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**MODELLING VARIATION IN THE GROWTH OF WILD AND CAPTIVE JUVENILE
VERVET MONKEYS IN RELATION TO DIET AND RESOURCE AVAILABILITY**

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Abstract

Objectives

To compare longitudinal weight gain in captive and wild juvenile vervet monkeys and conduct an empirical assessment of different mechanistic growth models.

Methods

Weights were collected from two groups of captive monkeys and two consecutive cohorts of wild monkeys until the end of the juvenile period (~800 days). The captive groups were each fed different diets, while the wild groups experienced different ecological conditions. Three different growth curve models were compared.

Results

By 800 days the wild juveniles were lighter, with a slower maximum growth rate, and reached asymptote earlier than their captive counterparts. There were overall differences in weight and growth rate across the two wild cohorts. This corresponded to differences in resource availability. There was considerable overlap in growth rate and predicted adult weight of male and females in the first, but not the second, wild cohort. Maternal parity was not influential. While the von Bertalanffy curve provided the best fit to the data sets modelled together, the Logistic curve best described growth in the wild cohorts when considered separately.

Conclusions

The growth curves of the two captive cohorts are likely to lie near the maximum attainable by juvenile vervets. It may be helpful to include deviations from these rates when assessing the

performance of wild vervet monkeys. The comparison of wild and captive juveniles confirmed the value of comparing different growth curve models, and an appreciation that the best models may well differ for different populations. Choice of mechanistic growth model can therefore be empirically justified, rather than theoretically predetermined.

Relative to other mammals, primates are characterized by a long juvenile period, and an extended period of growth before reaching sexual maturity (Pereira and Fairbanks, 1993). There is considerable interspecific diversity in the shape of growth curves across the primate order (Kirkwood, 1985). This diversity is thought to reflect variation in mortality rates and the timing of maturation, and the eventual trade-off between reproductive rate and the length of the reproductive lifespan (Charnov and Berrigan, 1993; Janson, 1993). Variation in growth rates within a species is equally of interest as it points to a norm of reaction in response to varying environmental conditions, interrogation of which can further enhance our understanding of primate life histories and their evolution (Lee, 2003).

Not surprisingly, given field constraints, most assessments of primate growth in the wild have relied on cross-sectional sampling, taking opportunities presented by capture or targeted immobilization to collect somatometric data (Strum, 1991; Cheverud et al., 1992; Whitten and Turner, 2009; Turner et al., 2018) from animals whose identities and ages may or may not be known. Longitudinal studies of juvenile growth variation within and among wild populations remain rare, no doubt due to the difficulty of collecting data repeatedly in the field. While repeated sampling of known individuals may be possible via capture or immobilization (Dietz et al., 1994; Huck et al., 2011), there are obvious risks and constraints associated with doing so. There are better prospects for repeated non-invasive growth data collection from long-term study sites where animals are well-habituated and can be followed through to adulthood. Recent advances in photogrammetrical techniques, for example, have exploited these features to provide insightful analyses of the factors affecting growth under conditions where body weight measurement is not practical (Berghänel et al., 2016). Where the terrain does facilitate it, and/or

where the animals are sufficiently terrestrial, it has been possible to obtain direct, repeated estimates of body weight from the same animals (Altmann and Alberts, 1987; Johnson, 2003).

The advantage of longitudinal data sets is that, while they can be parsed to provide cross-sectional weight-for-age estimates, they can also be used to probe the environmental and social correlates of individual life-history trajectories. Comparing the growth trajectories of animals raised under different nutritional conditions can help us identify more clearly the structure and bounds of life-history variation, such as growth rate, age and size at sexual maturity, and age and size at first reproduction. As a special instance of this, data from individuals that have had access to an artificially-enhanced diet can be used to set upper bounds on growth rates, providing a reference point against which to assess the life history trajectories of wild populations. Strum (1991), for example, used a von Bertalanffy growth curve (Zullinger et al., 1984) to model the growth of olive baboons (*Papio anubis*) in both wild-fed and food-enhanced groups. She found that animals of both sexes reached adult weights earlier in her food-enhanced group. Similarly, Altmann and Alberts (2005), using piecewise linear regression, recorded higher growth rates from juveniles in a food-enhanced group of yellow baboons (*Papio cynocephalus*), compared to their wild-fed counterparts, and showed that this underpinned accelerated sexual maturity. Comparison of growth trajectories can also be used to investigate trade-offs between growth, maintenance and reproduction (e.g., documenting the extent to which the energetic costs of mounting an immune response impede growth; how growth rates differ between the sexes in their response to nutritional conditions; and whether maternal parity has an impact on offspring growth rates: see Stulp and Barrett 2016 for human examples; also Altmann & Alberts 2005; Nuñez et al. 2015; Turner et al. 2018).

