1 **Anthropogenic food enhancement alters the timing of maturational landmarks among**
2 **wild savanna monkeys (*Chlorocebus pygerythrus*)**
3
4 Christopher A. Schmitt[1*], Alicia M. Rich[1*], Stacy-Anne R. Parke[1], Maryjka B. Blaszczyk[2], Jennifer
5 Danzy Cramer[3], Nelson B. Freimer[4], J. Paul Grobler[5], Trudy R. Turner[5,6]
6
7 [1]Department of Anthropology, Boston University, Boston MA
8 [2]Department of Anthropology, University of Texas Austin, Austin TX
9 [3]Department of Sociology and Anthropology, American Public University System, Charles Town,
10 WV
11 [4]Brain Research Institute, University of California Los Angeles, Los Angeles, CA
12 [5]Department of Genetics, University of the Free State, Bloemfontein, FS, South Africa
13 [6]Department of Anthropology, University of Wisconsin Milwaukee, Milwaukee, WI
14
15 * These authors contributed equally to this work.
16
17 Corresponding Author:
18 Christopher A. Schmitt
19 232 Bay State Road,
20 Boston MA, 02215 USA
21 +1 617 353 5026
22 caschmit@bu.edu
23
29
30
31 **RUNNING TITLE:** Food Enhancement and Reproductive Onset in Vervet Monkeys
32
33

34   **ABSTRACT:**
35
36   Anthropogenic landscapes are rapidly replacing natural nonhuman primate habitats. Yet,

37   the access to anthropogenic resources on primate biology, health, and fitness remain poorly

38   studied. Given their ubiquity across a range of human impacted landscapes, from cities to

39   national parks, savanna monkeys (*Chlorocebus* spp.) provide an excellent study system in

40   which to test these effects. We compared body condition and reproductive maturation in vervets

41   (*Chlorocebus pygerythrus*) inhabiting a private farm in !Gariep Dam, with ample access to

42   anthropogenic foods, and wild-foraging vervets in Soetdoring Nature Reserve, South Africa.

43   Overall, vervets in !Gariep show significantly thicker skin folds, and higher BMI and body mass,

44   than those in Soetdoring, suggesting increased fat deposition. Males in !Gariep have larger

45   relative testis volumes at peri-pubescent ages compared to those in Soetdoring, suggesting

46   early reproductive maturation associated with age-specific increases in body mass. Females

47   from !Gariep showed evidence of an earlier onset of reproduction than those in Soetdoring,

48   based on parity status as assessed by nipple length and evidence of lactation. Parity status at

49   sub-adult dental ages was also strongly associated with body mass. These results are

50   consistent with a positive effect of anthropogenic food-enhancement on body fat deposition,

51   potentially linked to an earlier onset of reproductive maturation. Further investigation into

52   primate responses to cultivated resources will inform our understanding of the broader effects of

53   food enhancement on developmental plasticity.

54
55   **KEYWORDS:** anthropogenic impacts, human-wildlife proximity, nutrition, menarche,
56   reproductive maturation, vervet monkeys
57

58   **INTRODUCTION**

59   Research on primate life histories often focuses on inter-specific variation across the

60   order. In these studies, variation presumably reflects adaptive responses to long-sustained

61   predation risks, dietary constraints, demographic variables, or other long-term socioecological

62   factors (Hill 2005; Kamilar & Cooper 2013). Within species, however, life histories may also be

63   highly plastic in response to the energetic constraints of the uterine and postnatal environment.

64   Testicular tissue generation and spermatogenesis are energetically costly developmental

65   processes (Rato et al. 2012), and female reproduction has been well-established as energy-

66   limited (Pusey 2012). The initiation of puberty in both males and females, for example, is

67   controlled indirectly by nutrition and adiposity via the permissive effects of the adipose-derived

68   hormone leptin (Elias 2012). Undernutrition *in utero* delays testis growth and puberty in male

69   offspring (Zambrano et al. 2014). While maternal undernutrition delays ovarian development

70   and menarche in females, maternal overnutrition leads to early menarche (Zambrano et al.

71   2014). Overall, increased nutrient availability during postnatal development accelerates the

72   onset of reproductive traits, including ovarian function and menarche, testis development, the

73   emergence of secondary sexual characteristics, and subsequent onset of reproduction (Ellison

74   1990; Koziel and Jankowska 2002; Setchell & Lee 2004; Gluckman and Hanson 2006a).

75   Given this, it is not surprising that primate populations living in nutrient- or calorie-rich

76   environments consistently show relatively rapid life histories for their species, including earlier

77   ages at sexual maturity and first reproduction (Altmann & Alberts 2003; Kuzawa & Bragg 2012).

78   With the rapid expansion of human landscapes (Estrada et al. 2017), crop foraging and

79   provisioning are growing sources of food for wild non-human primates (Naughton-Treves et al.

80   1998; Strum 2010; Lodge et al. 2013; Hill 2017). These anthropogenic foods are often more

81   accessible than wild forage (Altmann & Muruthi 1988; Cancelliere et al. 2018), allowing primates

82   to save energy that they might otherwise spend searching for and processing food. Crops may

83   also be higher in available energy content (Saj et al. 1999, 2001; Riley et al. 2013), allowing for

84   an earlier threshold of reproductive maturation. While ecologically-mediated malnutrition can

85   slow reproductive timing and introduce life-long constraints on reproduction (Bercovitch & Strum

86   1993; Lea et al. 2015), anthropogenic foods may provide a release from such constraints.

87   Human-provisioned yellow baboons, for example, grow one-third faster and to almost twice the

3

88   size of their wild-foraging counterparts (Altmann & Alberts 2005; Onyango et al. 2013). Similarly,

89   crop foraging baboons in Gashaka-Gumti National Park in Nigeria showed shorter inter-birth

90   intervals and lower infant mortality (Higham et al. 2009), while Japanese macaques (*Macaca*

91   *fuscata*) also began giving birth at younger ages during periods of nutritional provisioning (Mori

92   1979).

93   Savanna monkeys (*Chlorocebus* spp.) adapt well to anthropogenically impacted habitats

94   throughout their range (Brennan et al. 1985; Saj et al. 2001; Lee & Priston 2005). Wild

95   populations are ubiquitous across sub-Saharan Africa and can also be found in a range of

96   ecologies, from nature reserves to intensive agricultural areas, with varying proximity to

97   anthropogenic landscapes (Fourie et al. 2015; Turner et al. 2018). They are also particularly

98   well-characterized behaviorally, genomically, and physiologically, both in the wild (Jasinska et

99   al. 2013; Svardal et al. 2017; Turner et al. 2018) and in captivity (Kavanagh et al. 2007; Schmitt

100   et al. 2018).

101   The growth and reproductive ecology of savanna monkeys has also been well-

102   characterized. Wild savanna monkeys show a menstrual cycle lasting a median of 33 days

103   (range: 25-46 days; *Ch. pygerythrus* near Kampala, Uganda; Rowell 1970). Although females

104   may mate throughout their cycle (Rowell 1970; Andelman et al. 1985), most savanna monkeys

105   have a distinct mating season from April through July (McFarland et al. 2014; Blaszcyk 2016).

106   As such, pregnancy and birth is largely seasonal, with most births in South African populations

107   occurring between October and December (Cheney et al. 1988; Blaszczyk 2016, Jarrett et al.

108   2020). In wild vervet monkeys, lactation begins during pregnancy and lasts between 9 and 18.5

109   months after birth (Whitten 1982; Lee 1984). Provisioned vervets have a shorter time to

110   weaning and earlier subsequent conceptions (Whitten 1982). Birth cohorts of wild-feeding South

111   African vervet monkeys (*Ch. pygerythrus*) reach adult size more slowly and at a later age than

112   those in captivity (Jarrett et al. 2020). In wild green monkeys (*Ch. sabaeus*) in St. Kitts & Nevis,

113   this leads to clear increases in body mass and better body condition in captive adults (Turner et

4

114   al. 2016). Relatively malnourished wild cohorts also grow more slowly and to a lighter adult

115   weight than those with ample food (Jarrett et al. 2020). Wild male vervets reach pubertal

116   landmarks beginning between 23 and 37 months with the descent of the testes, followed by

117   detectable spermatogenesis at 48-60 months (Whitten & Turner 2009), and ejaculatory

118   copulation at 60 months of age (Cheney et al. 1988). Dispersing males typically leave their natal

119   group between 48 and 84 months, with the majority leaving by 72 months (Cheney & Seyfarth

120   1983). Females do not give birth until 52-68 months, although vervets provisioned with human

121   food waste or living in resource rich environments tend to give birth at earlier ages (Brennan et

122   al. 1985; Cheney et al. 1988). The ability to bring an infant to term in wild female vervets is

123   contingent on both age and rank. Both very young mothers and older females have a higher

124   probability of miscarriage (Turner et al. 1987). Low ranking females, with presumably lower

125   priority of access to resources, are unable to reproduce annually (and the lowest ranked for

126   multiple years) unlike those of higher rank (Turner et al. 1987). In all previous comparative

127   studies among vervet populations, stark differences in attaining growth and maturational

128   landmarks were noted based on resource availability and quality (Cheney et al. 1988; Turner et

129   al. 1997; Whitten & Turner 2009; Turner et al. 2018; Jarrett et al. 2020).

130   Here we compare aspects of reproductive maturation and body condition in two

131   populations of vervet monkeys in South Africa, each living in similar biomes with contrasting

132   human impacts. The first population, in Soetdoring Nature Reserve, subsists primarily on natural

133   forage while experiencing only moderate human impacts (Blasczyzk 2016). The second

134   population, on private farms near the !Gariep Dam, has ample access to anthropogenic foods

135   and experiences high human impacts. We predicted that food-enhanced vervets living on

136   private farms near the !Gariep Dam, compared to those living in the Soetdoring Nature Reserve,

137   would exhibit (1) body condition consistent with increased nutritional enhancement, including

138   heavier body weight, higher body mass index (BMI), and thicker skin folds, and (2) associated

139   evidence of earlier reproductive maturation, as illustrated by (2a) an earlier increase in testis

140   volume and pubertal growth spurt in males, and (2b) earlier average age at first birth in females,

141   using nipple morphology as an indicator of parity.

