

1 **Anthropogenic food enhancement alters the timing of maturational landmarks among**  
2 **wild savanna monkeys (*Chlorocebus pygerythrus*)**  
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25 MBB, JDC, JPG, and TRT conducted fieldwork. CAS, NBF, JPG, TRT secured funding and  
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27 and AMR implemented. CAS and AMR wrote the manuscript; TRT and other authors provided  
28 editorial advice.  
29  
30

31 **RUNNING TITLE:** Food Enhancement and Reproductive Onset in Vervet Monkeys  
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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 !Gariiep Dam, with ample access to

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

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

44 than those in Soetdoring, suggesting increased fat deposition. Males in !Gariiep 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 !Gariiep 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

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; Blaszczyk 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. sabaues*) in St. Kitts & Nevis,  
113 this leads to clear increases in body mass and better body condition in captive adults (Turner et

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).

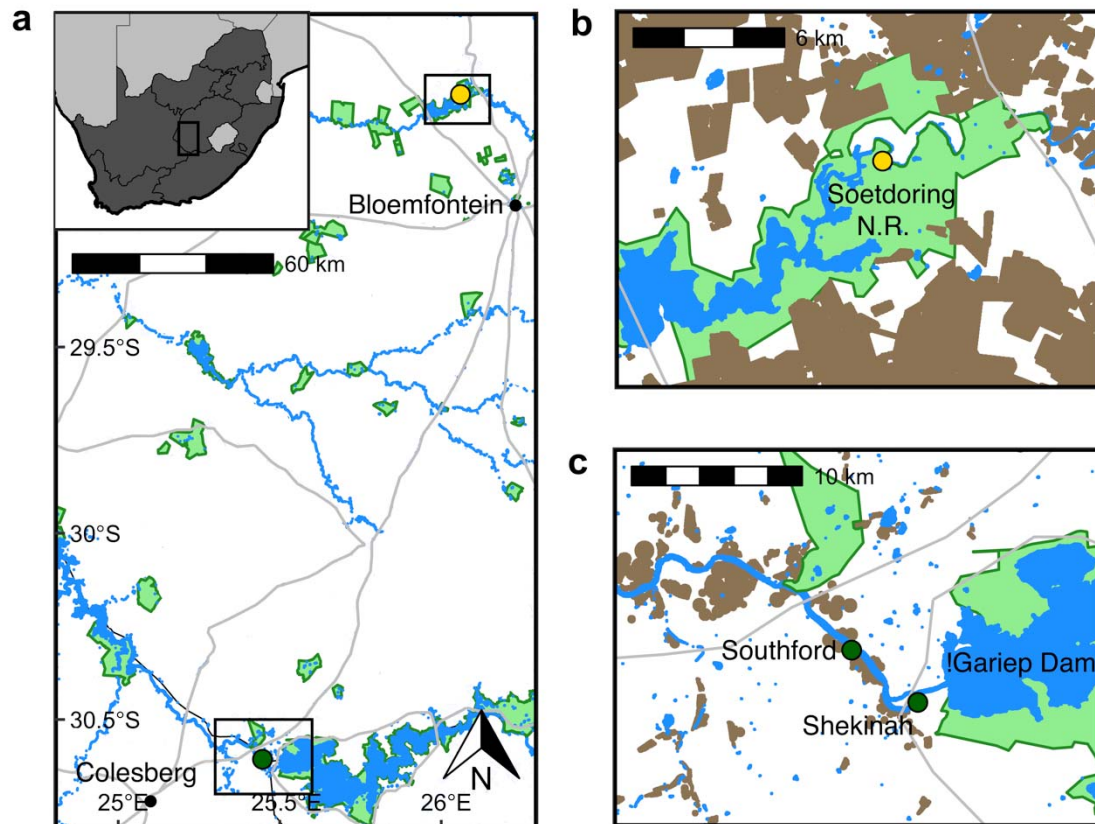
130         Here we compare aspects of reproductive maturation and body condition in two  
131 populations of vervet monkeys in South Africa, each living in similar biomes with contrasting  
132 human impacts. The first population, in Soetdoring Nature Reserve, subsists primarily on natural  
133 forage while experiencing only moderate human impacts (Blasczyk 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 **Figure 1.** Study sites in South Africa (a), with insets of b) Soetdoring Nature Reserve and c) the !Gariep  
146 Dam region. Brown areas indicate cropland, blue include rivers, and both naturally and dammed water  
147 sources, while green are protected natural areas. Soetdoring Nature Reserve (gold circle) has fewer  
148 human-wildlife interactions and provisioning, while private farms near the !Gariep Dam (green circles)  
149 facilitate crop foraging and high calorie provisioning. Both study areas include mosaics of grassland and  
150 Nama Karoo and have near identical ecological conditions outside immediate human impacts within their  
151 ranges.  
152

