when its P-value was < 0.05 . We were also interested in quantifying the importance
397 of inter-individual variation in developmental pace, and so tested the significance of the random
398 intercept, looking similarly at its P-value. For each model, we also checked graphically the
399 normality of the residuals' distribution and the accuracy of the number of knots used for the

400 age thin plate spline (this parameter constrains the ‘wiggleness’ of the smooth, i.e. the number
401 of bow points in the fitted curve) (Wood, 2003) using the ‘gam.check’ function of the ‘mgcv’
402 package (Wood, 2019). Graphical representations were made using the ‘mgcViz’ package
403 (Fasiolo, Nedellec, Goude, & Wood, 2018).

404

405 **RESULTS**

406 **1 Characterization of fur and skin color changes in chacma baboon infants**

407 All results associated with the characterization of fur and skin color changes in relation to age
408 are summarized in Figure 3. All baboons were fully grey (i.e., at all body parts) after 8 months
409 of age, with similar fur and skin coloration as adults. The fur, muzzle or hands and feet were
410 the first body parts to turn grey, on average between 1 and 2 months of age. Hands and feet, as
411 well as the muzzle, started to transition around 1 month old until becoming fully grey at approx.
412 4 months of age. Ears started to turn grey after 2 months and were totally grey by 5 months.
413 The last body parts to change color were the eye contours, the ischial callosities, and the tip of
414 the muzzle, which started to transition at approx. 3 months of age, and finished after 5 months.
415 The qualitative chronology of the transition was apparent in the correlation matrix (Table 1):
416 hands and feet scores were highly correlated with muzzle scores, and eye contours scores were
417 highly correlated with muzzle tip scores. Nonetheless, the order in which body parts change
418 color was not always consistent across individuals. For some infants, we observed ears turning
419 grey before muzzles and hands, or ischial callosities turning grey before the muzzle tip and ears.
420 Overall, a chacma baboon infant with entirely pink skin and black fur was almost always
421 younger than 2 months old, as at least the hands and feet started to turn grey after this age. An
422 infant with entirely grey skin and fur was at least 4 months old, as no infant was observed with
423 a grey tip of the muzzle before this age. Finally, a transitional infant was aged between 1 and 6
424 months old.

425

426 **2 Accuracy of age estimates based on color scores**

427 The color scores were strongly correlated with the known ages of infants for all body parts,
428 though correlation coefficients were slightly lower for the fur and the ischial callosities (Table
429 1). This means that the scores of these two body parts produce less precise age estimates,
430 probably due to higher inter-individual variation in the age of transition of these parts compared
431 to others. For example, a 3-month-old baboon could exhibit the full range of colors for ischial
432 callosities, from fully pink to fully grey; and a 1-month-old baboon could exhibit a fully black
433 or a fully grey fur (Figure 3).

434 In order to test the accuracy of infant body coloration as a method of age estimation, we
435 computed a composite score (using PCA) from 172 observations of all body parts from 51
436 infants of known ages (births observed, Sample 1), and then predicted this composite score to
437 estimate ages on an independent sample of 70 observations from 22 infants of known ages
438 (Sample 2). We obtained a median difference of 12 days between the actual age and the
439 estimated age using 70 observations, 7 body parts and a 5-level scale of color scores (Table 2).
440 We also investigated the effects of the number of body parts considered, and the number of
441 levels of the color scale. Decreasing the number of body parts considered only slightly
442 decreased the accuracy of age estimates (Table 2), and the same conclusion applied for using a
443 3-level color scale instead of a 5-level one – though using a 3-level scale in combination with
444 few body parts decreased accuracy more substantially (Table 2). Our best age estimations per
445 observation were computed when considering the skin across all 6 body parts but excluding the
446 fur, and using a 5-level color scale (absolute number of days of between actual and estimated
447 ages: median = 10.7, range = 0.1–86.4). We also investigated the effect of the number of
448 observations per infant on the accuracy of age estimates: the more observations, the more
449 accurate were the estimates (Figure S1, Supporting Information). Finally, the accuracy of age

450 estimates significantly decreased with age ($X_2 = 10.0$, P-value = 1.54×10^{-3}) (Figure S2,
451 Supporting Information), and were lower for photographic compared to field observations
452 (Figure S3, Supporting information), albeit the latter effect did not reach significance ($X_2 =$
453 3.63, P-value = 0.06).

454

455 **3 Determinants of individual variations in the pace of color changes**

456 Finally, we investigated the determinants of inter-individual variations in age-related color
457 scores, looking at ecological (food availability during pregnancy or during early-lactation, birth
458 timing), maternal (parity, rank) and individual (sex) predictors using GAMMs controlling for
459 age with a spline regression (Figure 4). The model explained 93% of the variation in the
460 weighted mean color scores. We detected significant inter-individual differences in mean color
461 scores (Table 3), and in most body parts (except for the muzzle tips, for which we had fewer
462 infants scored compared to other parts, see Table S3 in Supporting Information). Our index of
463 food availability during pregnancy influenced the weighted mean color score (controlled for
464 age): infants turned grey earlier considering all their body parts together when food during
465 pregnancy was abundant (Table 3, Figure 5). In contrast food availability during lactation did
466 not (Table S4, Supporting Information). We did not detect any effect of maternal (rank and
467 parity) nor individual (birth date and sex) traits on variation in infant mean color scores
468 controlled for age (Table 3). Looking at individual variation in color transitions for each body
469 part separately, we found a positive effect of food availability during pregnancy on the score of
470 ischial callosities only (Table S3, Supporting Information). We also found a positive effect of
471 the timing of birth on the scores of muzzle tips (maximizing scores for infants born in
472 December-January) but not for other body parts (Table S3, Supporting Information). We did
473 not detect any effect of food availability during lactation, maternal traits, i.e. maternal rank and
474 parity, on variation in infant color for any body part (Table S3, Supporting Information).

475

476 **DISCUSSION**

477 Our purpose in this study was twofold: (1) to assess how well infant chacma baboons with
478 unknown ages can be aged on the basis of their skin and fur color, and (2) to explore potential
479 environmental, maternal, and individual predictors of variation in the pace of infant color
480 development for infants with known ages. The age estimates obtained using infant color scores
481 were generally accurate (median number of days between actual age and estimate age per
482 observations = 10, range=0-86 days). All the tools required for estimating ages in a chacma
483 baboon population are provided in this paper. Figures 1 and 2 can be used to score baboon
484 coloration directly in the field (or using photographs), and the methods section details how the
485 first dimension of a composite score (using PCA), derived from these color scores, can be
486 computed to estimate ages. Various recommendations can be made to improve the accuracy of
487 age estimates:

- 488 1. Use the color scores from all body parts except fur, as age estimates were most accurate
489 with this configuration. However, decreasing the number of body parts considered does
490 not decrease the accuracy of age estimations dramatically. For example, considering
491 only two body parts (ears and muzzle tip) instead of six reduces the accuracy of age
492 estimations by only 4.5 days. Nonetheless, such a result may vary across primate
493 species, and one should establish the relevant body parts to be considered in different
494 species.
- 495 2. Score the same individual repeatedly, as an infant with 8 observations had a birth date
496 estimation error of 5 days in average, compared to more than 30 days for infants with
497 only a single observation. Ideally, infants should be scored as early as possible (as
498 accuracy decreases as infants age) and regularly until it turns fully grey.