142

143   **METHODS**

144   *Study Sites*
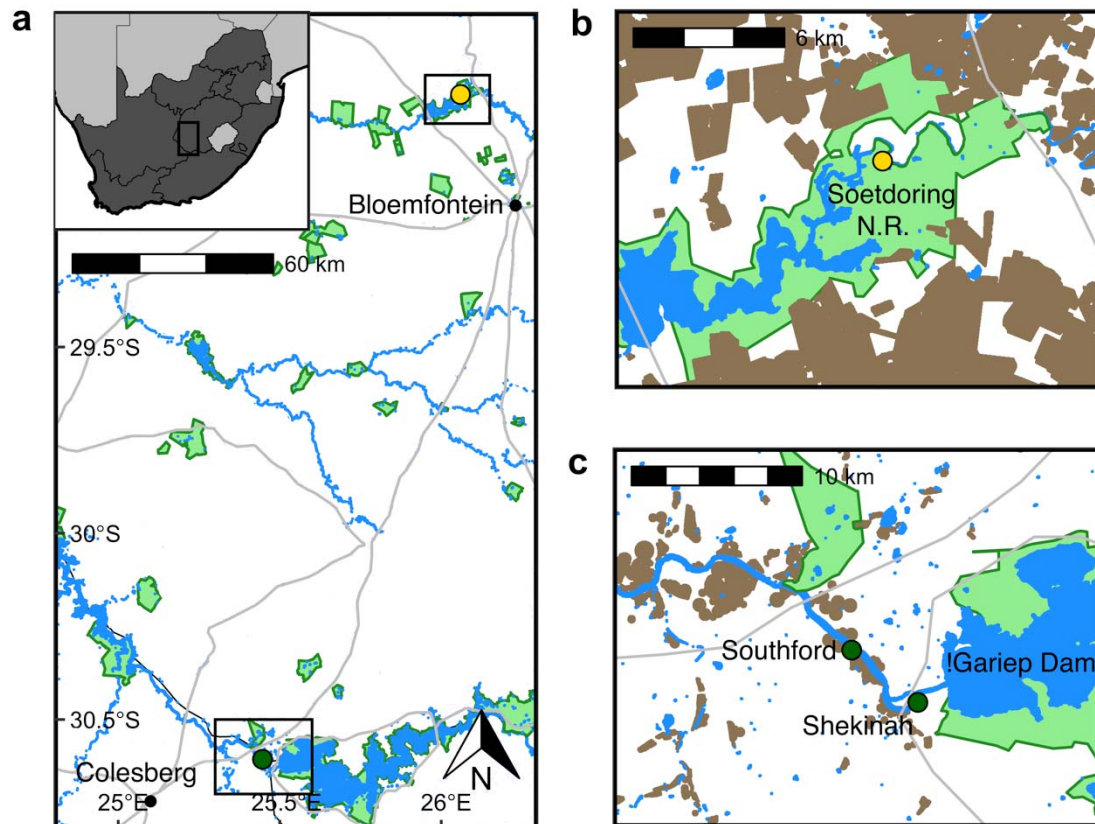
145
146   **Figure 1.** Study sites in South Africa (a), with insets of b) Soetdoring Nature Reserve and c) the !Gariep
147   Dam region. Brown areas indicate cropland, blue include rivers, and both naturally and dammed water
148   sources, while green are protected natural areas. Soetdoring Nature Reserve (gold circle) has fewer
149   human-wildlife interactions and provisioning, while private farms near the !Gariep Dam (green circles)
150   facilitate crop foraging and high calorie provisioning. Both study areas include mosaics of grassland and
151   Nama Karoo and have near identical ecological conditions outside immediate human impacts within their
152   ranges.

153
154   Both Soetdoring Nature Reserve and the !Gariep Dam farms occupy near-identical

155   grassland biomes (Janecke 2002; Janecke & du Preez 2005), at similar altitudes (1261 masl

156   and 1206 masl), and with similar levels of annual precipitation (79 mm and 72 mm) and

157   temperature (16.7° C and 16.9° C) over the past decade (Fig 1a). In both locations, vervet

6

158 groups primarily occupy riparian forest and adjacent *Acacia* thornveld (Blaszczyk 2016),

159 although the vervets in !Gariep spend much of their time in agricultural fields and orchards.

160 *Soetdoring Nature Reserve* (Fig 1b) occupies 6173 Ha of highveld grassland, including

161 the Modder River and the Krugersdrift Dam (Janecke & du Preez 2005). The vervet groups

162 studied here remain on the south side of the Modder River, primarily occupying riparian forest

163 and adjacent *Vachellia* thornveld near the eastern entrance to the reserve. Although they almost

164 exclusively subsist on natural forage, food scraps left by visitors were also eaten (Blaszczyk

165 2016). The landscape surrounding the reserve consists almost entirely of large-scale

166 agricultural fields consisting of maize, wheat, alfalfa, and sunflower cultivation.

167 *Southford Stud* and the *Shekinah Guest Farm* are private farms near the !Gariep Dam

168 (Fig 1c). Southford Stud is a 10,000-acre private farm primarily dedicated to horse husbandry,

169 straddling the Free State and Northern Cape provinces along the Orange River. It contains

170 several hundred acres of mixed pasture, riparian forest, and cropland including wheat, maize,

171 alfalfa, and pecans. Vervets at Southford Stud are also commonly seen eating the feed provided

172 *ad libitum* to the horses. The Shekinah Guest Farm, a 10 minute drive from Southford Stud, is a

173 tourist guest farm on the Orange River with riparian forest and small agricultural holdings,

174 including wheat and maize.

175

176 *Field Collections*

177 We trapped and sampled monkeys at both sites across four trapping seasons between

178 May and August in 2010 and 2016-2018 (Supplementary Table 1). Previous publications

179 provide greater detail on trapping and data collection methods (Jasinska et al. 2013; Turner et

180 al. 2018). We baited vervets with maize into modified drop traps (Grobler & Turner 2010), where

181 they were sedated by a veterinarian with 4 mg/kg of equal parts medetomidine/ketamine (2016-

182 2018) or ketamine/xylazine (2010). We placed subdermal microchips in the interscapular region

183 to facilitate identification. We collected morphological data as described by Turner et al. (1997;

7

184   2018): we used measuring tape for lower leg length (as the best proxy for body size in these

185   data, in keeping with Rodriguez et al. 2015), body length (for BMI, measured as body mass in

186   kg divided by body length in m squared) and waist circumference, a digital scale to measure

187   body mass, Lange calipers for skinfold thickness (mid-biceps, supra-iliac, sub-scapular, and

188   peri-umbilicus), and an ochidometer for testis volume (Karaman 2005; Cramer et al. 2013). We

189   assigned dental age categories and assessed approximate chronological ages using dental

190   eruption patterns as described in Turner et al. (2018) (Table 1). We assigned female parity

191   status based on nipple morphology (Altmann et al. 1981) and used digital photographs of the

192   torso taken during trapping to confirm field-based assignments. Female parity status was

193   determined based on nipple length as defined by Turner et al. (1997): nulliparous, wherein

194   nipples are flat to the chest; primiparous, wherein nipples are firm and noticeably protrude less

195   than a centimeter from the body; and multiparous, wherein nipples are limp and extend over a

196   centimeter from the body. We used transabdominal or rectal palpation to assess pregnancy

197   status (Turner et al. 1987; Eley 1992), and assessed lactation by the presence of expressible

198   milk from the nipple (Whitten & Turner 2009). Given that collections occurred over the first few

199   months after the breeding season, and that the earliest potential detection of pregnancy using

200   these methods in captive primates is ~30 days post-conception (van Pelt 1974; Eley 1992), it is

201   possible that females in our non-pregnant sample were in the early stages of pregnancy but not

202   detectable. We urge caution in interpreting the results specific to pregnancy status given that

203   maternal weight gain in primates can begin before the time when pregnancy is detectable by

204   palpation (e.g., in macaques: Kohrs et al. 1976; Kemnitz et al. 1984).

205

206   **Table 1**: Dental age categories based on tooth eruption sequences in Chlorocebus (from Turner

207   et al., 2018). Age range listed is the lower range for the initiation of that age class.

Dental age class	Permanent dentition present	Age range (months)
1	All deciduous	6 – 115 days

2	M1	12 – 14
3	M1, I1, I2	22 – 27
4	M1, I1, I2, M2	26 – 31
5	M1, I1, I2, M2, P3, P4	32 – 40
6	M1, I1, I2, M2, P3, P4, C	38 – 41
Adult	Eruption of M3	> 38

208

209

210   *Ethical Note*

211   These methods have been used with great success in these populations since 2009

212   (Jasinska et al. 2013; Turner et al. 2019). The processing of anesthetized animals rarely lasts

213   longer than 20 minutes, and all animals sampled in this study were successfully released back

214   to their social groups unharmed. Consistent with South African law, a licensed South African

215   veterinarian applied or supervised all invasive methods. The animal care and use committees at

216   Boston University, University of California at Los Angeles, the University of Wisconsin at

217   Milwaukee, and the University of the Free State approved all methods. All methods are

218   consistent with the Principles for the Ethical Treatment of Non-Human Primates by the

219   American Society of Primatologists.

220

221   *Statistical Analysis*

222   The sample for this study includes 245 wild vervets, including 135 males and 110

223   females (Table 2). We included only the initial trapping data for any vervets re-trapped within or

224   across field seasons. We conducted all analyses using R v. 3.6.1 (R Core Team 2019).

225   Measures indicative of body condition–including body mass, BMI, waist circumference, and

226   skinfold thicknesses–are all significantly correlated with each other. Previous work in *Macaca*

227   also show all of these measures scale strongly with adiposity (Colman et al. 1999). Colman et

228   al. (1999) found waist circumference to be the strongest indicator of central adiposity in *Macaca*.

229   In our sample, however, waist circumference showed an unacceptable level of variance across

9

230   sampling periods, so we discarded it. The 2010 sample lacked skinfold thickness measures, so

231   we used body mass and BMI as indicators of adiposity in our models.

232

233   **Table 2**: Summary statistics of vervet body measures.