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

158 groups primarily occupy riparian forest and adjacent *Acacia* thornveld (Błaszczuk 2016),  
159 although the vervets in !Gariiep 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 (Błaszczuk  
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 !Gariiep 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;

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 ochildometer 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

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.

		Soetdoring				!Gariiep			
		Males		Females		Males		Females	
Trait	Dental Age	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 (0.21)	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		69		66		59		51
		135				110			
		245							
BMI	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
	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		69		66		59		51	
		135				110			
		245							
Subscapular SFT (cm)	Dental Age	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
	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

	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)	<b>Dental Age</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>
	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)	<b>Dental Age</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>
	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)	<b>Dental Age</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>
	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)
		50		48		33		31	
	Total	98				64			
		162							
	<b>Dental</b>								
	<b>Age</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>
	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)
		50		48		33		31	
	Total	98				64			
		162							
	<b>Dental</b>								
	<b>Age</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>	<b>n</b>	<b>Mean (SD)</b>
	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)	-	-
		69		0		59		0	
	Total	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 !Gariiep (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  $R^2 = 1 - \frac{\text{Residual Deviance}}{\text{Null Deviance}}$ . 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

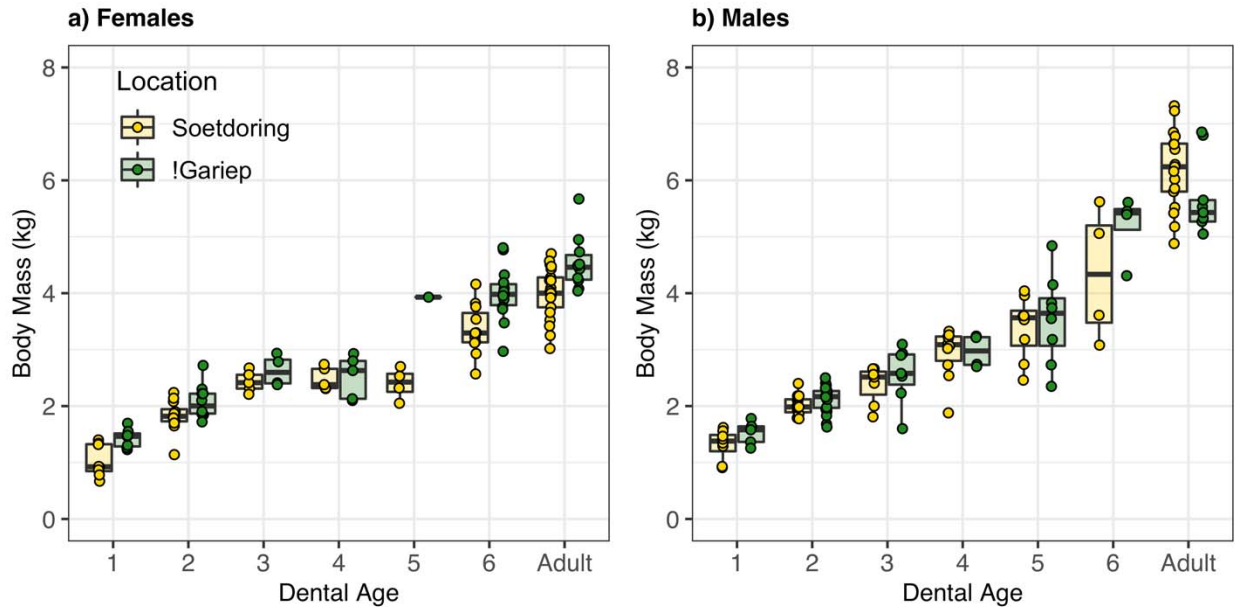
## 264 **RESULTS**

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 =  $2.40 \pm \text{SD } 0.28$   
272 kg). At dental age 6, females in !Gariep were heavier than in Soetdoring (Games-Howell:  $\Delta_{\text{mean}} =$   
273 0.64 kg,  $t = 3.50$ ,  $df = 22.13$ ,  $P = 0.082$ ), and this difference continued into adulthood (Games-  
274 Howell:  $\Delta_{\text{mean}} = 0.60$  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 ( $N_{\text{preg}} = 6$  of 10,  $\Delta_{\text{mean}} = 0.25$  kg), while in !Gariep  
283 pregnant females were 11% heavier than non-pregnant females ( $N_{\text{preg}} = 5$  of 11,  $\Delta_{\text{mean}} = 0.46$   
284 kg). Although pregnant adult females in Soetdoring were 13% heavier than non-pregnant adult  
285 females ( $N_{\text{preg}} = 2$  of 12;  $\Delta_{\text{mean}} = 0.54$  kg), there was no detectable difference in body mass  
286 based on pregnancy in !Gariep adults ( $N_{\text{preg}} = 2$  of 6;  $\Delta_{\text{mean}} = 0.05$  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 ( $F_{1,47} = 12.82$ ,  $P <$

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 ( $N_{\text{lact}} = 7$  of 14;  $\Delta_{\text{mean}} = 0.63$  kg); no females in dental age 6 in Soetdoring were  
294 observed to be lactating.



295

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.