- 499 3. Prioritize field observations. Photographic evidence can be less accurate because color
500 scores may be influenced by fluctuating light conditions. If necessary, photographic
501 approaches should exploit multiple high-resolution photographs of the same individual
502 on a given day at different times and angles to control for light variation.
- 503 4. Consider using a 3-level color scale, which is slightly less accurate than a 5-level scale
504 but also more practical, and may maximize inter-observer reliability. However, such
505 choice depends on the trade-off between the accuracy targeted and the conditions of
506 data collection (e.g., single versus multiple observers).

507 In addition, this study opens the possibility of a similar application for machine learning where
508 an algorithm could predict the age of an infant based on pictures, as long as a large set of high-
509 quality pictures (see recommendation #3) of known-age individuals is available to initialize the
510 algorithm. This relatively recent method is based on mathematical and statistical approaches
511 through which computers can ‘learn’ from data to then make predictions. Such methods have
512 been used in a wide range of field applications, and are becoming increasingly common (Al-
513 Jarrah, Yoo, Muhaidat, Karagiannidis, & Taha, 2015).

514 Changes in the pigmentation of infants’ ears and muzzles at Tsaobis follow a similar pattern
515 to that observed in another population of wild chacma baboon living in Mkuzi Game Reserve
516 (South Africa), with an onset of grey coloration appearing around 1-2 months, and the full
517 transition completed around 4-6 months of age (Whitehead et al., 1990). Our detailed
518 characterization of the age at which fur and skin turn grey indicates that infant chacma baboons’
519 coloration develops faster than yellow baboons (Altmann & Altmann, 1981; Rasmussen, 1979).
520 Whilst chacma baboon infants have all turned grey by 8 months of age, most yellow baboon
521 infants are still in the transition phase at this age, and only exhibit adult color around 12 to 14
522 months of age, depending on the population (Altmann & Altmann, 1981; Rasmussen, 1979). In
523 addition, in contrast to yellow baboons, the order in which body parts change color was not

524 always consistent across individuals in this study. Discrepancies observed in the age and
525 chronology of transition between baboon species highlight that such patterns are species-
526 specific, and that the methodology presented here should be developed and validated separately
527 for each species.

528 Inter-individual variation in the rate of maturation was high for each body part considered
529 in this study, as found in yellow baboons (Altmann & Altmann, 1981; Rasmussen, 1979).
530 Specifically, the change in fur color was a less accurate indicator of age, as fur turned grey
531 relatively early and showed marked individual variation. Failure to derive accurate age
532 estimates remains non-negligible (we had a maximum of 86 days difference between actual and
533 estimated age when relying on 6 body parts), due to the existence of outlier individuals with
534 very fast or slow development. This suggests that, whilst this method of age estimation is not
535 perfect, infant coloration can provide a simple and non-invasive proxy to detect individual
536 variation in developmental pace on a semi-quantitative scale. Nevertheless, despite their utility
537 for tracking other developmental factors (Barthold et al., 2009; Treves, 1997), studies linking
538 age-related changes in color to other indicators of developmental pace are very rare in baboons.
539 Only one study on Amboseli yellow baboons recorded that late changes in paracallosal skin
540 color can be seen as a first sign of developmental abnormality, being followed by delayed
541 maturation, locomotor disability and finally death (Altmann & Altmann, 1981).

542 Regarding the determinants of individual variations in color-for-age considering all body
543 parts together, we found that higher food availability during pregnancy, but not during early-
544 lactation, accelerated the transition towards adult coloration. In line with this, infant yellow
545 baboons from a food-enhanced group grew more rapidly than individuals from wild-foraging
546 groups (Altmann & Alberts, 2005). Similarly, in Phayre's leaf monkeys (*Trachypithecus*
547 *phayrea*) infants in larger groups transitioned from natal to adult fur color later, suggesting that
548 food competition affects infant color maturation and development (Borries et al., 2008). Here,

549 we distinguished pre-natal from post-natal food availability, and our results emphasize the
550 importance of maternal condition during pregnancy for infant post-natal color development. In
551 capital breeders like baboons or humans, females can store energy to use it later, and conception
552 likelihood generally peaks during periods of high food availability to increase the success of
553 their reproductive attempt (Brockman & van Schaik, 2005). Numerous human studies similarly
554 show that maternal nutritional status during pregnancy has a significant impact on infant birth
555 weight, early-life development, health and survival (Emery Thompson, 2013; Martorell &
556 Gonzalez-Cossio, 1987). This study, by highlighting the effect of prenatal food availability on
557 inter-individual variations in color-for-age, suggests that similar effects could occur in baboons,
558 and that color-for-age may thus be a reliable indicator of other developmental dimensions.

559 Studies on various primates including baboons have also shown that the infants of dominant
560 females exhibit faster development in terms of growth rate and age at weaning (Altmann &
561 Alberts, 2005; Fedigan, 1983; Pusey, 2012). Yet, surprisingly, maternal rank did not affect
562 individual variation in infant color in this study. Given that color scores reflect inter-individual
563 variation in maternal nutritional condition (see above), it is possible that rank does not capture
564 such differences at Tsaobis, perhaps because most food resources are not monopolizable, or
565 because subordinate females adopt foraging and social strategies that help to mitigate the costs
566 of their low rank (Marshall, Carter, Ashford, Rowcliffe, & Cowlishaw, 2015; Sick et al., 2014).

567 Interestingly, looking at the color development of each body part separately, we found that
568 the only body part affected by prenatal food availability was the ischial callosities. This suggests
569 that the color scoring of different body parts could be used for different purposes; for example,
570 ischial callosities are a better indicator of developmental pace than of age. Further investigations
571 of the determinants of color changes at specific body parts showed that infants born in
572 December-January have greyer muzzle tips for their age than others. However, the muzzle tip
573 was scored on the lowest number of infants (N = 16), and such a small sample size questions

574 the robustness of this result that was not replicated using other body parts. Using a larger dataset
575 will be necessary to reach conclusive results.

576 Our study of the determinants of inter-individual variation of color-for-age is preliminary
577 for several reasons. First, we were not able to explore the impact of other factors that are known
578 to influence infant color transitions, like variation in social dynamics and infanticide risk
579 (Bădescu et al., 2016) that are probably of considerable evolutionary significance for young
580 chacma baboons (Cheney et al., 2004; Palombit, 2003). Second, further studies are needed to
581 explore the correlation between age-related changes in coloration and developmental
582 milestones like weaning age for chacma baboons. Testing whether color development co-varies
583 with other dimensions of development would indicate if it could be used as a reliable indicator
584 of developmental pace that may ultimately be connected to fitness. In line with this suggestion,
585 the transition from natal to adult fur coloration of wild ursine colobus (*Colobus vellerosus*)
586 infants has been used as a proxy of developmental pace to show that high infanticide risk
587 accelerates infant development (Bădescu et al., 2016). Finally, examining the potential effects
588 of infant coloration on protective behavior from other group members, and on the level of
589 alloparenting care received wherever it is relevant (Brent, Teichroeb, & Sicotte, 2008; Ross &
590 Regan, 2000) could be an interesting perspective to test other hypotheses proposed to account
591 for the evolution of natal coat in primates.