Trait	Dental Age	Soetdoring				!Gariep			
		\multicolumn{2}{c}{Males}	\multicolumn{2}{c}{Females}	\multicolumn{2}{c}{Males}	\multicolumn{2}{c}{Females}
		n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
Body Mass (kg)	1	8	1.32 (0.27)	8	1.03 (0.28)	5	1.52 (021)	7	1.43 (0.17)
	2	15	2.02 (0.17)	12	1.82 (0.28)	22	2.13 (0.23)	10	2.08 (0.30)
	3	7	2.37 (0.34)	5	2.43 (0.19)	7	2.55 (0.51)	4	2.63 (0.28)
	4	10	2.94 (0.45)	5	2.48 (0.20)	4	2.97 (0.29)	5	2.52 (0.38)
	5	8	3.39 (0.56)	4	2.40 (0.28)	8	3.55 (0.79)	1	3.93
	6	4	4.34 (1.19)	11	3.35 (0.45)	4	5.19 (0.60)	14	4.00 (0.47)
	Adult	17	6.20 (0.70)	21	4.00 (0.44)	9	5.66 (0.69)	10	4.54 (0.49)
	Total	\multicolumn{2}{c}{69}	\multicolumn{2}{c}{66}	\multicolumn{2}{c}{59}	\multicolumn{2}{c}{51}
		\multicolumn{4}{c}{135}	\multicolumn{4}{c}{110}
		245
	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
BMI	1	8	21.58 (1.37)	8	18.90 (4.21)	5	22.65 (1.31)	7	22.02 (3.36)
	2	15	22.66 (2.18)	12	20.53 (1.86)	22	24.00 (2.46)	10	22.64 (2.39)
	3	7	22.43 (1.78)	5	24.39 (1.56)	7	25.06 (4.34)	4	24.54 (2.13)
	4	10	23.65 (2.24)	5	22.97 (1.81)	4	24.80 (2.29)	5	23.58 (1.36)
	5	8	26.25 (1.89)	4	22.42 (2.95)	8	27.14 (5.32)	1	29.50
	6	4	26.99 (3.08)	11	25.09 (3.73)	4	36.31 (5.81)	14	30.61 (2.94)
	Adult	17	32.47 (3.12)	21	27.46 (2.36)	9	31.38 (2.70)	10	29.36 (3.45)
	Total	\multicolumn{2}{c}{69}	\multicolumn{2}{c}{66}	\multicolumn{2}{c}{59}	\multicolumn{2}{c}{51}
		\multicolumn{4}{c}{135}	\multicolumn{4}{c}{110}
		245
	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
Subscapular SFT (cm)	1	5	1.7 (0.5)	6	1.4 (0.5)	5	2.1 (0.2)	6	2.1 (0.2)
	2	11	1.9 (0.4)	8	1.9 (0.2)	15	2.0 (0.1)	10	2.3 (0.5)
	3	6	1.8 (0.3)	5	1.8 (0.3)	4	2.8 (0.5)	1	2.5
	4	6	1.8 (0.4)	4	1.9 (0.3)	4	2.4 (0.5)	1	2.0

	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
	5	5	2.2 (0.5)	3	2.0 (0.0)	3	2.3 (0.5)	1	3.0
	6	3	2.3 (0.6)	10	1.9 (0.5)	1	2.0	7	2.9 (0.5)
	Adult	14	1.9 (0.4)	12	2.0 (0.3)	1	3.0	5	2.9 (0.2)
	Total	50		48		33		31	
		98				64			
		162							
Above Umbilicus SFT (cm)	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
	1	5	1.9 (0.2)	6	1.5 (0.5)	5	2.3 (0.5)	6	2.3 (0.3)
	2	11	1.9 (0.4)	8	1.6 (0.4)	15	2.0 (0.5)	10	2.4 (0.5)
	3	6	1.7 (0.4)	5	1.3 (0.7)	4	2.8 (1.0)	1	2.5
	4	6	2.0 (0.0)	4	1.8 (0.5)	4	2.8 (0.5)	1	2.5
	5	5	2.2 (0.5)	3	2.2 (0.8)	3	2.3 (0.6)	1	3.5
	6	3	2.0 (0.0)	10	2.4 (1.0)	1	2.0	7	4.1 (1.6)
	Adult	14	1.9 (0.6)	12	1.9 (0.8)	1	4.0	5	2.6 (1.3)
	Total	50		48		33		31	
		98				64			
		162							
Below Umbilicus SFT (cm)	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
	1	5	1.3 (0.3)	6	1.2 (0.3)	5	2.0 (0.6)	6	2.2 (0.3)
	2	11	1.4 (0.4)	8	1.3 (0.4)	15	1.8 (0.5)	10	1.8 (0.4)
	3	6	1.5 (0.6)	5	1.4 (0.6)	4	2.4 (0.5)	1	2.0
	4	6	1.8 (0.4)	4	1.8 (0.5)	4	2.0 (0.0)	1	2.0
	5	5	2.1 (0.7)	3	1.7 (0.3)	3	2.2 (0.8)	1	2.0
	6	3	2.3 (0.6)	10	2.1 (0.8)	1	2.0	7	2.8 (0.8)
	Adult	14	1.5 (0.4)	12	1.7 (0.8)	1	2.5	5	2.1 (0.6)
	Total	50		48		33		31	
		98				64			
		162							
Mid-Biceps SFT (cm)	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
	1	5	1.8 (0.3)	6	1.2 (0.4)	5	2.0 (0.4)	6	1.8 (0.3)
	2	11	1.7 (0.5)	8	1.4 (0.4)	15	1.8 (0.3)	10	1.8 (0.3)
	3	6	1.4 (0.4)	5	1.5 (0.5)	4	2.0 (0.0)	1	2.0
	4	6	1.8 (0.3)	4	1.9 (0.3)	4	2.0 (0.0)	1	2.0
	5	5	2.0 (0.0)	3	2.0 (0.0)	3	2.0 (0.5)	1	2.0
	6	3	2.0 (0.0)	10	1.8 (0.5)	1	2.0	7	1.9 (0.5)

	Adult	14	2.1 (0.2)	12	1.6 (0.5)	1	2.0	5	1.8 (0.3)
	Total		50		48		33		31
			98				64		
					162				

	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
Suprailiac SFT (cm)	1	5	1.5 (0.4)	6	1.25 (0.4)	5	2.3 (0.7)	6	2.2 (0.5)
	2	11	1.5 (0.5)	8	1.25 (0.4)	15	1.9 (0.4)	10	2.3 (0.4)
	3	6	1.3 (0.5)	5	1.5 (0.5)	4	2.3 (0.5)	1	2.0
	4	6	1.7 (0.4)	4	1.4 (0.5)	4	2.3 (0.5)	1	2.0
	5	5	1.8 (0.5)	3	2.0 (0.0)	3	1.7 (0.6)	1	3.0
	6	3	2.0 (0.0)	10	1.8 (0.5)	1	2.0	7	2.4 (0.5)
	Adult	14	1.8 (0.4)	12	1.6 (0.5)	1	2.0	5	2.4 (0.6)
	Total		50		48		33		31
			98				64		
					162				

	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
Testis Volume (cc)	1	8	0.6 (0.2)	-	-	5	0.6 (0.2)	-	-
	2	15	0.7 (0.4)	-	-	22	1.0 (1.0)	-	-
	3	7	0.6 (0.2)	-	-	7	1.1 (0.5)	-	-
	4	10	1.0 (0.4)	-	-	4	0.8 (0.3)	-	-
	5	8	1.2 (0.5)	-	-	8	2.1 (0.8)	-	-
	6	4	5.6 (3.9)	-	-	4	13.0 (6.3)	-	-
	Adult	17	17.4 (5.9)	-	-	9	14.8 (6.0)	-	-
	Total		69		0		59		0
			69				59		
					128				

234

235   We compared body measures across age, sex, and site using Welch's ANOVA, with

236   non-parametric Games-Howell post-hoc tests to account for differences in variance and small

237   sample sizes across categories. We ran a separate Type II ANOVA with Games-Howell post-

238   hoc tests on subsets of females for which pregnancy or lactation were noted in dental age 6 and

239   adulthood to assess the impact of these statuses on body mass, BMI, and skinfold thickness.

240   Dental age 5 was excluded from ANOVAs analyzing female variation due to low sample size in

241   !Gariep (n = 1). Although both pregnancy and lactation status were accompanied by significantly

242   heavier body mass and higher BMI in dental ages 6 and adulthood among these subsets (see

243   Results and Supplemental Information), we did not include them as covariates in maturation

244   models as doing so would have significantly reduced our sample size.

245   We modeled indicators of maturation in two phases: a pre-pubertal phase with relative

246   stasis in trait state, and a peri-pubertal phase with marked change across age categories

247   through adulthood. We placed the dividing line for these models at dental age 4 in both sexes.

248   For males, we modeled testis volume as a continuous variable, cube root transformed to reduce

249   the measure to one dimension, using loess curves for visualization and generalized linear

250   regression with a Gamma error family and log link function with location, dental age, and

251   indicators of body condition as covariates. We used the Akaike Information Criterion with a

252   correction for small sample size (AICc) and likelihood ratio tests to assess covariate inclusion.

253   We assessed model fit as $R^2 = 1 - \frac{Residual\ Deviance}{Null\ Deviance}$. For females, there was no variation in

254   nipple morphology prior to dental age 4, so we did not model this trait for the pre-pubertal

255   phase. In the female peri-pubertal phase, we binned parity status into a binary variable –

256   nulliparous vs. parous – modeled using logistic regression with location, dental age, and

257   indicators of body condition as covariates. We also used Fisher's exact tests to assess relative

258   proportions of parity in each age category between sites.

259

260   *Data Availability*

261   The final datasets generated and analyzed during this study are available from the

262   corresponding author upon reasonable request.

263

264   **RESULTS**

265   *Morphometric indicators of body condition*

266   Individuals in !Gariep were, overall, significantly heavier than those in Soetdoring for

267   both females (ANOVA: $F_{1,103}$ = 29.68, P < 0.001), and males ($F_{1,114}$ = 3.64, P = 0.059), although

268   these differences only emerged beginning in the peri-pubertal phase (dental age 5, or 32-40

269   months of age; Fig. 2). Only one female from dental age 5 was sampled in !Gariep (body mass

270   = 3.93 kg), making comparison across sites difficult at this age, although she weighed much

271   more than any female sampled in that age category at Soetdoring (body mass = 2.40 ± SD 0.28

272   kg). At dental age 6, females in !Gariep were heavier than in Soetdoring (Games-Howell: Δ_{mean} =

273   0.64 kg, t = 3.50, df = 22.13, P = 0.082), and this difference continued into adulthood (Games-

274   Howell: Δ_{mean} = 0.60 kg, t = 3.48, df = 22.91, P = 0.084). Males showed no significant

275   differences in body mass within age categories across sites ($F_{6,114}$ = 1.03, P = 0.407).