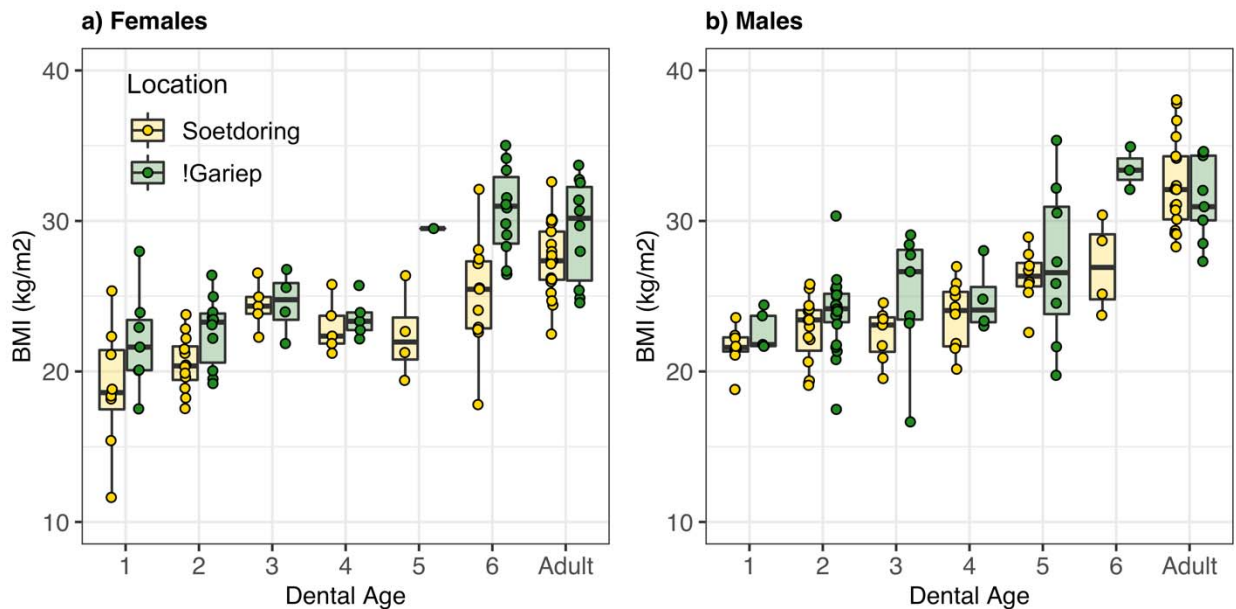
298

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:  $\Delta_{\text{mean}} = 5.52$  kg/m<sup>2</sup>,  $t = 4.02$ ,  $df$   
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 ( $\Delta_{\text{mean}} = 2.7 \text{ kg/m}^2$ ), no difference  
310 was seen in !Gariep ( $\Delta_{\text{mean}} = 0.0 \text{ kg/m}^2$ ). In dental age 6, pregnant females in Soetdoring had  
311 10% higher BMI than non-pregnant ( $\Delta_{\text{mean}} = 2.7 \text{ kg/m}^2$ ), and in !Gariep the BMI of pregnant  
312 females was 3% higher ( $\Delta_{\text{mean}} = 0.9 \text{ kg/m}^2$ ). 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 ( $\Delta_{\text{mean}} = 0.5 \text{ kg/m}^2$ ) and in !Gariep had 13% higher BMI ( $\Delta_{\text{mean}} =$   