In vervets, growth has recently been modelled using both cross-sectional data from wild animals (Turner et al., 2018) and longitudinal data from captive animals (Schmitt et al., 2018), although acknowledged limitations to the datasets and how they've been analyzed call for further study. Using data from wild-trapped vervet monkeys, Turner et al. (2018) modelled cross-sectional growth using loess regression curves. They found qualitative differences in growth between sites that appeared to correspond to large-scale geographic differences: animals in East Africa grew more rapidly to a smaller adult body size than those in South or West Africa. They also found qualitative differences in growth based on human impacts, with animals in environments of high human impact growing for longer and reaching larger adult size, presumably based on availability of human foods (e.g. Turner et al., 1997). Nevertheless, categorical ages based on dental eruption sequences limit the interpretive value of their results, as age categories cover long stretches of developmental time and may not be consistent across regional populations or species, while the method of data collection and the scale of their analysis did not permit a nuanced analysis of diet (Turner et al., 2018). Schmitt et al. (2018) used logistic growth curves to model the growth of captive vervet monkeys (*Ch. sabaues*) gestated on different maternal diets and found evidence not only of the influence of diet during the juvenile phase, but also that vervets gestated on a high-fiber high-protein diet generally grew at slower rates and with longer trajectories than those gestated on a commercial chow diet (see below). While a genetic component to growth was demonstrated, it accounted for a relatively small proportion of variation in growth rate or duration (~12-23%). Although the results are compelling, this study did not test other models that may have more effectively described growth in this population, nor did it provide much detail regarding dietary influences on the juvenile phase of growth between dietary conditions.

The most obvious explanations for differences between wild-fed and food-enhanced or captive groups is that wild populations expend more energy and/or ingest a less nutritious diet (Altmann et al., 1993; Turner et al., 2016), but other factors may also play a role. For example, Pereira (1988) found that aggressive interactions between adult and juvenile yellow baboons reduced the foraging efficiency of juveniles. There is also evidence to suggest that juveniles are less efficient foragers because they lack the strength and/or knowledge to forage as effectively as adults (Altmann, 1980; Boinski and Fragaszy, 1989). Certain aspects of the maternal phenotype have also been shown to influence infant growth rates: Altmann and Alberts (2005) showed that, in both wild-fed and food-enhanced groups, 80% of the offspring born to primiparous mothers were relatively small as juveniles and, among wild-fed groups only, offspring of higher-ranking mothers were heavier. Finally, Strum (1991) suggested that highly seasonal environments could result in large variations in juvenile growth rate within and between years. Thus, variation in rates of aggression, diet composition, environmental variability, and the influence of maternal reproductive and social status are also likely to contribute to variation in growth rates within and between populations. It remains the case, though, that we need more and better data from a wider range of species and populations if we are to begin to build a more comprehensive picture of how and why growth rates vary in the wild.

Here, we use longitudinal data from two cohorts of wild (*Ch. pygerythrus*) and two groups of captive (*Ch. sabaesus*) vervet monkeys, a moderately sexually dimorphic taxon group (Turner et al., 2018). The members of the genus *Chlorocebus* were previously considered to be members of a single species, but are now considered to be separate species given evidence of certain phylogenetic constraints on morphology and behavior (Turner et al., 2019a). The captive vervets were obtained from the island of St. Kitts in the Caribbean, and are of West African

origin. Here, we examine growth rates under wild and captive dietary regimes, although we remain aware that any observed differences may be moderated by factors in addition to dietary quality. Our aims are to:

(i) Determine how growth rates in our wild population compare to the growth potential provided by the captive setting. In addition to the intrinsic value of this comparison, outlined above, we are also interested in using the captive data as a benchmark against which to gauge the performance of our population, which inhabits a semi-arid habitat (Pasternak et al., 2013), where marked drought cycles (McDougall et al., 2010) result in correspondingly large inter-annual variations in resource availability.