592 Our study demonstrates that monitoring the skin color transition of infant baboons is a non-
593 invasive and accurate method to estimate age up to 8 months old, with a median accuracy of 10
594 days, which can decrease further if the same individual is scored repeatedly. Our study
595 additionally highlights inter-individual variability in the ages of color transitions. This suggests
596 that scoring the change in infants' body coloration can also be used to detect individual variation
597 of developmental pace, and certain body parts are more variable than others for a given age,
598 and thus represent promising candidates in this respect. In this context, food availability during

599 prenatal life affected infant color-for-age in our population, suggesting that maternal nutritional
600 condition during pregnancy plays a central role in infant color development. Further research
601 is necessary to determine whether such scores correlate with broader aspects of development
602 (morphological, behavioral, and physiological), and which body parts are most useful.

603

604 **DATA AVAILABILITY STATEMENT**

605 The data that support the findings of this study are openly available in Mendeley data:
606 <http://dx.doi.org/10.17632/65vk9tck25.1>

607

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619

620 **CONFLICT OF INTEREST STATEMENT**

621 The authors do not have any conflict of interest to declare.

622

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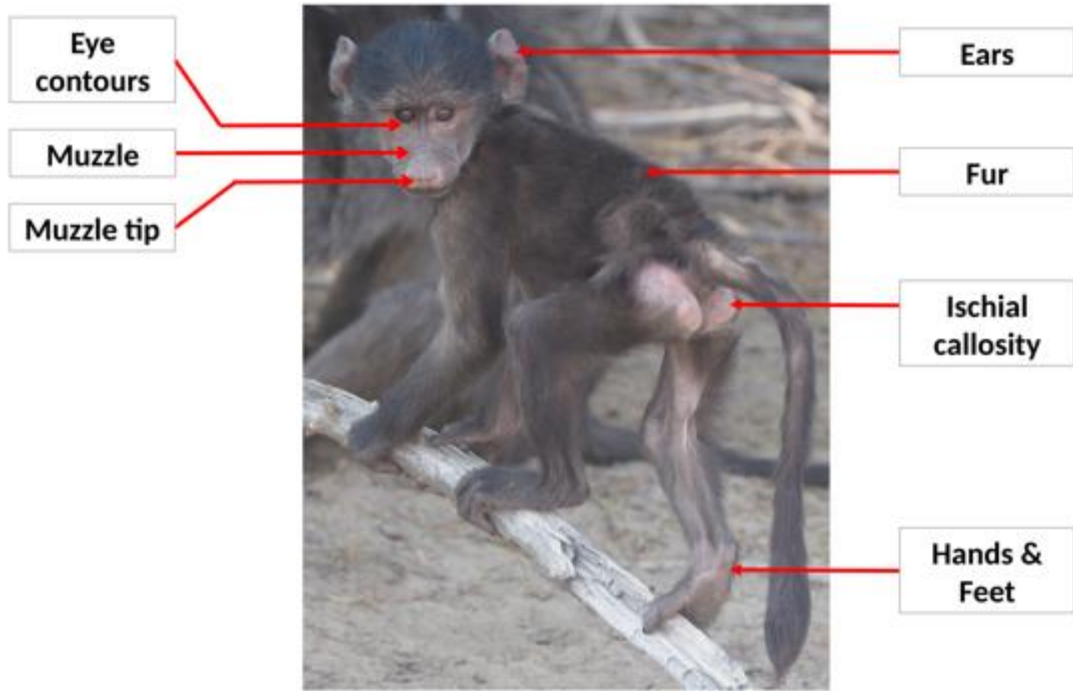
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786 **FIGURE LEGENDS**
































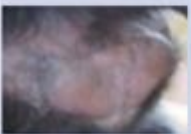

787 **Figure 1:** Picture of an infant chacma baboon showing the different body parts scored in this
788 study.



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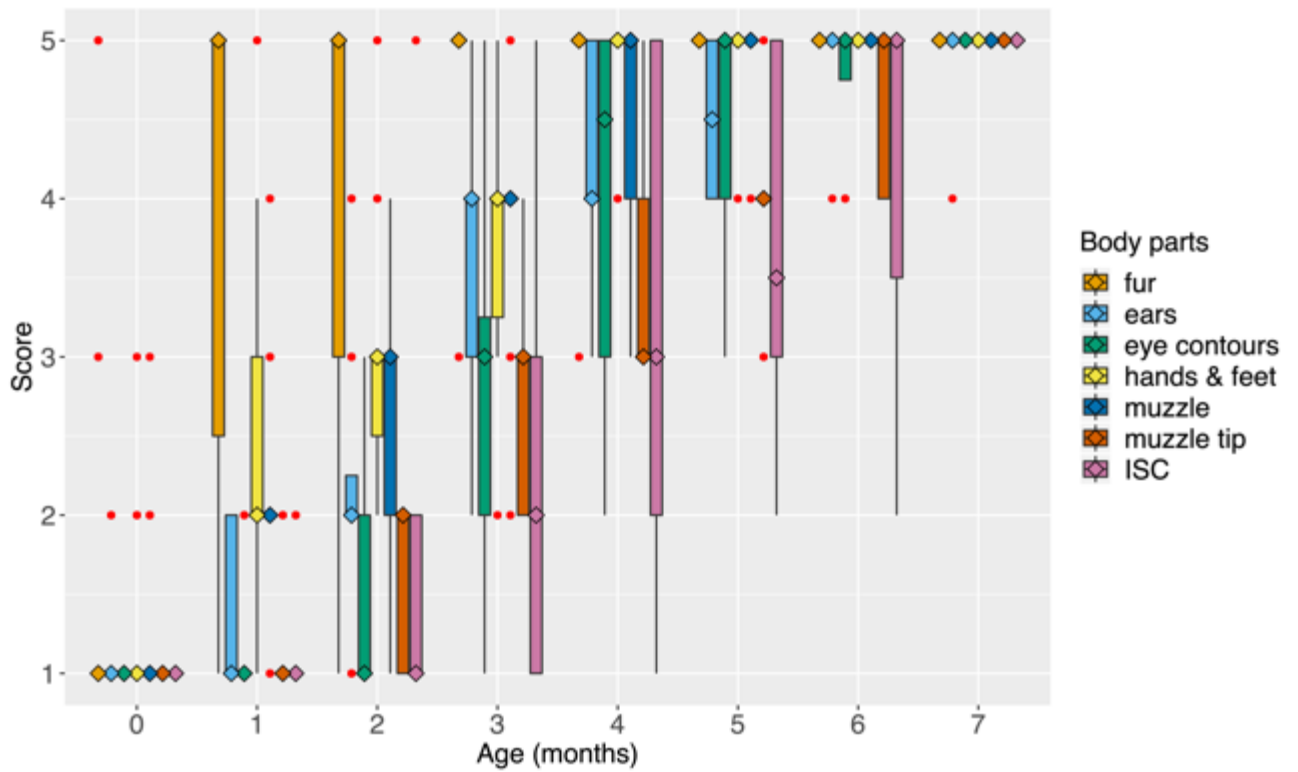
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791 **Figure 2:** Pictures showing examples of color scores for different body parts. The first column
 792 refers to score 1, i.e. pink skin for each body part, and black fur. The second column refers to
 793 score 2, i.e., body parts that are pinker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