315  $4.1 \text{ kg/m}^2$ ), although neither difference was statistically significant. Lactating females in dental  
316 age 6 in !Gariep had 8% higher BMI than non-lactating females ( $\Delta_{\text{mean}} = 2.6 \text{ kg/m}^2$ ).  
317



318

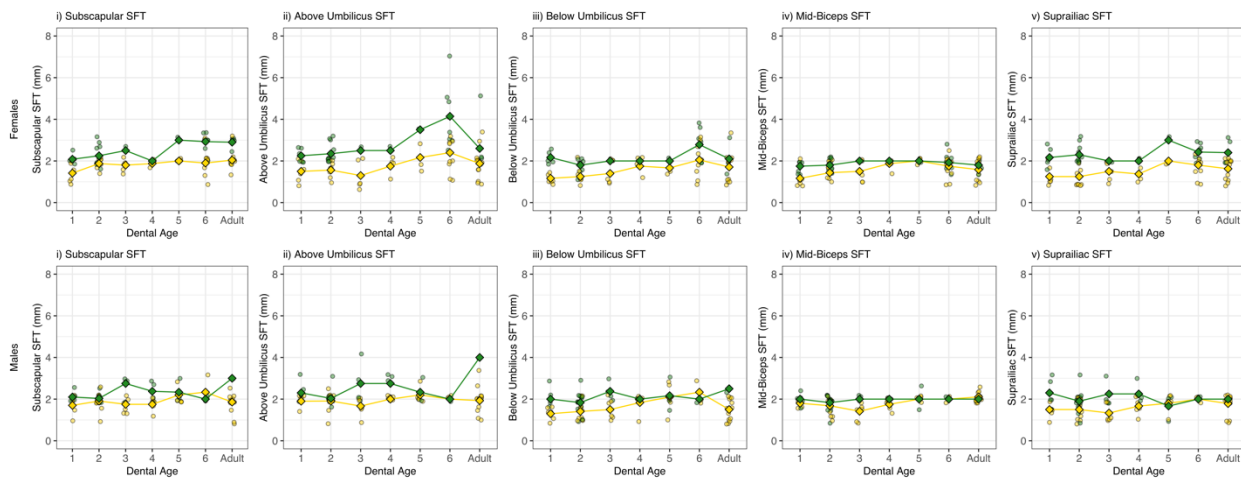
319 **Figure 3.** Body mass index or BMI ( $\text{kg/m}^2$ ) in a) female and b) male vervet monkeys across each dental  
320 age category. For estimated chronological ages, see Table 1.

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 !Gariiep ( $F_{1,27} = 7.51$ ,  $P = 0.011$ ). The suprailiac skin fold was also thicker in  
 334 Soetdoring but thinner in !Gariiep in lactating compared to non-lactating females ( $F_{1,27} = 4.39$ ,  $P$   
 335  $= 0.045$ ; Supplementary Table 15).