In this regard, the first of the wild cohorts (2013) was distinctive, following as it did two years of very few births – 17% of females in 2011 and 11% of females in 2012 – and almost no infant survival beyond three months in either of these two cohorts. Coupled with a strong improvement in rainfall and resource availability during 2012 that persisted through to 2016, this meant that 83% of females gave birth in 2013 to offspring who then, as juveniles, also experienced excellent conditions when making the transition to independent foraging. We consider it likely that growth rates for juveniles in this cohort represent the best achievable in our study habitat (see Young et al. in prep.). Much the same is true for the 2014 cohort during their early development, with the exception of a notable decline in resource availability later on in their development. Additionally, given that most of the females (89%) had previously given birth in 2013, there was little release from gestational and lactation costs.

(ii) Consequently, we assess whether the growth curve model that best captures the combined wild and captive data also describes the wild data considered separately. We do so because it cannot be assumed that a single model will, in principle, describe all growth rates measured in a

taxon or larger taxon grouping (Curran et al., 2010) and that, therefore, the use of growth curve estimates in further analyses requires empirical validation in each case.

(iii) Following this, our third objective is to determine whether growth parameters vary across our two annual cohorts and then, if so,

(iv) Whether the variation in growth parameters across our two wild cohorts corresponds to variation measured in the environmental conditions experienced by each.

Methods

Study populations

For the wild population, where the birth season lasts for approximately three months (October - December), we measured juvenile's body weight from two consecutive birth cohorts (Cohort 2013: N=26, Males =14, Females =12; Cohort 2014: N=24, Males =14, Females=10) from three troops (PT, RBM, RST) of vervet monkeys (*Chlorocebus pygerythrus*) in the Samara Private Game Reserve in the Karoo, Eastern Cape, South Africa (32°22'S, 24°52'E; Pasternak et al., 2013). All three troops are fully habituated, with RST and RBM studied since September 2008 and PT since January 2012.

Subjects were on average 126.70 (\pm 25 SD) days of age when body weight data collection commenced and 780.02 (\pm 17 SD) days old at the end of the study period. The beginning of this period coincides with the onset of weaning (Lee, 1987; Sashaw, 2012), and it ends just before the onset of the male growth spurt, conservatively signalling the end of the juvenile period (Turner et al., 1997). We modelled data from individuals only if they had five or more recordings spanning this period.

Body weights for the captive population were collected from a multi-generational pedigree study of vervets (*Chlorocebus sabaesus*) at the Wake Forest School of Medicine, Winston-Salem, North Carolina, USA. The vervets were originally from the island of St. Kitts in the Caribbean and the colony was housed previously at UCLA (until February 2008). Body weights from 148 individuals were available for the present study. All mothers and infants/juveniles had *ad libitum* access to water, and opportunities for exercise were available to all animals throughout the study period. The diets of all animals were supplemented with fruits and vegetables 1-5 days per week, though these represented only a small proportion of overall caloric intake.

Measurement of body weight

Wild vervets were weighed using a portable field scale (Adam Equipment CPW Plus-15 Weighing Scale), to which a wooden platform (70x70cm) was added to increase surface area (see Fig. S1 in supplementary material). To entice the animals onto the scale, a teaspoon of honey was smeared thinly across a 4cm² area at the centre of the platform, and baby toys (three teething rings) were attached to the platform with cable ties, after which the scale was reset to zero. These measures increased the length of time that animals spent on the platform, enabling stable weights to be recorded. Body weight was recorded to a precision of <5.0 g. If more than one individual was on the scale, we recorded the total body weight, and then recorded the change in weight as animals left, making it possible to obtain individual weights by subtraction. Animals approached and climbed on the scale voluntarily, i.e., there was no formal training of the animals. Body weights were obtained opportunistically throughout the day, whenever the animals were moving in an area to which it was possible to transport the scale (which was stored

in the project vehicle). We recorded 1034 body weight data points across the two cohorts (2013: N=707, M=370, F=337; 2014: N=327, M=195, F=132), averaging 20.68 (\pm 12.4 SD) weights per individual.