276   Although pregnancy and lactation both were accompanied by significant increases in

277   body mass for females (see below), site and age category showed larger effects, with adult

278   females being significantly heavier than subadults (ANOVA: $F_{5,31}$ = 19.67, P < 0.001;

279   Supplementary Table 2) and females in !Gariep being significantly heavier than those in

280   Soetdoring ($F_{1,31}$ = 32.27, P < 0.001). Pregnant females were heavier, overall, than non-

281   pregnant females ($F_{1,31}$ = 5.40, P = 0.027). In dental age 6, pregnant females in Soetdoring were

282   7% heavier than non-pregnant females (N_{preg} = 6 of 10, Δ_{mean} = 0.25 kg), while in !Gariep

283   pregnant females were 11% heavier than non-pregnant females (N_{preg} = 5 of 11, Δ_{mean} = 0.46

284   kg). Although pregnant adult females in Soetdoring were 13% heavier than non-pregnant adult

285   females (N_{preg} = 2 of 12; Δ_{mean} = 0.54 kg), there was no detectable difference in body mass

286   based on pregnancy in !Gariep adults (N_{preg} = 2 of 6; Δ_{mean} = 0.05 kg). Similarly, although

287   lactating females were, overall, heavier than non-lactating females ($F_{1,47}$ = 8.35, P = 0.006;

288   Supplementary Table 9), these differences were small compared to those between subadults

289   and adults ($F_{1,47}$ = 13.22, P < 0.001) and between !Gariep and Soetdoring ($F_{1,47}$ = 12.82, P <

14

290   0.001). There was no statistically significant difference in body mass by lactation status within

291   each site among adults, although lactating adult females were ~6% heavier than non-lactating

292   females in each. Lactating females in !Gariep at dental age 6 were heavier (11%) than non-

293   lactating females (N_{lact} = 7 of 14; Δ_{mean} = 0.63 kg); no females in dental age 6 in Soetdoring were
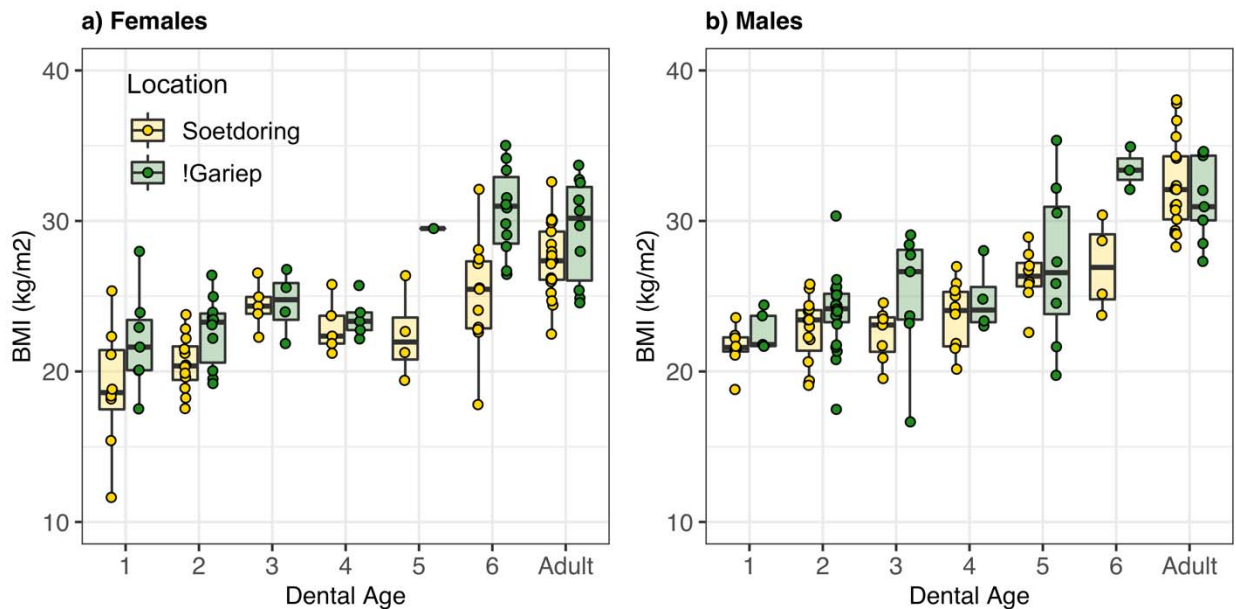
294   observed to be lactating.
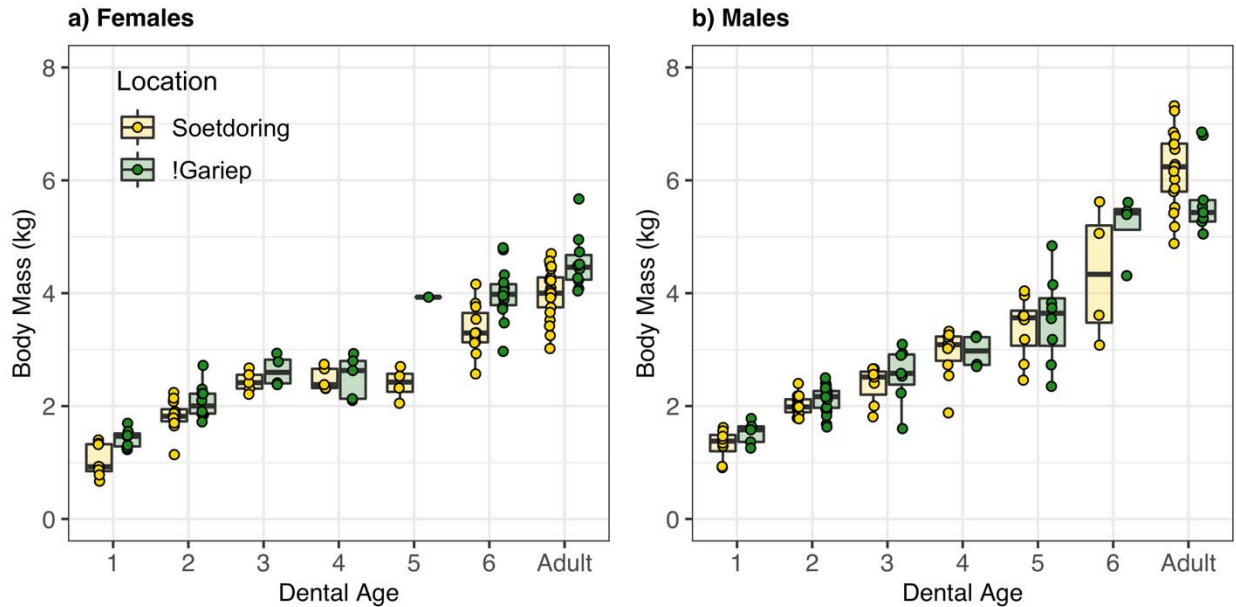
296   **Figure 2.** Body mass (kg) in a) female and b) male vervet monkeys across each dental age category. For
297   estimated chronological ages, see Table 1.
298

299   BMI was significantly higher overall for females in !Gariep compared to Soetdoring

300   (ANOVA: $F_{1,103}$ = 14.47, P < 0.001), but BMI did not differ significantly between the two sites

301   within any particular age/sex class except at dental age 6, in which !Gariep females had

302   significantly higher BMI than those in Soetdoring (Games-Howell: Δ_{mean} = 5.52 kg/m^2, t = 4.02, df

303   = 18.75, P = 0.033). BMI was also significantly higher, overall, in !Gariep males than in males at

304   Soetdoring ($F_{1,114}$ = 5.23, P = 0.024), but there were no significant differences within age

305   classes across sites.

306   Pregnant females had a significantly higher BMI, overall, than non-pregnant females

307   (ANOVA: $F_{1,31}$ = 4.64, P = 0.039; Supplementary Table 3), but this was overshadowed by

308   differences between sites ($F_{1,31}$ = 17.63, P < 0.001). Although pregnant adult females had 9%

309   higher BMI than non-pregnant adult females in Soetdoring (Δ_{mean} = 2.7 kg/m^2), no difference

310   was seen in !Gariep (Δ_{mean} = 0.0 kg/m^2). In dental age 6, pregnant females in Soetdoring had

311   10% higher BMI than non-pregnant (Δ_{mean} = 2.7 kg/m^2), and in !Gariep the BMI of pregnant

312   females was 3% higher (Δ_{mean} = 0.9 kg/m^2). Lactating females, overall, had higher BMI than

313   non-lactating ($F_{1,47}$ = 4.05, P = 0.050; Supplementary Table 10). Lactating adult females in

314   Soetdoring had 2% higher BMI (Δ_{mean} = 0.5 kg/m^2) and in !Gariep had 13% higher BMI (Δ_{mean} =

315   4.1 kg/m^2), although neither difference was statistically significant. Lactating females in dental

316   age 6 in !Gariep had 8% higher BMI than non-lactating females (Δ_{mean} = 2.6 kg/m^2).

317

319   **Figure 3.** Body mass index or BMI (kg/m^2) in a) female and b) male vervet monkeys across each dental
320   age category. For estimated chronological ages, see Table 1.
321

322   All skin folds measured were significantly thicker in !Gariep compared to Soetdoring (Fig

323   4), except for mid-biceps in males. There were no significant age-related differences in any skin

324   fold thickness. Overall, vervets in !Gariep showed significantly thicker skin folds, including the

325   subscapular (males, $F_{1,81}$ = 13.34, P < 0.001; females, $F_{1,78}$ = 33.15, P < 0.001), above

326   umbilicus (males, $F_{1,81}$ = 10.63, P = 0.0016; females, $F_{1,78}$ = 18.35, P < 0.001), below umbilicus

327   (males, $F_{1,81}$ = 11.10, P = 0.0013; females, $F_{1,78}$ = 15.44, P < 0.001), mid-biceps (males, $F_{1,81}$ =

328   1.34, P = 0.25; females, $F_{1,78}$ = 8.53, P = 0.0046), and suprailiac (males, $F_{1,81}$ = 12.97, P <

329   0.001; females, $F_{1,78}$ = 50.35, P < 0.001). Pregnancy was generally not associated with thicker

330   skin folds (Supplementary Tables 4-8, 11-15), with the notable exceptions of the mid-biceps

331   (ANOVA: $F_{1,27}$ = 10.00, P = 0.0039; Supplementary Table 7) and suprailiac ($F_{1,27}$ = 4.12, P =

332   0.052; Supplementary Table 8), which were thicker during pregnancy in Soetdoring but thinner

333   during pregnancy in !Gariep ($F_{1,27}$ = 7.51, P = 0.011). The suprailiac skin fold was also thicker in