Score	1	2	3	4	5
Fur					
Ears					
Eye contours					
Hands & feet					
Muzzle					
Muzzle tip					
Ischial callosity					

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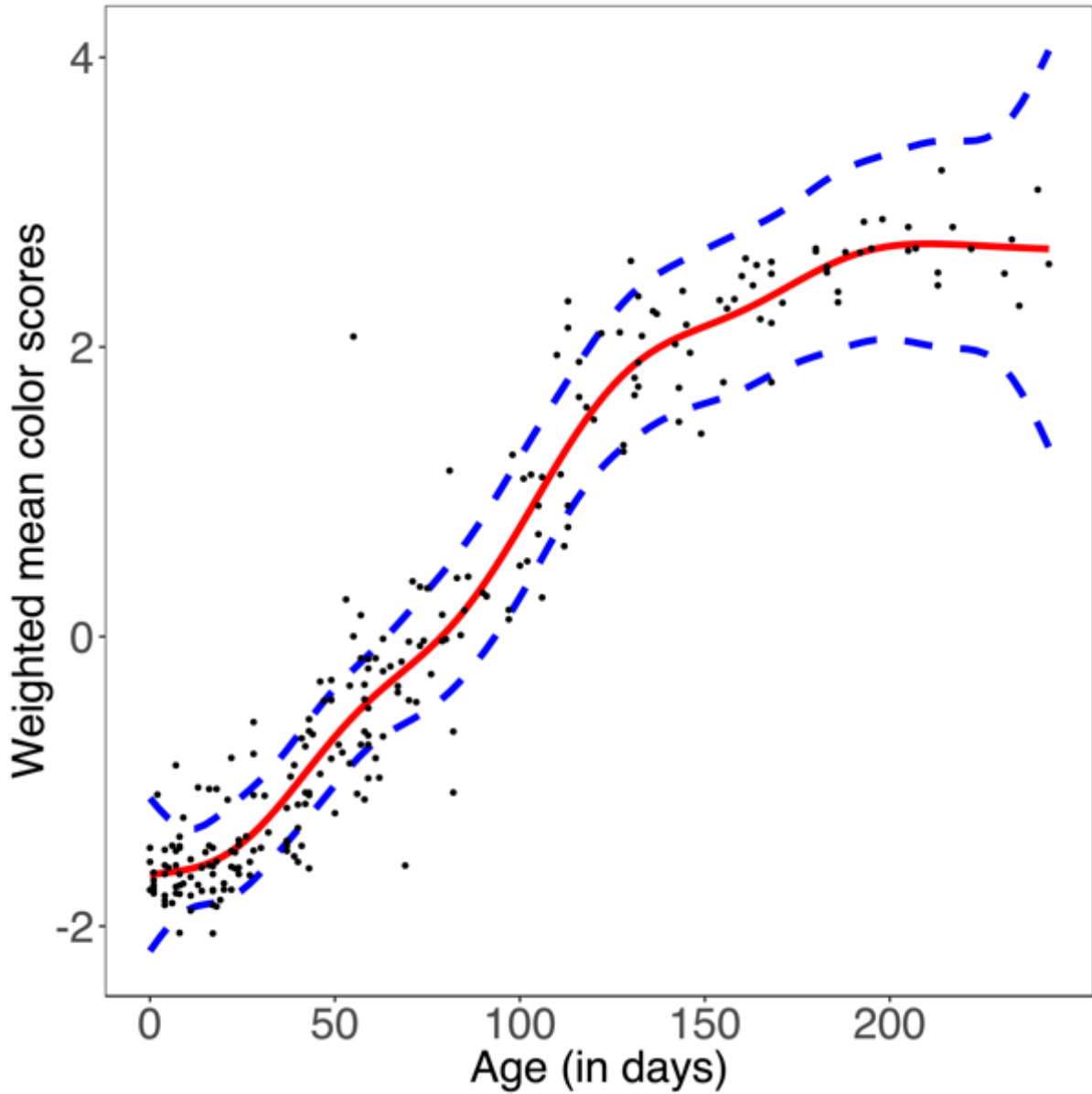
799 **Figure 3:** Color scores (from 1 to 5) of the different body parts of an infant according to its age
 800 (in months), using 242 observations on 73 infants with known birth date (Cohort 1). Month 0
 801 indicates an infant less than 1 month old, Month 1 indicates an infant aged between 1 and 2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