Body weights from the captive population were collected annually from 2000 to 2007, and three times annually from 2008 to 2015. Individuals were sedated with intramuscular ketamine (8 to 10 mg/kg), and body weight was measured (in g) using an electronic scale. Body weights were collected from animals that had been raised on one of two prescribed diets: (1) a standard monkey diet (referred to hereafter as “Standard”) Purina LabDiet 5038) with a caloric content of 69% carbohydrates, 18% protein, 13% fat, with 5% weight as crude fibre, and (2) an intervention diet (hereafter “Intervention”), which was higher in fibre and protein (caloric content: 58% carbohydrates, 27% protein, 15% fat, with 12.4% weight as crude fibre – Purina LabDiet Fiber-Balanced Monkey Diet 5052; this diet is no longer available from Purina). For further information on these diets, see Fairbanks et al. (2010) and Schmitt et al. (2018). For the Standard diet, data are presented from animals born between 2010-2012, whose mothers had been fed the Standard diet throughout gestation and lactation, and whose offspring were fed the Standard diet thereafter (45 females and 53 males). For the Intervention diet, data are presented for animals born between 2005-2006, whose mothers were fed the Intervention diet from gestation and throughout lactation, and whose offspring were also fed the same diet after weaning (26 females, 24 males). In total, 1035 data points were collected (Standard = 674, M=367, F=307; Intervention = 361, M=177, F=184), averaging 6.99 (\pm SD 1.61) data points per individual.

Modelling approach

To capture the growth patterns for the wild and captive populations and within the wild population, we fitted the three most commonly used mechanistic growth curve functions, namely von Bertalanffy, Gompertz, and Logistic growth curves (Zullinger et al., 1984), as outlined below:

$$(1) \textit{ von Bertalanffy} \quad W_t = a \left(1 - \frac{1}{3} e^{-k(t-t_0)} \right)^3$$

$$(2) \textit{ Gompertz} \quad W_t = a e^{-e^{-k(t-t_0)}}$$

$$(3) \textit{ Logistic} \quad W_t = \frac{a}{1 + e^{-k(t-t_0)}}$$

All three equations have previously been used to describe growth rates in mammals (Ricklefs, 1967; Gaillard et al., 1997; Strathe et al., 2010; English et al., 2012) and are informed by the same three growth parameters: a , k and t_0 ; where a is the asymptotic weight, k is the growth rate constant, and t_0 is the age of inflection in the growth curve (the point at which the acceleration in growth changes from positive to negative). These three parameters together determine the shape of the growth curve. We converted the growth rate constant into *maximum growth rate* (grams/day) by multiplying k by estimated weight at the inflection point (von Bertalanffy: $W_{t_0} = A \cdot \frac{8}{27}$; Gompertz: $W_{t_0} = A \cdot \frac{1}{e}$; Logistic: $W_{t_0} = \frac{1}{2} \cdot A$) to make the measure of k more biologically meaningful (Case, 1978; Zullinger et al., 1984). The main difference in the shape of the three models is the assumption of where the inflection point lies. The von Bertalanffy assumes the inflexion point is reached at 30% of adult weight, the Gompertz at 37%, and Logistic at 50%

(Zullinger et al., 1984). Thus, the estimated age at which the inflection point occurs is highest in the Logistic model and lowest in the von Bertalanffy. When applying the growth curve functions to the same datasets, there are consistent differences in the estimated values as a result of the specific shape of the growth function's curve. The von Bertalanffy model predicts the highest asymptotic weight of the three, whereas the Logistic predicts the lowest. The Logistic model generally predicts the largest k , and the von Bertalanffy the lowest (Zullinger et al., 1984).