334   Soetdoring but thinner in !Gariep in lactating compared to non-lactating females ($F_{1,27}$ = 4.39, P

335   = 0.045; Supplementary Table 15).
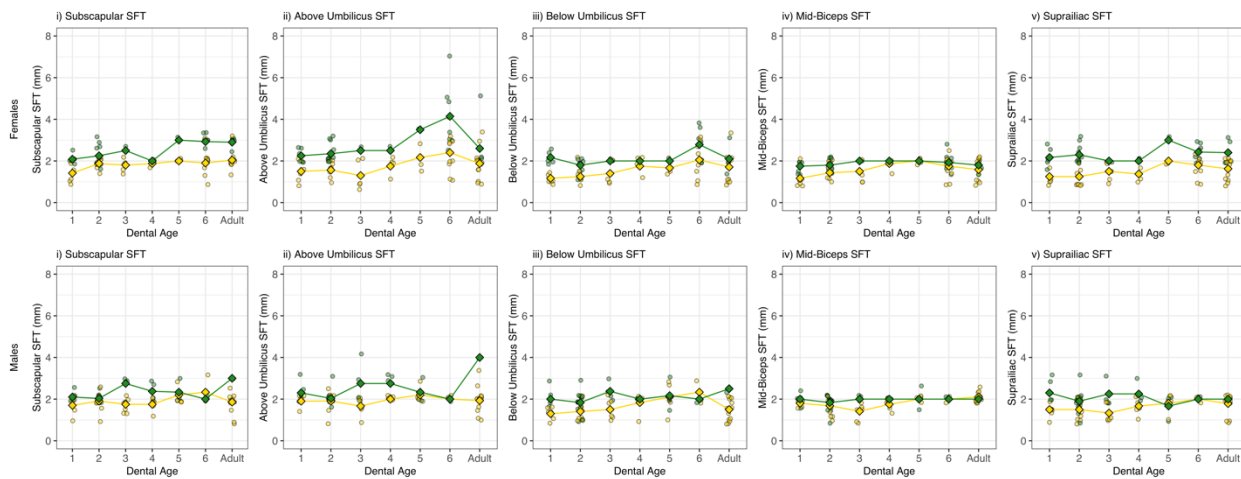
336

337   **Figure 4**. Mean i) subscapular, ii) above umbilicus, iii) below umbilicus, iv) mid-biceps, and v) suprailiac

338   skin fold thickness in a) females, and b) males for vervets sampled in !Gariep (green) and Soetdoring

339   (gold). Individual measurements are shown to demonstrate range.

340

341   *Male maturation – Relative testis volume*

342   Differing patterns of testis growth distinguished males in Soetdoring from those in

343   !Gariep, using both absolute and relative testis volume as measures (Fig 5). Although both

344   absolute and relative testis volume appears larger in !Gariep for age categories 5 and 6, these

17

345   differences were not significant. In adulthood, both relative and absolute testis volume was the

346   same between the two sites.
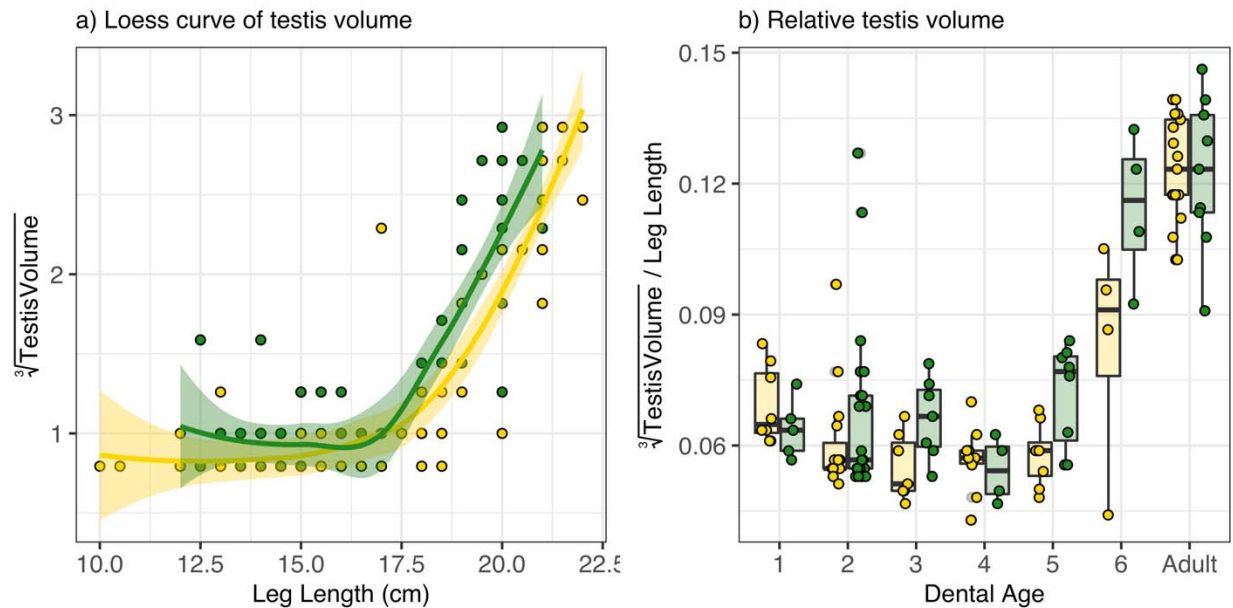
347
348   **Figure 5.** Boxplot of a) loess curves representing growth in absolute testis volume by body mass, and b)
349   relative testis volume in males (testis volume/leg length) across each dental age category. See Table 2
350   for sample sizes. Gold indicates males sampled at Soetdoring Nature Reserve, while green represents
351   males sampled in the !Gariep Dam region.
352

353   The pre-pubertal model with the lowest AICc included only body mass as a significant

354   negative covariate of relative testis volume, albeit of small effect (β = -0.042, P = 0.0048; R^2 =

355   0.12; Table 3a). The peri-pubertal model with the lowest AICc included location (Soetdoring vs.

356   !Gariep), dental age category, body mass, and an interaction term between age and body mass

357   as covariates (Table 3b). In this model, males in !Gariep had significantly larger relative testis

358   volume overall compared to those in Soetdoring (β = 0.088, P = 0.019; R^2 = 88.47). After

359   accounting for body mass, dental age category was not significantly related to relative testis

360   volume. Males in age category 6, however, showed a significantly larger increase in relative

361   testis size as body mass increased (β = 0.295, P = 0.008).

362

363   **Table 3**: Models of Relative Testis Volume

364

18

a) Pre-Pubertal (Age Categories 1 - 4) Model

RTV ~ Body Mass	Estimate	Error	p value	
Intercept	-2.673	0.059	< 0.001	***
Body Mass	-0.081	0.026	0.003	**

b) Peri-Pubertal (Age Categories 4 - Adult) Model

RTV ~ Age * Body Mass + Location		Estimate	Error	p value	
Intercept		-2.820	0.279	< 0.001	***
Location (!Gariep)		0.088	0.037	0.019	*
Age Category		-	-	-	
	5	0.038	0.334	0.909	
	6	-0.842	0.377	0.029	*
	Adult	0.021	0.363	0.954	
Body Mass		-0.029	0.094	0.760	
Body Mass : Age Category 5		0.028	0.107	0.797	
Body Mass : Age Category 6		0.295	0.107	0.008	**
Body Mass : Age Category Adult		0.140	0.102	0.174	

365

366

367 *Female maturation – Parity status by nipple length*

368   As indicated by nipple morphology, no female sampled in Soetdoring showed signs of

369 parity before dental age 6 (Fig 6). Two Soetdoring females in the adult sample were

370 primiparous. In !Gariep, primiparity began at dental age 4 (26-31 months), and eight females

371 were already multiparous by dental age 6. All adult females (N = 30) had given birth at least

372 once. The model with the lowest AICc for parity included body mass and location as covariates,

373 along with their interaction term (R^2=0.796; Table 4). Body mass, overall, had a significant

374 positive association with parity status (β = 0.745, P = 0.009). No Fisher's exact test of parity

375 status across sites within age categories showed significant differences.

376
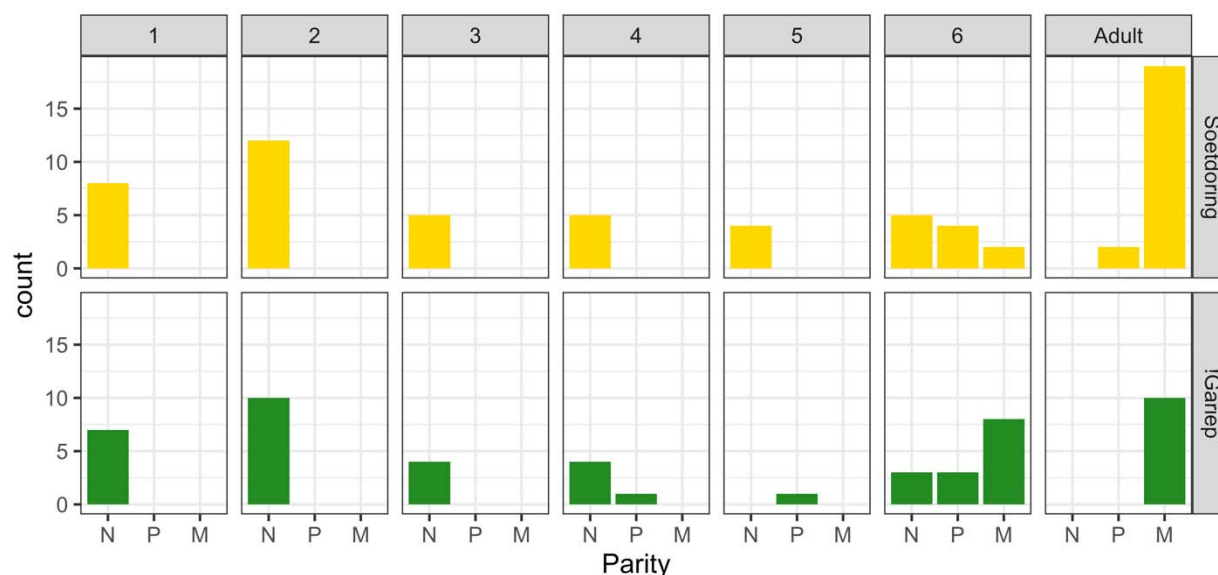
Figure 6. The number of females exhibiting nipple morphology indicative of each parity category (N = Nulliparous, P = Primiparous, M = Multiparous) within each dental age, compared between sites.