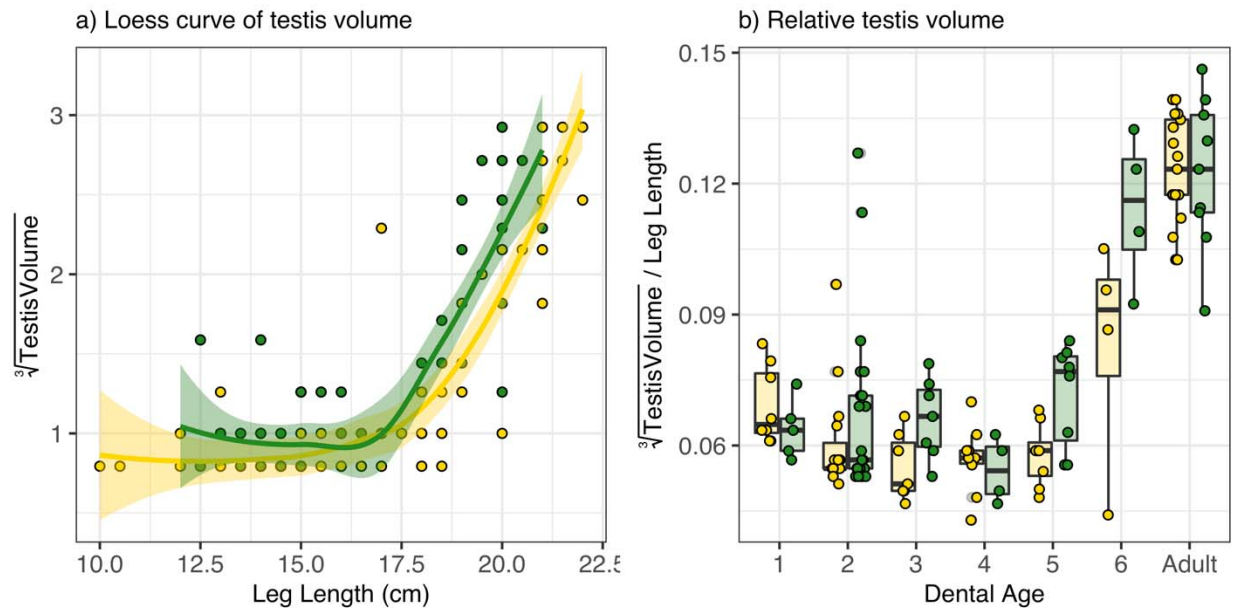
336  
 337 **Figure 4.** Mean i) subscapular, ii) above umbilicus, iii) below umbilicus, iv) mid-biceps, and v) suprailiac  
 338 skin fold thickness in a) females, and b) males for vervets sampled in !Gariiep (green) and Soetdoring  
 339 (gold). Individual measurements are shown to demonstrate range.

340

341 *Male maturation – Relative testis volume*

342 Differing patterns of testis growth distinguished males in Soetdoring from those in  
 343 !Gariiep, using both absolute and relative testis volume as measures (Fig 5). Although both  
 344 absolute and relative testis volume appears larger in !Gariiep for age categories 5 and 6, these

345 differences were not significant. In adulthood, both relative and absolute testis volume was the  
346 same between the two sites.



347 **Figure 5.** Boxplot of a) loess curves representing growth in absolute testis volume by body mass, and b)  
348 relative testis volume in males (testis volume/leg length) across each dental age category. See Table 2  
349 for sample sizes. Gold indicates males sampled at Soetdoring Nature Reserve, while green represents  
350 males sampled in the !Gariiep Dam region.  
351  
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 ( $\beta = -0.042$ ,  $P = 0.0048$ ;  $R^2 =$   
355  $0.12$ ; Table 3a). The peri-pubertal model with the lowest AICc included location (Soetdoring vs.  
356 !Gariiep), dental age category, body mass, and an interaction term between age and body mass  
357 as covariates (Table 3b). In this model, males in !Gariiep had significantly larger relative testis  
358 volume overall compared to those in Soetdoring ( $\beta = 0.088$ ,  $P = 0.019$ ;  $R^2 = 88.47$ ). 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 ( $\beta = 0.295$ ,  $P = 0.008$ ).

362

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

364

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

---

RTV ~ Body Mass		Estimate	Error	p value	
<b>Intercept</b>		<b>-2.673</b>	<b>0.059</b>	<b>&lt; 0.001</b>	<b>***</b>
<b>Body Mass</b>		<b>-0.081</b>	<b>0.026</b>	<b>0.003</b>	<b>**</b>