We fitted each of the three growth curve functions to a dataset consisting of observed growth data from the captive and both wild cohort populations considered together, as well as to the dataset from the wild population alone. To estimate the fit of the three growth models, we used the Watanabe-Akaike information criterion (WAIC. McElreath, 2016) to identify the best fitting growth curve for both datasets (i.e., wild-captive comparison, and within-wild cohort comparison). For both datasets, we allowed all three growth parameters, a , k and t_0 , to vary by ecological context (i.e., wild versus captive, or 2013 versus 2014 cohort) and by the sex of the individual. We also allowed sex-specific adjustments to account for any interaction effects between sex and context. For example, estimates for females in the 2014 cohort were based on an adjustment for being female, an adjustment for being in the 2014 cohort, followed by an adjustment for being both female and in the 2014 cohort. We also modelled parity (i.e. whether the mother was primiparous or multiparous) as a fixed effect in the wild cohort comparison, principally to serve as a statistical control for potentially lower growth rates by the offspring of young mothers (Setchell et al., 2001). Finally, we included a random effect of individual identity (ID) on a , k , and t_0 . Model equations for both the between- and within-population comparisons are available in supplementary Equation S1 (wild-captive comparison) and Equation S2 (within-wild cohort comparison).

We applied the growth curve function using a Bayesian framework with r-STAN v.2.14 (Stan-Development-Team, 2017) in R 3.3.1 (R-Core-Team, 2016), using the `map2stan` function in the *'rethinking'* package (McElreath, 2016). The parameter a is the only parameter for which an informed prior was specified. We used the mean body weight of adult males from Samara as our informed prior for a ($\sim N(5,15)$), and applied a large standard error (SE) around the weight to highlight our uncertainty. All other parameters were given priors of ($\sim N(0,1)$), and age and body weights were scaled to the standard deviation (SD) of all body weights, but not centred on the mean.

We assessed the differences in resource availability experienced by each cohort using the Normalized Difference Vegetation Index (NDVI). We used the Normalized Difference Vegetation Index (NDVI), indexed as a value from -1 – +1, as a proxy for net primary vegetation productivity, as it is a strong correlate of food available to wild vervets (Willems et al., 2009). Although these remotely sensed data are quick and easy to obtain, and provide a useful and accurate proxy of overall resource availability, it should be noted that NDVI remains rather a crude proxy measure; it does not allow a detailed assessment of the availability of specific species and food items eaten by the vervets, nor does it provide any information on nutritional quality as such. For our purposes here, however, an assessment of growth in relation to NDVI was sufficient to assess whether growth rates are sensitive to ecological conditions. Any such effects can thus provide the basis for more detailed analyses.

To generate estimates of NDVI, we downloaded MODIS NDVI data from NASA's EarthExplorer site (Didan, 2015). MODIS data are collected by the Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1) with a repeat cycle of 16 days. MODIS data were then imported into ArcGIS where they were overlaid onto the territories of the

three troops, which were represented as a regular series of points 10m apart. NDVI values were then extracted from the MODIS rasters at each point. Once extracted, all NDVI values for each territory were averaged to produce an area weighted average of NDVI for the territory for each troop. The weighted estimate is the average NDVI within the 95% isopleth weighted by the usage of the home range, and each date represents a window that is 33 days wide, 16 days post and prior to the specified date. Therefore, we were able to generate NDVI values that reflected immediate 'local' changes in resource availability (Fig. 2). This then allowed us to capture the difference in resource availability between the two cohorts. We used a Bayesian t-test (Kruschke, 2013) to model the mean and standard deviation sigma of the environmental condition (NDVI) difference between the two cohorts, in order to determine whether there was a difference in experienced NDVI.

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Ethical statement

Data for the wild population body weight collection protocols were approved by the University of Lethbridge Animal Welfare Committee (Protocol #1505). The captive data collection protocols were approved by the Institutional Animal Care and Use Committees of both UCLA and Wake Forest School of Medicine. Both protocols adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

Results

Comparison between captive and wild animals

The von Bertalanffy curve described the combined captive and wild data best (Table 1). We therefore used this growth curve function to quantify between-population differences in growth. The equation describing adjustments for diet, cohort, and sex, and interaction between sex with diet and cohort is provided in supplementary materials (Equation S1).