Table 4: Logistic Regression Model for Female Parity

Parity ~ Body Mass*Location	Estimate	Error	p value	
Intercept	-23.482	9.094	0.010	**
Body Mass	7.445	2.857	0.009	**
Location (!Gariep)	11.486	9.736	0.238	
Body Mass : Location(!Gariep)	-3.900	3.020	0.197	

DISCUSSION

The vervets in !Gariep show clear evidence of better body condition, with significantly thicker skin folds in all parts of the body measured, with significantly higher body mass and BMI overall, as well as within specific age/sex categories. Differences in body mass between the two sites become apparent in males at dental age 6 (Fig 2), when !Gariep males appear heavier than in Soetdoring. This timing is generally consistent with the pubertal growth spurt for males of this taxon (Turner et al. 2019; Jarrett et al. 2020). Given that males in !Gariep are not then

20

392   significantly heavier in adulthood than those in Soetdoring, we interpret as evidence of an earlier

393   peak of growth at !Gariep. Turner et al. (2019) note a typical pubertal growth spurt in female

394   vervets in dental age 4 or 5 (after approximately 24 months), consistent with the generally

395   earlier onset of reproduction in cercopithecine females relative to males (Bercovitch 2000).

396   Although our sample size for these age categories is unfortunately small, we do note that the

397   one !Gariep female sampled at dental age 5 was comparable in weight to dental age 6 females,

398   and females remain significantly heavier in !Gariep compared to Soetdoring from this age

399   through adulthood.

400   Given the earlier and more exaggerated increases in mass at !Gariep, it is unclear why

401   adult males do not also appear heavier in !Gariep. That much larger male body size in

402   provisioned groups appears to be the norm in previously studied populations (e.g., Altmann &

403   Alberts 2005) makes this more puzzling. This could potentially be explained by male-biased

404   dispersal in vervets, particularly in the context of these study groups (Henzi and Lucas 1980;

405   Cheney and Seyfarth 1983; Turner et al. 2019). Provisioning is rare for the vervets in Soetdoring

406   Nature Reserve, but the reserve is bordered entirely by cropland (Fig 1b). No one has observed

407   the entire study groups sampled here crossing the Modder River into these agricultural areas,

408   although on two separate occasions individuals, including an identified subadult male, were

409   observed to swim across the river and back (Blaszczyk 2016; Nick Theron, personal

410   communication). As such, although males may cross the Modder River on occasion and for

411   dispersal purposes, the river may serve as a barrier limiting regular access to anthropogenic

412   foods for females. Adult males that disperse into our study groups from these farms may have

413   benefitted from consistent food enhancement from crops during development. Conversely, the

414   farms in !Gariep are relatively isolated agricultural areas surrounded by bushveld and nature

415   reserves (Fig 1c), suggesting that adult males dispersing into these farms may come from less

416   well-provisioned areas. Given this, it is possible that we are seeing heavier than expected males

417   in Soetdoring, and lighter than expected males in !Gariep, given the nutritional environments to

418   which pre- and peri-pubertal males in these populations have access.

419   Our best model for pre-pubertal testis size suggests a significant decrease in relative

420   testis size with age until puberty. This result reflects a relative stasis in testis size as body mass

421   increases through the juvenile phase of development. Along with an earlier significant increase

422   in body mass, peri-pubertal males in !Gariep show significantly larger relative testis volume than

423   in Soetdoring in dental ages 5 and 6 (Fig 3), ultimately leading to similar relative testis volumes

424   by adulthood. Increases in testosterone levels accompanied by a 15% increase in testis volume

425   in captive vervets during the breeding season suggest that a larger testis volume may confer a

426   higher chance of fertilization (Eley et al. 1986; Eley 1992). Sample collection was limited to June

427   through August, which is just after the peak breeding season, characterized as April to June

428   throughout South Africa (Blaszczyk 2016; McFarland et al. 2014). Given that our sampling was

429   constrained to this season alone, we do not think that seasonal effects are a concern.

430   Intraspecific variation in testis size is associated with higher circulating testosterone

431   concentration, sperm quality, and fitness (Schulte-Hostedde et al. 2004; Hamada et al. 2005).

432   However, the larger testis volume during these ages in !Gariep appears to be a developmental

433   pattern, not leading to substantial adult differences translatable to long-term increases in fertility

434   beyond a potentially earlier initiation of reproduction. This earlier reproductive maturation, if

435   paired with an earlier age at dispersal, could lead to an earlier age at first reproduction in males

436   and higher fitness. Previous work in Soetdoring, however, only observed the intergroup transfer

437   of adults and one very large subadult male (Blasczyzk 2016); we have not yet carried out long

438   term behavioral observations in !Gariep populations. To assess whether the earlier increase in

439   testis volume in !Gariep could lead to earlier reproduction will require more extensive behavioral

440   observations and direct continuous monitoring of these populations.

441   Despite evidence of primiparity at dental ages 4 and 5 in !Gariep, our sample size limits

442   our ability to interpret the relative timing of reproductive onset in females between these

22

443   populations. Given that nipple morphology appears to be directly related to use, this suggests

444   that female vervets begin nursing at a younger age on the !Gariep farms, indicating earlier onset

445   of reproduction. Additionally, nearly half of the females in dental age 6 in !Gariep were observed

446   to be lactating, compared to none in Soetdoring (although nearly half of the females in this age

447   category were noted to be pregnant in both populations). Given these indicators are reliable

448   signs of earlier reproduction in !Gariep, it would be consistent with the human and non-human

449   primate literature showing strong correlations between nutritional enrichment and earlier

450   menarche and age at first birth (Mori 1979; Cheney et al. 1988; Altmann and Alberts 2005;

451   Gluckman and Hanson 2006a), having reached a critical threshold of body fatness or body

452   mass for reproductive viability at an earlier age (e.g., Wade & Schneider 1996). The overall

453   higher body mass and BMI of pregnant and lactating females in both dental age 6 and

454   adulthood could reflect that pattern, and suggest that the earlier attainment of heavier body

455   mass allowed !Gariep females to initiate reproduction sooner. Alternatively, the added weight

456   and BMI could be a byproduct of their reproductive status, reflecting weight-gain associated with

457   pregnancy or in preparation for extended lactation (McFarland 1997).

458   One weakness of this study is that we lack longitudinal behavioral observations of

459   foraging/feeding, copulation, and birth to pair with these proxy measures. Calorie-rich crop

460   foraging is a logical conclusion given the otherwise uniform natural ecologies of these sites. Still,

461   without foraging observations we cannot demonstrate which environmental factor at !Gariep is

462   directly responsible for the earlier attainment of these maturational landmarks. We were also

463   unable to control for behavioral factors that may have influenced access to anthropogenic

464   resources, including rank. In wild populations, rank mediates priority of access to resources,

465   leading to accelerated growth and earlier maturation in more highly ranked individuals (Whitten

466   1983; Bercovitch & Strum 1993; Onyango et al., 2013; Jarrett et al., 2020). This same priority of

467   access influences access to anthropogenic food resources in urban macaques, with males and

468   high ranking females getting more caloric benefits, potentially limiting the fitness benefits of

469   these foods for lower-ranking females (Marty et al. 2019).

470   Additionally, without hormonal data it is difficult to directly link the evidently higher body

471   fatness in !Gariep with the apparently earlier onset of reproduction. In many cases of early

472   reproductive onset in humans and non-human primates, increased caloric intake is thought to

473   drive this pattern (Altmann and Alberts 2005; Gluckman and Hanson 2006a; Wade & Schneider

474   1996). However, there are known mediating factors. Low birth weight derived from insufficient

475   nutrition *in utero*, and rapid postnatal growth during critical developmental stages, for example,

476   often precede early reproductive maturation in human and non-human primates of both sexes

477   (Ibáñez et al. 2000; Kuzawa et al. 2010). High age-specific levels of body fatness and

478   associated hormone levels, such as elevated circulating levels of the adipose-derived hormone

479   leptin, are also associated with accelerated developmental trajectories and the earlier timing of

480   reproductive maturation (Bercovitch 2000; Whitten & Turner 2009; Gluckman and Hanson

481   2006b). An assessment of circulating leptin levels and sex steroids would make the link

482   between body fatness and early reproductive onset more clear. Future research should also

483   consider other environmental factors that could alter developmental constraints on growth and

484   secondary sexual characteristics, including potential anthropogenic determinants like endocrine-

485   disrupting agrochemicals (e.g., English et al. 2012; Blanck et al. 2000).

486   While we have focused on the benefits of anthropogenic food-enhancement in

487   developmental timing in these populations, the costs of human-wildlife conflict may also be

488   affecting life history and development in !Gariep. Vervets are classified as 'vermin' in South

489   Africa, and permits are not required to kill them on private property. We have not observed

490   attempts to capture or harm vervet monkeys on the farms in !Gariep first-hand, but several

491   monkeys present with missing legs (indicating past encounters with snares), evidence of

492   electrocution (presumably by power lines), and metal BBs under their skin (suggesting their

493   having been shot by humans). Although the owners of each farm in !Gariep Dam, by all

24

494   accounts, treat the resident monkeys quite well, this does not preclude conflict on other lands.

495   Indeed, most evidence of these risks is seen in adult males, who no doubt emigrated into our

496   study groups. High psychosocial stress is associated with delays in growth and reproductive

497   onset (Johnson 2003; Onyango et al., 2013), but such unpredictable and dangerous

498   environments are also associated with an earlier onset of menarche and first birth (Chisolm et

499   al. 2005; Ellis et al. 2009). A closer examination of individual risks and stressors in each

500   landscape would be required to tease out what role, if any, the stressors of each environment

501   play independently of nutrition in the timing of reproductive onset.

502   Addressing potential demographic effects on the timing of maturation was beyond the

503   scope of this project, but should be considered in studies with longitudinal or more diverse

504   population samples. In Amboseli baboons, relatively small populations appear to experience

505   earlier maturation, presumably due to lower competition for resources (Altmann & Alberts 2003).

506   While the !Gariep populations are larger and occur at a higher density than those in Soetdoring

507   (Schmitt, unpublished data), this does not appear to limit growth and maturation. This may be

508   because demography has not yet outstripped the available food resources for these monkeys.

509   However, high population density and the hypothesized risks of high mortality environments are

510   thought to occur hand-in-hand (Ellis et al. 2009). Such populations may then also experience

511   selection for faster life histories with earlier reproductive maturity (Ellis et al. 2009; Wells 2012).

512   A better understanding of the risks and stresses faced by each population is necessary to clarify

513   how these factors may also contribute to the timing of maturation.

514   This work demonstrates a potential effect of anthropogenic food enhancement on the

515   reproductive maturation among wild vervet monkeys, underscoring previous research on this

516   topic. Our results add to the evidence indicating an increase in body condition and more rapid

517   reproduction for primates living in anthropogenic environments. Future research on these

518   populations should add to these results with detailed behavioral and nutritional data, more

519   detailed data on ecological stressors, and physiological indicators of energy balance and

520   maturation. The continued incursion of human environments on non-human primate habitats

521   around the world (Estrada et al. 2017) demand increased attention to the effects of human

522   presence and resources on primate biology and health.