---

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

---

RTV ~ Age * Body Mass + Location		Estimate	Error	p value	
<b>Intercept</b>		<b>-2.820</b>	<b>0.279</b>	<b>&lt; 0.001</b>	<b>***</b>
<b>Location (!Gariep)</b>		<b>0.088</b>	<b>0.037</b>	<b>0.019</b>	<b>*</b>
<b>Age Category</b>		-	-	-	
	5	0.038	0.334	0.909	
	<b>6</b>	<b>-0.842</b>	<b>0.377</b>	<b>0.029</b>	<b>*</b>
	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	
<b>Body Mass : Age Category 6</b>		<b>0.295</b>	<b>0.107</b>	<b>0.008</b>	<b>**</b>
Body Mass : Age Category Adult		0.140	0.102	0.174	

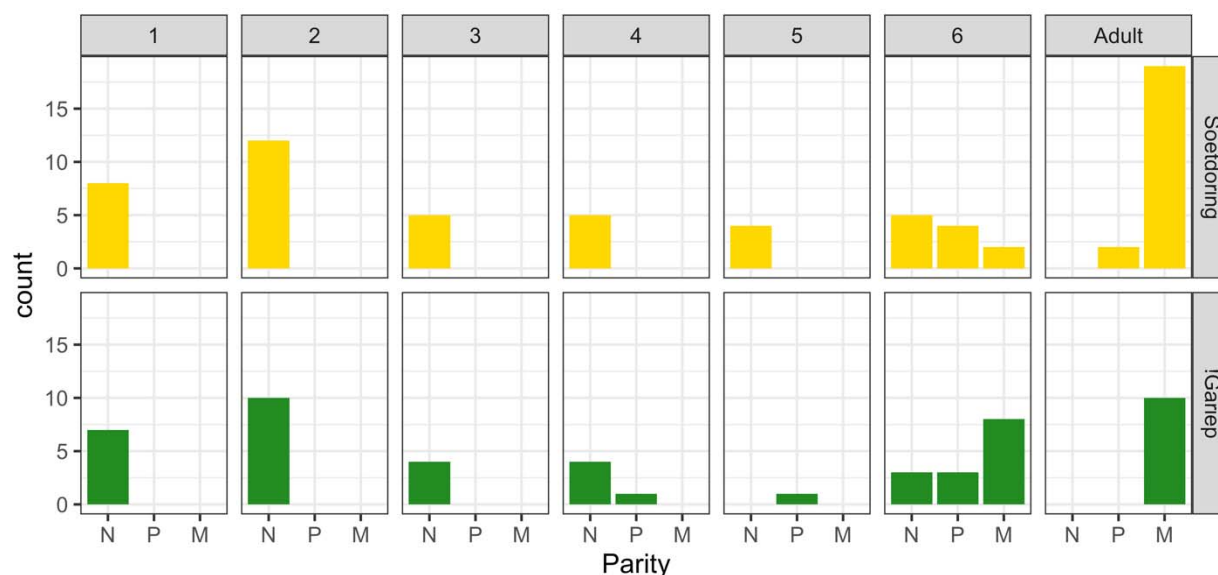
365

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 ( $\beta = 0.745$ ,  $P = 0.009$ ). No Fisher's exact test of parity  
 375 status across sites within age categories showed significant differences.

376



377  
378 **Figure 6.** The number of females exhibiting nipple morphology indicative of each parity category (N =  
379 Nulliparous, P = Primiparous, M = Multiparous) within each dental age, compared between sites.  
380

381

382 **Table 4:** Logistic Regression Model for Female Parity

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

383

384

## 385 DISCUSSION

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

392 significantly heavier in adulthood than those in Soetdoring, we interpret as evidence of an earlier  
393 peak of growth at !Gariiep. 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 !Gariiep female sampled at dental age 5 was comparable in weight to dental age 6 females,  
398 and females remain significantly heavier in !Gariiep compared to Soetdoring from this age  
399 through adulthood.

400         Given the earlier and more exaggerated increases in mass at !Gariiep, it is unclear why  
401 adult males do not also appear heavier in !Gariiep. 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 !Gariiep 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 !Gariiep, 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 !Gariiep 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 !Gariiep 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 (Blaszczyk 2016); we have not yet carried out long  
438 term behavioral observations in !Gariiep populations. To assess whether the earlier increase in  
439 testis volume in !Gariiep 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 !Gariiep, our sample size limits  
442 our ability to interpret the relative timing of reproductive onset in females between these

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 !Gariiep 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 !Gariiep. 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 !Gariiep 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 !Gariiep Dam, by all



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 !Gariap 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

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555

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