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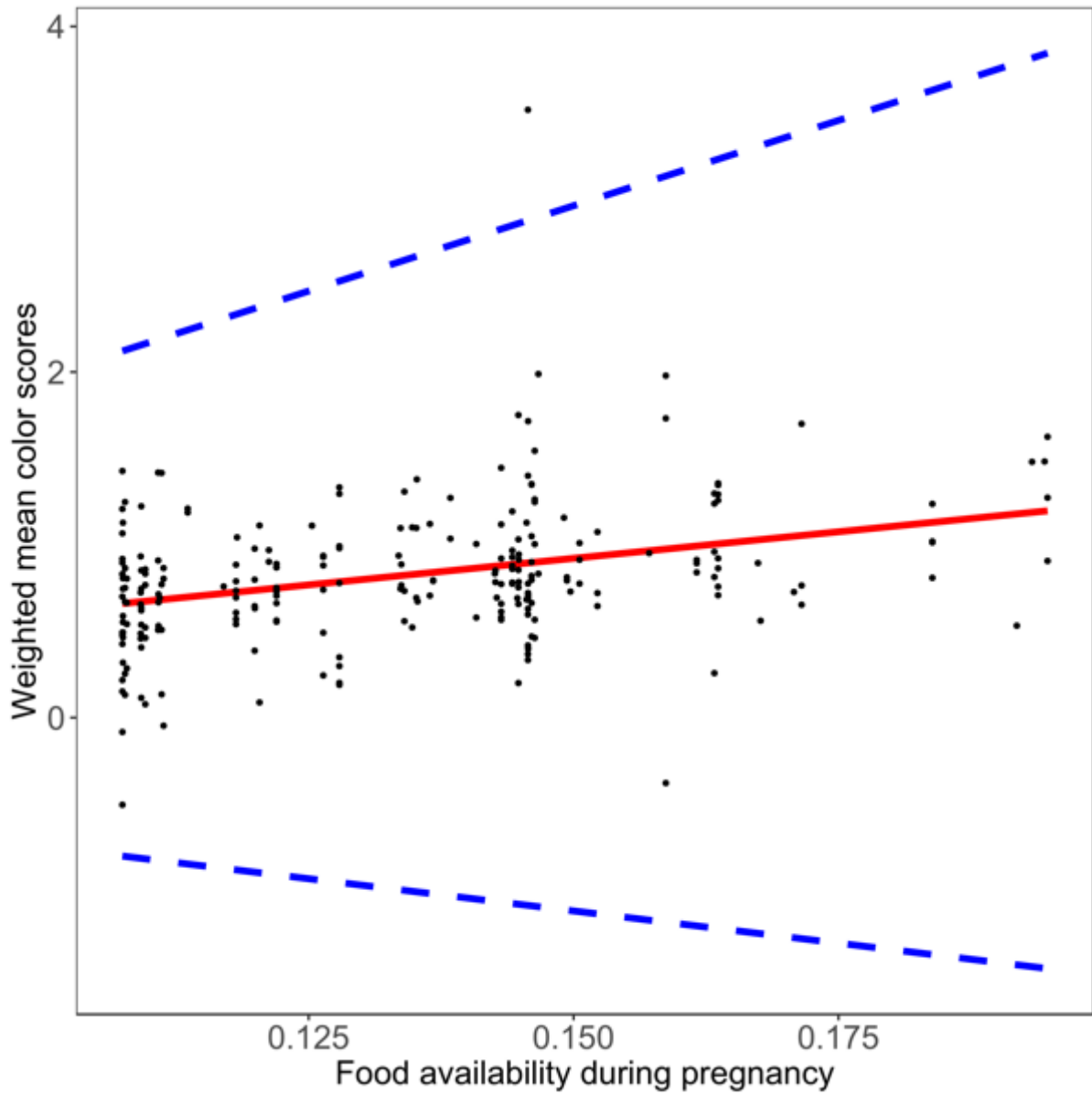
807 **Figure 4:** Weighted mean color score according to infant age (in days). Each dot represents the
808 age component smooth function of the weighted mean color score according to individual age.
809 The red curve shows the fitted smooth effect, and the 95% upper and lower confidence intervals
810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



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



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Tables for:

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Developmental transitions in body color in chacma baboon infants:

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implications to estimate age and developmental pace

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TABLE 1: Correlation table between known ages and age estimates for each body part. The

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correlation matrix was built using Spearman rank coefficients and using the full sample (242

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observations from 73 infants).

Variable	Age (Months)	Fur	Ears	Eye contours	Hands & feet	Muzzle	Muzzle tip
Fur	0.86						
Ears	0.93	0.86					
Eye contours	0.90	0.84	0.92				
Hands & feet	0.95	0.89	0.94	0.92			
Muzzle	0.93	0.88	0.94	0.92	0.97		
Muzzle tip	0.91	0.85	0.93	0.95	0.92	0.93	
Ischial callosity	0.81	0.78	0.82	0.88	0.82	0.82	0.87

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829 **TABLE 2:** Accuracy of age estimates using 70 observations from 22 infants (Sample 2),
 830 depending on the number of body parts considered, and on the number of levels of the color-
 831 scoring scale (3 or 5). Accuracies were measured by the absolute number of days between actual
 832 and estimate age for each observation, which are given with their median and range.

Number of body parts considered †	7	6	5	4	3	2
5-level color scale						
Median	12.2	10.7	12.9	10.9	16.4	15.2
Range	0.1 - 95.3	0.1 - 86.4	0.1 - 79.2	0.5 - 87.3	0.5 - 82.4	1.4 - 70.8
3-level color scale						
Median	11.5	11.9	12.8	15.5	17.0	18.5
Range	0.1 - 93.2	0.2 - 95.0	0.1 - 97.0	0.6 - 70.9	1.2 - 74.5	0.1 - 70.2

833 †: We considered respectively the scores of the ears, muzzle tips, eye contours, muzzles, ischial
 834 callosities and hands and feet when 6; of the ears, muzzle tips, eye contours, muzzles and ischial
 835 callosities when 5; ears, muzzle tips, eye contours and muzzles when 4; ears, muzzle tips and
 836 eye contours when 3; and finally ears and muzzle tips when 2.

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838 **TABLE 3:** Determinants of inter-individual variation in weighted mean color scores. We
839 computed parameter estimates (with their standard deviations) for each fixed effect, the Wald
840 statistic (X^2) test, and P-values. For categorical parameters, the tested category is indicated
841 between brackets. Food availability was indexed by the mean daily NDVI during pregnancy
842 and an infant's birth timing in the annual cycle was represented by a sinusoidal term (with a
843 phase of $\pi/3$). For smooth effects, we gave the effective degrees of freedom (Edf), the residual
844 degree of freedom (Ref.df), the Wald Statistic (X^2) and the P-value. Significant effects are
845 indicated in bold. Similar models were run on each body part separately, and corresponding
846 results are presented in the electronic supplementary materials (Table S3).

Fixed effects	Estimate	Standard error	X^2	P-value
Intercept	2.88	0.11		
Food availability during pregnancy	0.13	0.06	5.10	0.025
Birth timing	0.06	0.10	0.33	0.57
Sex (Male)	0.03	0.12	0.08	0.77
Rank	0.10	0.06	2.63	0.11
Parity (Primiparous)	0.10	0.18	0.31	0.58
Group (L)	0.15	0.12	1.60	0.21
Smooth effects	Edf	Ref.df	X^2	P-value
Age	7.10	8.03	219.9	<1.10⁻³
Infant identity	40.9	66	1.88	<1.10⁻³

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851 **Supporting Information for:**
852 **Developmental transitions in body color in chacma baboon infants:**
853 **implications to estimate age and developmental pace**

854 Jules Dezeure¹, Julie Dagorrette¹, Alice Baniel², Alecia J. Carter³, Guy Cowlshaw⁴, Harry H.
855 Marshall⁵, Claudia Martina^{3,4,6}, Cassandra Raby^{4,7}, Elise Huchard¹

856 ¹Institute of Evolutionary Biology of Montpellier (ISEM), Université de Montpellier, CNRS,
857 IRD, EPHE, Montpellier, France.

858 ²Department of Anthropology, Stony Brook University, Stony Brook, NY, USA

859 ³Department of Anthropology, University College London, London, UK

860 ⁴Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY

861 ⁵Centre for Research in Ecology, Evolution and Behaviour, Department of Life Sciences,
862 University of Roehampton, London, SW15 4JD, UK

863 ⁶Department of Behavioural Biology, University of Vienna, Althanstrasse 14, 1090, Austria

864 ⁷Institute of Integrative Biology, University of Liverpool, Biosciences Building, Liverpool,
865 L69 7ZB, UK

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867 **Corresponding author:**

868 Jules Dezeure, Institute of Evolution Science of Montpellier, UMR 5554, University of
869 Montpellier, CNRS, IRD, EPHE, Place Eugène Bataillon, Cc 065, 34095 Montpellier Cedex
870 05, France.