523

26

546   Environment and Nature Conservation; the South Africa Department of Agriculture, Forestry &

547   Fisheries; and the South African National Department of Environmental Affairs. All procedures

548   involving the capture, sample collection, and handling of live non-human primates were

549   approved by the Boston University Institutional Animal Care and Use Committee; University of

550   Wisconsin, Milwaukee IACUC; the UCLA Animal Research Committee; and University of the

551   Free State Animal Research Ethics Committee.

552

555

556   **Conflict of Interest**: The authors declare that they have no conflicts of interest.

REFERENCES

Altmann, J., & Alberts, S. C. (2003). Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology*, 15, 401-409.

Altmann, J., & Alberts, S. C. (2005). Growth rates in a wild primate population: Ecological influences and maternal effects. *Behavioral Ecology & Sociobiology*, 57, 490–501.

Altmann, J., Altmann, S., & Hausfater, G. (1981). Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. *American Journal of Primatology*, 1, 389–399.

Altmann, J., & Muruthi, P. (1988). Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology*, 15, 213–221.

Andelman, S. J., Else, J. G., Hearn, J. P., & Hodges, J. P. (1985). The non-invasive monitoring of reproductive events in wild vervet monkeys (*Cercopithecus aethiops*) using urinary pregnadiol-3α-glucuronide and its correlation with behavioural observations. *Journal of Zoology*, 205, 467-477.

Bercovitch, F. B. (1993). Dominance rank and reproductive maturation in male rhesus macaques, *Macaca mulatta. Journal of Reproduction and Fertility*, 99, 113-120.

Bercovitch, F. B. (2000). Behavioral ecology and socioendocrinology of reproductive maturation in cercopithecine monkeys. In P. F. Whitehead and Jolly, C. J. (Eds.), *Old World Monkeys* (pp. 298-320). Cambridge: Cambridge University Press.

Bercovitch, F. B., & Strum SC. (1993). Dominance rank, resource availability, and reproductive maturation in female savanna baboons. *Behavioral Ecology & Sociobiology*, 33, 313-318.

Blanck, H. M., Marcus, M., Tolbert, P. E., Rubin, C., Henderson, A. K., Hertzberg, V. S., Zhang, R. H., & Cameron, L. (2000). Age at menarche and Tanner stage in girls exposed *in utero* and postnatally to polybrominated biphenyl. *Epidemiology*, 11, 641–647.

Blaszczyk, M. B. (2016). Personality and social niche specialization in wild vervet monkeys (Unpublished Doctoral Dissertation). New York University, New York, NY.

Brennan, E. J., Else, J. G., & Altmann, J. (1985). Ecology and behaviour of a pest primate: vervet monkeys in a tourist-lodge habitat. *African Journal of Ecology*, 23, 35–44.

Cancelliere, E. C., Chapman, C. A., Twinomugisha, D., & Rothman, J. M. (2018). The nutritional value of feeding on crops: diets of vervet monkeys in a humanized landscape. *African Journal of Ecology*, 56, 160-167.

Cheney, D. L., & Seyfarth, R. M. (1983). Nonrandom dispersal in free-ranging vervet monkeys: Social and genetic consequences. *American Naturalist*, 122, 392–412.

Cheney, D. L., Seyfarth, R. M., Andelman, S. J., & Lee, P. C. (1988). Reproductive success in vervet monkeys. In T. H. Clutton-Brock (Ed.), *Reproductive success: studies of individual variation in contrasting breeding systems* (pp. 384-402). Chicago, IL: University of Chicago Press.

594 Chisolm, J. S., Quinlivan, J. A., Petersen, R. W., & Coall, D. A. (2005). Early stress predicts age
595   at menarche and first birth, adult attachment, and expected lifespan. *Human Nature*, 16,
596   233-265.

597 Colman, R. J., Hudson, J. C., Barden, H. S., & Kemnitz, J. W. (1999). A comparison of dual-
598   energy x-ray absorptiometry and somatometrics for determining body fat in rhesus
599   macaques. *Obesity Research*, 7, 90-96.

600 Cramer, J. D., Gaetano, T. J., Gray, J. P., Grobler, J. P., Lorenz, J., Freimer, N. B., Schmitt, C.
601   A., & Turner, T. R. (2013). Variation in scrotal color among widely distributed vervet
602   monkey populations (*C. a. pygerythrus* and *C. a. sabaeus*). *American Journal of
603   Primatology*, 75, 752-762.

604 Eley, R. M. (1992). Reproductive biology of the vervet monkey (*Cercopithecus aethiops*): A
605   review. *Utafiti*, 4, 1-33.

606 Eley, R. M., Else, J. G., Gulamhusein, N., & Lequin, R. M. (1986). Reproduction in the vervet
607   monkey (*Cercopithecus aethiops*): I.Testicular volume, testosterone, and seasonality.
608   *American Journal of Primatology*, 10, 229-235.

609 Elias, C. F. (2012). Leptin action in pubertal development: recent advances and unanswered
610   questions. *Trends in Endocrinology & Metabolism*, 23, 9-15.

611 Ellis, B. J., Figueredo, A. J., Brumback, B. H., & Schlomer, G. L. (2009). Fundamental
612   dimensions of environmental risk. *Human Nature*, 20, 204-268.

613 Ellison, P. T. (1990). Human ovarian function and reproductive ecology: New hypotheses.
614   *American Anthropologist*, 92, 933–952.

615 Ellison, P. T. (2003). Energetics and reproductive effort. *American Journal of Human Biology*,
616   15, 342–351.

617 English, R. G., Perry, M., Lee, M. M., Hoffman, E., Delport, S., & Dalvie, M. A. (2012). Farm
618   residence and reproductive health among boys in rural South Africa. *Environment
619   International*, 47, 73-79.

620 Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A.,
621   Nekaris, K. A. I., Nijman, V., Heymann, E. W., Lambert, J. E., Rovero, F., Barelli, C.,
622   Setchell, J. M., Gillespie, T. R., Mittermeier, R. A., Arregoitia, L. V., de Guinea, M.,
623   Gouveia, S., Dobrovolski, R., Shanee, S., Shanee, N., Boyle, S. A., Fuentes, A.,
624   MacKinnon, K. C., Amato, K. R., Meyer, A. L. S., Wich, S., Sussman, R. W., Pan, R., Kone,
625   I., & Li, B. (2017). Impending extinction crisis of the world's primates: Why primates matter.
626   Science Advances 3: e1600946. doi: 10.1126/sciadv.1600946

627 Fourie, N. H., Turner, T. R., Brown, J. L., Pampush, J. D., Lorenz, J. G., & Bernstein, R. M.
628   (2015). Variation in vervet (*Chlorocebus aethiops*) hair cortisol concentrations reflects
629   ecological disturbance by humans. *Primates*, 56, 365–373.

630 Gluckman, P. D., & Hanson, M. A. (2006a). Changing times: the evolution of puberty. *Molecular
631   and Cellular Endocrinology*, 254-255, 26–31.

632 Gluckman, P. D., & Hanson, M. A. (2006b). Evolution, development and timing of puberty.

633   *Trends in Endocrinology & Metabolism*, 17, 7–12.

634   Grobler, J. P., & Turner, T. R. (2010). A novel trap design for the capture and sedation of vervet
635   monkeys (*Chlorocebus aethiops*). *South African Journal of Wildlife Research*, 40, 163–168.

636   Hamada, Y., Suzuki, J., Ohkura, S., & Hayakawa, S. (2005). Changes in testicular and nipple
637   volume related to age and seasonality in Japanese macaques (*Macaca fuscata*), especially
638   in the pre- and post-pubertal periods**.** *Primates*, 46, 33-45.

639   Henzi, S. P., & Lucas J. W. (1980). Observations on the inter-troop movement of adult vervet
640   monkeys (*Cercopithecus aethiops*). *Folia Primatologica*, 33, 220–235.

641   Higham, J. P., Warren, Y., Adanu, J., Umaru, B. N., MacLarnon, A. M., Sommer, V., & Ross C.
642   (2009). Living on the edge: life-history of olive baboons at Gashaka-Gumti National Park,
643   Nigeria. *American Journal of Primatology*, 71, 293-304.

644   Hill, C. M. (2017). Primate crop feeding behavior, crop protection, and conservation.
645   *International Journal of Primatology*, 38, 385-400.

646   Hill, K. (2005). Life history theory and evolutionary anthropology. *Evolutionary Anthropology*, 2,
647   78–88.

648   Ibáñez, L., Ferrer, A., Marcos, M. V., Hierro, F. R., & de Zegher, F. (2000). Early puberty: rapid
649   progression and reduced final height in girls with low birth weight. *Pediatrics* 106:E72. doi:
650   10.1542/peds.106.5.e72

651   Janecke, B. B. (2002). Vegetation ecology of Soetdoring Nature Reserve: Pan, grassland, and
652   Karroid communities. Bloemfontein: University of the Free State.

653   Janecke, B. B., & du Preez, P. (2005). A synoptic view on the grassland vegetation of
654   Soetdoring Nature Reserve, Free State Province. *South African Journal of Botany*, 71, 339-
655   348.

656   Jarrett, J. D., Bonnell, T., Jorgensen, M. J., Schmitt, C. A., Young, C., Dostie, M., Barrett, L., &
657   Henzi, S. P. (2020). Modeling variation in the growth of wild and captive juvenile vervet
658   monkeys in relation to diet and resource availability. *American Journal of Physical
659   Anthropology*, 171, 19-99.

660   Jasinska, A. J., Schmitt, C. A., Service, S. K., Cantor, R. M., Dewar, K., Jentsch, J. D., Kaplan,
661   J. R., Turner, T. R., Warren, W. C., Weinstock, G. M., Woods, R. P., & Freimer, N. B.
662   (2013). Systems biology of the vervet monkey. *Journal of the Institute for Laboratory Animal
663   Research*, 54, 122–143.

664   Johnson, S. E. (2003). Life history and the competitive environment: trajectories of growth,
665   maturation, and reproductive output among chacma baboons. *American Journal of Physical
666   Anthropology*, 120, 83–98.

667   Kaburu, S. S. K., Marty, P. R., Beisner, B., Balasubramaniam, K. N., Bliss-Moreau, E., Kaur, K.,
668   Mohan, L., & McCowan, B. (2019). Rates of human-macaque interactions affect grooming
669   behavior among urban-dwelling rhesus macaques (*Macaca mulatta*). *American Journal of
670   Physical Anthropology*, 168, 92–103.