871 Email: jules.dezeure@etu.umontpellier.fr

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873 **Table S1:** Intra-class coefficients (ICC) for each body part. We also computed the 95%
874 confidence limits for ICC of each body part (ICC lower and upper limits), and indicated the
875 number of observations used for this test (N), which varies across body parts.

Body Part	ICC	ICC lower	ICC upper	N
Fur	0.8	0.71	0.86	60
Ears	0.96	0.93	0.97	58
Eye contours	0.96	0.93	0.97	55
Hands & Feet	0.93	0.89	0.96	38
Muzzle	0.94	0.90	0.96	58
Muzzle tip	0.96	0.93	0.97	54
Ischial callosity	0.9	0.66	0.97	8

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878 **Table S2:** Model selection performed to identify the best age fit to predict weighted mean
879 color scores. We ran four GAMMs with infant identity set as random effect and different
880 functions of age as fixed effects. For each model, we computed the log likelihood, degrees of
881 freedom, Akaike Information Criterion (AIC) and Δ AIC which is the AIC value between a
882 given model and the model with the lowest AIC (indicated in bold).

Age effect	Log Likelihood	Model degrees of freedom	AIC	Δ AIC
Age	-140.9	52.9	387.7	53.6
Age + Age ²	-141.7	46.5	376.5	42.4
Age + Age ² + Age ³	-118.2	51.6	339.5	5.4
spline(Age)	-112.91	54.1	334.1	0

883

884 **Table S3:** No significant effects of food availability during early-lactation on variation in
885 weighted mean color scores. We computed parameter estimates (with their standard
886 deviations) for each fixed effect, Wald statistics (X^2) and P-values. For categorical
887 parameters, the tested category is indicated between brackets. For smooth effects, we gave the
888 effective degrees of freedom (Edf), the residual degree of freedom (Ref.df), the Wald Statistic
889 (X^2) and the P-value. The food availability was indexed by the mean daily NDVI between
890 infant birth and observation date (i.e. during lactation), and an infant's birth timing in the
891 annual cycle was represented by a sinusoidal term of its date of birth, with a phase of $\pi/3$.
892 Significant effects are indicated in bold.

Fixed effects	Estimate	Standard error	X^2	P-value
Intercept	2.89	0.11		
Food availability during lactation	0.07	0.05	1.91	0.17
Birth timing	-0.05	0.10	0.22	0.64
Sex (Male)	0.03	0.12	0.08	0.78
Rank	0.10	0.06	2.54	0.11
Parity (Primiparous)	0.12	0.19	0.43	0.78
Group (L)	0.12	0.12	1.02	0.31
Smooth effects	Edf	Ref.df	X^2	P-value
Age	7.10	8.04	221.2	<1.10⁻³
Infant identity	41.5	67	2.04	<1.10⁻³

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895 **Table S4:** Determinants of variation in color scores for each body part. We computed
896 parameter estimates (with their standard deviations) for each fixed effect, Wald statistics (X^2)
897 and P-values. For categorical parameters, the tested category is indicated between brackets.
898 For smooth effects, we gave the effective degrees of freedom (Edf), the residual degree of
899 freedom (Ref.df), the Wald Statistic (X^2) and the P-value. We indicated the number of
900 observations (Nobs) and of scored individuals (Nind) for each response variable, i.e. for each
901 body part. The food availability was indexed by the mean daily NDVI between infant
902 conception and birth (i.e. during pregnancy), and an infant's birth timing in the annual cycle
903 was represented by a sinusoidal term of its date of birth (with a phase of 0 for fur, $\pi/6$ for eye
904 contours, $\pi/3$ for hands and feet and muzzle, and $\pi/2$ for ears, muzzle tips and ischial
905 callosities). Significant effects are indicated in bold. Note that given the number of models
906 ($n=7$), the significance threshold falls to $\alpha=0.007$ when applying a Bonferroni correction.

Scores of body part (response variable)	Fixed effects	Estimate	Standard error	X^2	P- value
Fur (Nobs=239 on Nind=73)	Intercept	-3.68	3.96		
	Food availability	40.1	26.8	2.25	0.13
	Infant date of birth	0.57	0.81	0.49	0.48
	Group (L)	-0.07	1.10	0.01	0.95
	Sex (Male)	-0.09	1.07	0.01	0.93
	Rank	0.58	1.68	0.12	0.73
	Parity (Primiparous)	-0.72	1.73	0.17	0.68
	Smooth effects	EDF	Ref.df	X^2	P- value
	Age	3.75	4.58	73.8	<1.10_{.3}
	Infant identity	32.8	66.0	75.4	<1.10_{.3}
Ears (Nobs=238 on Nind=73)	Intercept	-0.55	2.54		
	Food availability	9.35	16.67	0.31	0.58
	Infant date of birth	1.10	0.66	2.79	0.09
	Group (L)	1.19	0.71	2.84	0.09
	Sex (Male)	-0.19	0.71	0.07	0.79
	Rank	1.06	1.09	0.94	0.33
	Parity (Primiparous)	-0.15	1.13	0.02	0.89
	Smooth effects	EDF	Ref.df	X^2	P- value

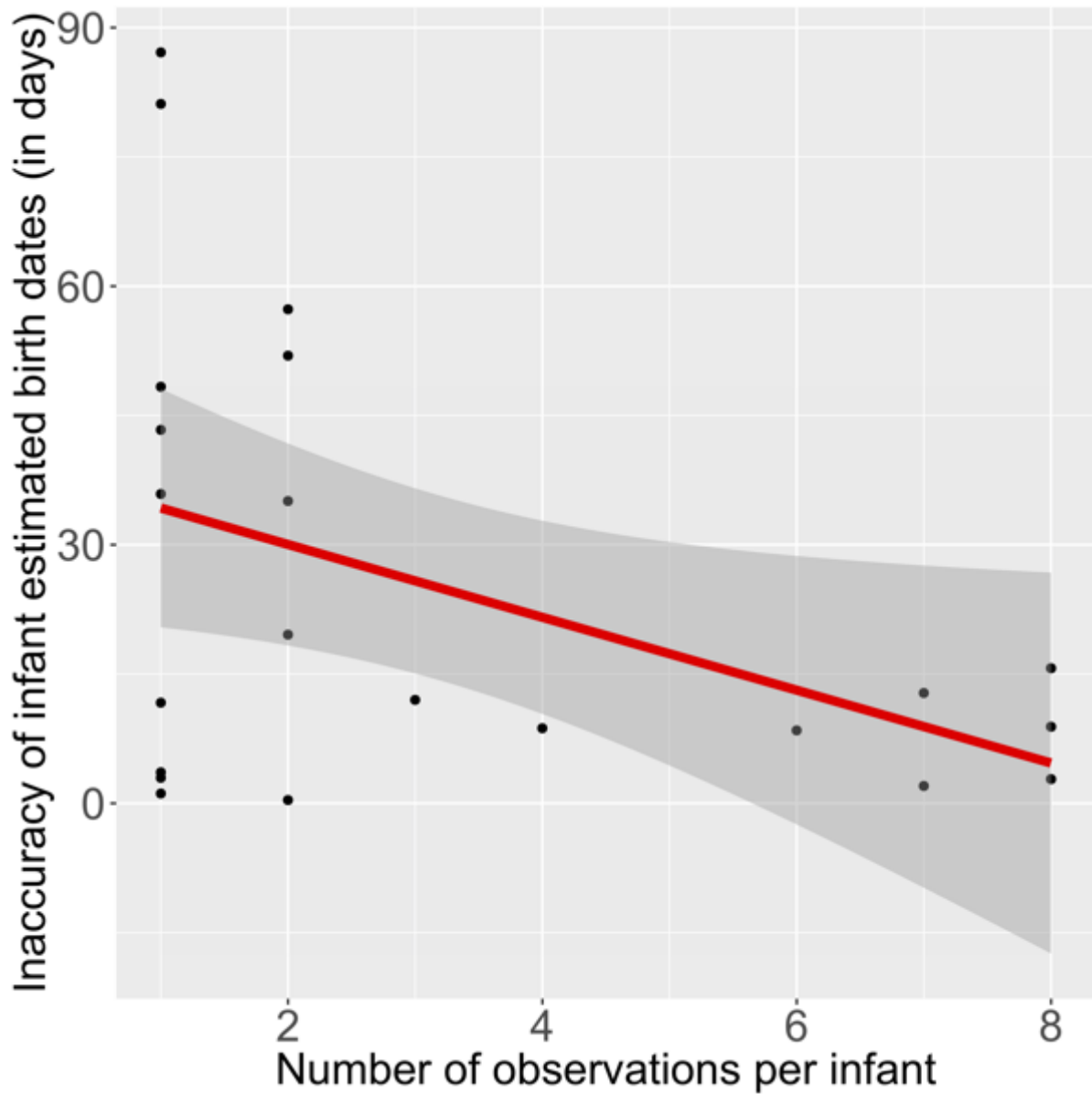
	Age	2.94	3.65	455.4	<1.10⁻³
	Infant identity	21.96	66.0	49.9	<1.10⁻³
	Intercept	-11.4	5.11		
	Food availability	59.3	30.3	3.83	0.05
	Infant date of birth	1.02	1.25	0.66	0.42
	Group (L)	1.28	1.51	0.72	0.40
Eye contours (Nobs=202 on Nind=64)	Sex (Male)	3.19	1.56	4.21	0.04
	Rank	1.91	2.33	0.68	0.41
	Parity (Primiparous)	-1.39	2.24	0.38	0.54
					P-
	Smooth effects	EDF	Ref.df	X ²	value
	Age	3.24	4.00	260	<1.10⁻³
	Infant identity	24.0	57.0	96.7	<1.10⁻³
	Intercept	4.14	3.24		
	Food availability	6.97	21.8	0.10	0.75
	Infant date of birth	0.89	0.90	0.96	0.33
	Group (L)	0.49	1.00	0.24	0.62
Hands & feet (Nobs=204 on Nind=66)	Sex (Male)	-0.49	1.01	0.24	0.63
	Rank	1.67	1.60	1.08	0.30
	Parity (Primiparous)	-1.21	1.53	0.63	0.43
					P-
	Smooth effects	EDF	Ref.df	X ²	value
	Age	3.33	4.11	325	<1.10⁻³
	Infant identity	33.9	59.0	120	<1.10⁻³
	Intercept	-1.88	3.84		
	Food availability	46.7	24.8	3.55	0.06
	Infant date of birth	1.81	1.00	3.24	0.07
	Group (L)	0.98	1.09	0.81	0.37
Muzzle (Nobs=240 on Nind=73)	Sex (Male)	2.25	1.11	4.07	0.04
	Rank	1.57	1.70	0.86	0.35
	Parity (Primiparous)	-0.40	1.62	0.06	0.81
					P-
	Smooth effects	EDF	Ref.df	X ²	value
	Age	3.83	4.67	451	<1.10⁻³
	Infant identity	42.7	66.0	184	<1.10⁻³
	Intercept	3.74	9.47		
	Food availability	-26.0	79.4	0.11	0.74
	Infant date of birth	3.59	1.16	9.65	2.10⁻³
	Group (L)	0.50	0.98	0.26	0.61
Muzzle tip (Nobs=92 on Nind=16)	Sex (Male)	-0.31	1.01	0.09	0.76
	Rank	1.46	1.53	0.91	0.34
	Parity (Primiparous)	-0.69	2.30	0.09	0.76
					P-
	Smooth effects	EDF	Ref.df	X ²	value
	Age	1.00	1.00	138	<1.10⁻³
	Infant identity	0.76	9.00	0.89	0.31

	Intercept	-9.66	3.24		
	Food availability	65.1	20.2	10.4	1.10⁻³
	Infant date of birth	2.06	0.83	6.18	0.01
Ischial	Group (L)	-0.59	1.00	0.35	0.00
callosity	Sex (Male)	0.00	1.02	0.00	0.99
(Nobs=144 on	Rank	1.44	1.68	0.73	0.39
Nind=47)	Parity (Primiparous)	1.60	1.52	1.12	0.29
	Smooth effects	EDF	Ref.df	X ²	P-value
	Age	1.00	1.00	98.8	<1.10⁻³
	Infant identity	17.9	40.0	42.0	<1.10⁻³