671   Kamilar, J. M., & Cooper, N. (2013). Phylogenetic signal in primate behavior, ecology, and life

672   history. *Proceedings of the Royal Society B*, 368, 20120341. doi:10.1098/rstb.2012.0341

673   Karaman, M. I., Kaya, C., Caskurlu, T., Guney, S., & Ergenkon, E. (2005). Measurement of
674   pediatric testicular volume with Prader orchidometer: comparison of different hands.
675   *Pediatric Surgery International*, 21, 517-520.

676   Kavanagh, K., Jones, K. L., Sawyer, J., Kelley, K., Carr, J. J., Wagner, J. D., & Rudel, L. L.
677   (2007). Trans fat diet induces abdominal obesity and changes in insulin sensitivity in
678   monkeys. *Obesity*, 15, 1675–1684.

679   Kemnitz, J. W., Eisele, S. G., Lindsay, K. A., Engle, M. J., Perelman, R. H., & Farrell, P. M.
680   (1984). Changes in food intake during menstrual cycles and pregnancy of normal and
681   diabetic rhesus monkeys. *Diabetologia*, 26, 60-64.

682   Kohrs, M. B., Harper, A. E., & Kerr, G. R. (1976). Effects of a low-protein diet during pregnancy
683   of the rhesus monkey I. Reproductive efficiency. *American Journal of Clinical Nutrition*, 29,
684   136-145.

685   Koziel, S., & Jankowska, E. A. (2002). Effect of low versus normal birthweight on menarche in
686   14-year-old Polish girls. *Journal of Paediatrics & Child Health*, 38, 268–271.

687   Kuzawa, C. W., & Bragg, J. M. (2012). Plasticity in human life history strategy: implications for
688   contemporary human variation and the evolution of genus *Homo*. *Current Anthropology*,
689   53(S6), S369-S382.

690   Kuzawa, C. W., McDade, T. W., Adair, L.S., & Lee, N. (2010). Rapid weight gain after birth
691   predicts life history and reproductive strategy in Filipino males. *Proceedings of the National
692   Academy of Sciences*, 107, 16800–16805.

693   Lea, A. J., Altmann, J., Alberts, S. C., & Tung, J. (2015). Developmental constraints in a wild
694   primate. *American Naturalist*, 185, 809-821.

695   Lee, P. C. (1984). Ecological constraints to the social development of vervet monkeys.
696   *Behaviour*, 94, 245-262.

697   Lee, P. C., & Priston, N. E. C. (2005). Human attitudes to primates: Perceptions of pests,
698   conflict and consequences for primate conservation. In J. D. Paterson, Wallis, J. (Eds.),
699   *Commensalism and Conflict: The Primate-Human Interface* (pp. 1-23). Winnipeg: Higwell
700   Printing.

701   Lodge, E., Ross, C., Ortmann, S., & MacLarnon, A. M. (2013). Influence of diet and stress on
702   reproductive hormones in Nigerian olive baboons. *General and Comparative
703   Endocrinology*, 191, 146-154.

704   Marty, P. R., Balasubramaniam, K. N., Kaburu, S. S. K., Hubbard, J., Beisner, B., Bliss-Moreau,
705   E., Ruppert, N., Arlet, M. E., Sah, S. A. M., Ismail, A., Mohan, L., Rattan, S. K.,
706   Kodandaramaiah, U., & McCowan, B. (2019). Individuals in urban dwelling primate species
707   face unequal benefits associated with living in an anthropogenic environment. *Primates*.
708   doi: 10.1007/s13029-019-00775-4

709   McFarland, R., Barrett, L., Boner, R., Freeman, N. J., & Henzi, S. P. (2014). Behavioral flexibility
710   of vervet monkeys in response to climatic and social variability. *American Journal of*

711   *Physical Anthropology*, 154, 357-364.

712   McFarland, R. (1997). Female primates: Fat or fit? In M.E. Morbeck, Galloway, A., & Zihlman, A.
713   (Eds.), *The Evolving Female: A Life-History Perspective* (pp. 163-175). Princeton, NJ:
714   Princeton University Press.

715   Møller, A. P. (1988). Ejaculate quality, testes size and sperm competition in primates. *Journal of*
716   *Human Evolution*, 17, 479–488.

717   Mori, A. (1979). Analysis of population changes by measurement of body weight in the Koshima
718   troop of Japanese monkeys. *Primates*, 20, 371–397.

719   Naughton-Treves, L., Treves, A., Chapman, C., & Wrangham, R. (1998). Temporal patterns of
720   crop-raiding by primates: Linking food availability in croplands and adjacent forest. *Journal*
721   *of Applied Ecology*, 35, 596-606.

722   Onyango, P. O., Gesquiere, L. R., Altmann, J., & Alberts, S. C. (2013). Puberty and dispersal in
723   a wild primate population. *Hormones and Behavior*, 64, 240-249.

724   Pusey, A. E. (2012). Magnitude and sources of variation in female reproductive performance. In
725   J. C. Mitani, Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.), *The Evolution of*
726   *Primate Societies* (pp. 343-363). Chicago: University of Chicago Press.

727   Rato, L., Alves, M. G., Socorro, S., Duarte, A. I., Cavaco, J. E., & Oliveira, P. F. (2012).
728   Metabolic regulation is important for spermatogenesis. *Nature Reviews Urology*, 9, 330–
729   338.

730   R Core Team. (2019). R: A language and environment for statistical computing. Vienna, Austria:
731   R Foundation for Statistical Computing.

732   Riley, E. P., Tolbert, B., Farida, W. R. (2013). Nutritional content explains the attractiveness of
733   cacao to crop raiding Tonkean macaques. *Current Zoology*, 59, 160-169.

734   Rodriguez, R. L., Cramer, J. D., Schmitt, C. A., Gaetano, T. J., Grobler, J. P., Freimer, N. B., &
735   Turner, T. R. (2015). The static allometry of sexual and non-sexual traits in vervet monkeys.
736   *Biological Journal of the Linnean Society*, 114, 527-537.

737   Rowell, T. E. (1970). Reproductive cycles of two *Cercopithecus* monkeys. *Journal of*
738   *Reproduction and Fertility*, 22, 321-338.

739   Saj, T. L., Sicotte, P., & Paterson, J. D. (2001). The conflict between vervet monkeys and
740   farmers at the forest edge in Entebbe, Uganda. *African Journal of Ecology*, 39, 195–199.

741   Saj, T., Sicotte, P., & Paterson, J. D. (1999). Influence of human food consumption on the time
742   budget of vervets. *International Journal of Primatology*, 20, 977–994.

743   Schmitt, C. A., Service, S. K., Jasinska, A. J., Dyer, T. D., Jorgensen, M. J., Cantor, R. M.,
744   Weinstock, G. M., Blangero, J., Kaplan, J. R., & Freimer, N. B. (2018). Obesity and
745   obesogenic growth are both highly heritable and modified by diet in a nonhuman primate
746   model, the African green monkey (*Chlorocebus aethiops sabaeus*). *International Journal of*
747   *Obesity*, 42, 765–774.

748   Schulte-Hostedde, A. I., & Millar, J. S. (2004). Intraspecific variation of testis size and sperm

length in the yellow-pine chipmunk (*Tamias amoenus*): implications for sperm competition and reproductive success. *Behavioral Ecology & Sociobiology*, 55, 272-277.

Setchell, J. M., & Lee, P. C. (2004). Development and sexual selection in primates. In P. M. Kappeler, & van Schaik, C. P. (Eds.), *Sexual Selection in Primates: New and Comparative Perspectives* (pp. 175-195). Cambridge: Cambridge University Press.

Strum, S. C. (2010). The development of primate raiding: Implications for management and conservation. *International Journal of Primatology*, 31, 133-156.

Sugiyama, Y., & Ohsawa, H. (1982). Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. *Folia Primatologica*, 39, 238–263.

Svardal, H., Jasinska, A. J., Apetrei, C., Coppola, G., Huang, Y., Schmitt, C. A., Jacquelin, B., Ramensky, V., Müller-Trutwin, M., Antonio, M., Weinstock, G., Grobler, J. P., Dewar, K., Wilson, R. K., Turner, T. R., Warren, W. C., Freimer, N. B., & Nordborg, M. (2017). Ancient hybridization and strong adaptation to viruses across African vervet monkey populations. *Nature Genetics*, 49, 1705–1713.

Turner, T. R., Anapol, F., & Jolly, C. J. (1997). Growth, development, and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *American Journal of Physical Anthropology*, 103, 19-35.

Turner, T. R., Cramer, J. D., Nisbett, A., & Gray, J. P. (2016). A comparison of adult body size between captive and wild vervet monkeys (*Chlorocebus aethiops sabaeus*) on the island of St. Kitts. *Primates*, 57, 211-220.

Turner, T. R., Schmitt, C. A., & Cramer, J. D. (2019). *Savanna Monkeys: The Genus Chlorocebus*. Cambridge: Cambridge University Press.

Turner, T. R., Schmitt, C. A., Cramer, J. D., Lorenz, J., Grobler, J. P., Jolly, C. J., & Freimer, N. B. (2018). Morphological variation in the genus *Chlorocebus*: Ecogeographic and anthropogenically mediated variation in body mass, postcranial morphology, and growth. *American Journal of Physical Anthropology*, 166, 682-707.

Turner, T. R., Whitten, P. L., Jolly, C. J., & Else, J. E. (1987). Pregnancy outcomes in free-ranging vervet monkeys: a preliminary report. *American Journal of Primatology*, 12, 197-203.

van Pelt, L. F. (1974). Clinical assessment of reproductive function in female rhesus monkeys: Individual physical examination. *Laboratory Animals*, 8, 199-212.

Wade, G. N., Schneider, J. E., & Li, H. I. (1996). Control of fertility by metabolic cues. *American Journal of Physiology-Endocrinology and Metabolism*, 270, E1-E19.

Wells, J. C. K. (2012). The evolution of human adiposity and obesity: where did it all go wrong? *Disease Models & Mechanisms*, 5, 595–607.

Whitten, P. L. (1982). Female reproductive strategies among vervet monkeys (Unpublished Doctoral Dissertation). Harvard University, Cambridge, MA.

Whitten, P. L. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology*, 5, 139-159.

788   Whitten, P. L., & Turner, T. R. (2009). Endocrine mechanisms of primate life history trade-offs:
789   Growth and reproductive maturation in vervet monkeys. *American Journal of Human*
790   *Biology*, 21, 754-761.

791   Zambrano, E., Guzmán, C., Rodríguez-González, G. L., Durand-Carbajal, M., Nathanielsz, P.W.
792   (2014). Fetal programming of sexual development and reproductive function. Molecular and
793   Cellular Endocrinology, 382, 538-549.