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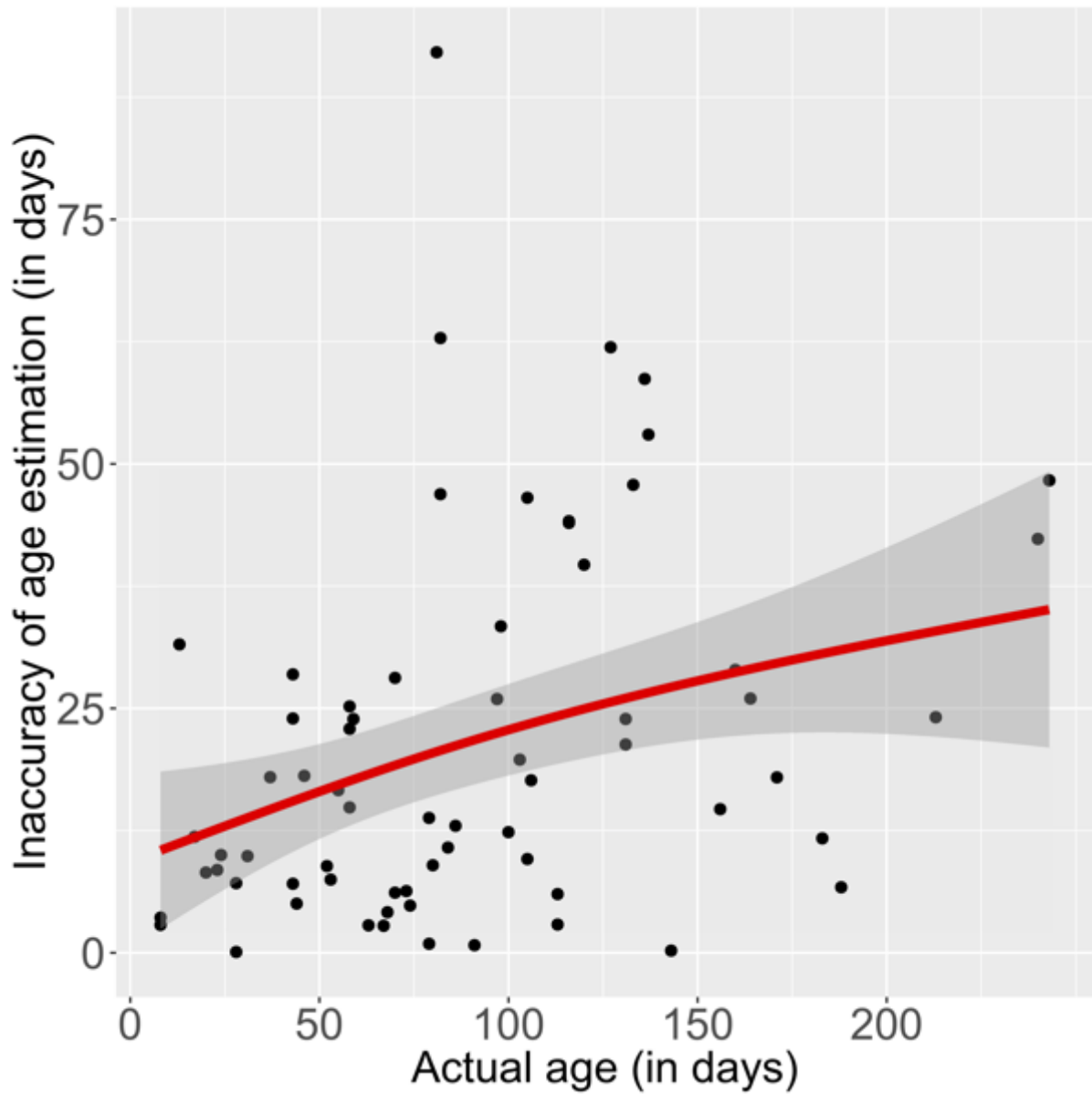
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909 **Figure S1:** Decreased inaccuracy of infant estimated birth dates (in days) in relation to the
910 number of observations per infant. The inaccuracy is the absolute number of days between an
911 infant actual birth date and its estimated birth date. The red curve shows the linear fit, and the
912 shaded area indicates the 95% confidence interval around it.



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918 **Figure S2:** Increased inaccuracy of age estimation (in days) in relation to the actual age of the
919 infant (in days). The inaccuracy is the absolute number of days between an infant actual and
920 estimated age per observation. The red curve shows the linear fit, and the shaded area
921 indicates the 95% confidence interval around it.



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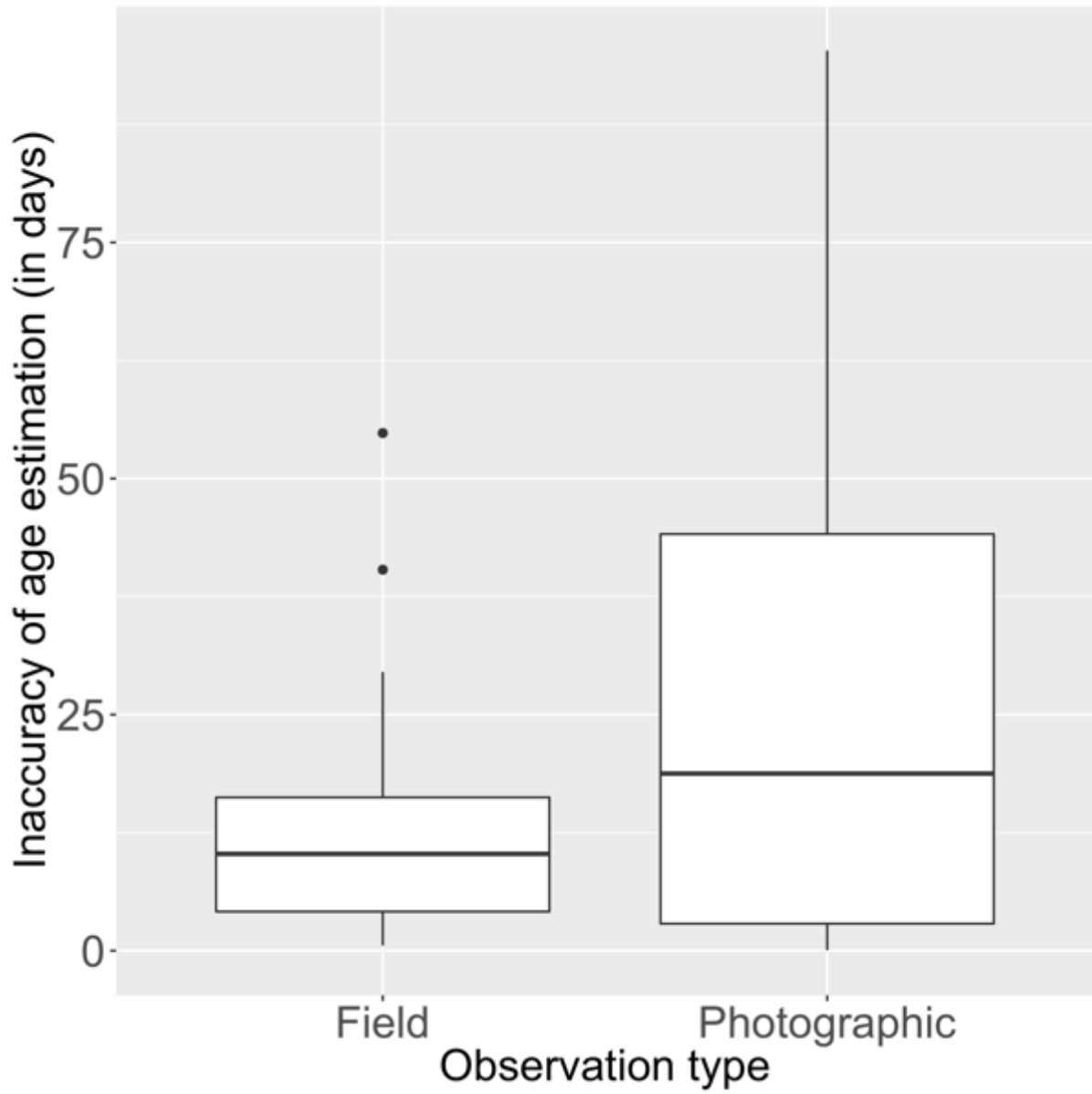
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927 **Figure S3:** Inaccuracy of infant age per estimation (in days) according to the observation
928 type, i.e. field of photographic observation. The inaccuracy is the absolute number of days
929 between an infant actual and estimated age per observation.



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