In summary, the wild population was estimated to achieve a maximum growth rate that was lower by 0.72g per day, that reached its maximum 119.41 days sooner than the captive population and to have been younger at the point of inflection (Fig. 1). Growth parameters specified by the von Bertalanffy curves are provided for the different juvenile vervet groups in Table 2 (see supplementary material Table S1 for model output). Captive animals on the Intervention diet reached heavier asymptotic weights than did those on the Standard diet, with growth rates that differed by sex. Inflection points indicate that juveniles on the Intervention diet grew faster for longer.

In line with the estimated growth curve parameters, we expect an individual in the wild population to weigh 0.80kg less than its captive counterpart at 800 days, with the heaviest

Table 1. The comparison of the growth curve functions for the combined datasets of the captive and wild populations. The table provides a Widely Applicable Information Criterion (WAIC) value for each model (smaller WAIC indicate better estimated out-of-sample deviance). The pWAIC value is the estimated effective number of parameters. The dWAIC value is the difference between each WAIC and the lowest WAIC. The dSE value is the standard error of the differences in WAIC between each model and the top-ranked model (i.e. smallest WAIC). Lastly, w is the Akaike weight for each model.

| <i>Model</i> | <i>WAIC</i> | <i>pWAIC</i> | <i>dWAIC</i> | <i>dSE</i> | <i>w</i> |
|------------------------|----------------|--------------|--------------|--------------|----------|
| <i>von Bertalanffy</i> | <i>-7518.5</i> | <i>357.2</i> | <i>0</i> | <i>NA</i> | <i>1</i> |
| <i>Gompertz</i> | <i>-7379.6</i> | <i>383.7</i> | <i>138.9</i> | <i>11.66</i> | <i>0</i> |
| <i>Logistic</i> | <i>-6838.4</i> | <i>444.1</i> | <i>680.1</i> | <i>40.02</i> | <i>0</i> |

Table 2. Growth parameters specified by the von Bertalanffy model for each juvenile vervet category group in the between-population comparison, where a is the asymptotic weight, maximum growth rate is given in grams/day (estimated by multiplying the growth rate constant, k , by estimated weight at the inflection point of the curve) and t_0 is the age (in days) at inflexion in the growth curve (the point at which the acceleration in growth changes from positive to negative).

| <i>Growth Parameters</i> | <i>Mean (kg)</i> | <i>SE</i> | <i>L95% CI</i> | <i>U95% CI</i> |
|----------------------------|------------------|-------------|----------------|----------------|
| <i>a</i> | | | | |
| <i>Standard Male</i> | <i>2.97</i> | <i>0.06</i> | <i>2.84</i> | <i>3.08</i> |
| <i>Standard Female</i> | <i>2.82</i> | <i>0.07</i> | <i>2.69</i> | <i>2.95</i> |
| <i>Intervention Male</i> | <i>3.63</i> | <i>0.11</i> | <i>3.42</i> | <i>3.85</i> |
| <i>Intervention Female</i> | <i>3.41</i> | <i>0.11</i> | <i>3.20</i> | <i>3.64</i> |
| <i>2013 Male</i> | <i>2.23</i> | <i>0.10</i> | <i>2.04</i> | <i>2.43</i> |
| <i>2013 Female</i> | <i>2.16</i> | <i>0.11</i> | <i>1.95</i> | <i>2.37</i> |
| <i>2014 Male</i> | <i>1.91</i> | <i>0.10</i> | <i>1.72</i> | <i>2.11</i> |
| <i>2014Female</i> | <i>2.06</i> | <i>0.13</i> | <i>1.80</i> | <i>2.32</i> |
| <i>Maximum growth rate</i> | | | | |
| <i>Standard Male</i> | <i>2.80</i> | <i>0.26</i> | <i>2.30</i> | <i>3.28</i> |

| | | | | |
|----------------------------|---------------|--------------|---------------|---------------|
| <i>Standard Female</i> | <i>2.51</i> | <i>0.29</i> | <i>1.99</i> | <i>3.16</i> |
| <i>Intervention Male</i> | <i>2.85</i> | <i>0.31</i> | <i>2.21</i> | <i>3.44</i> |
| <i>Intervention Female</i> | <i>2.45</i> | <i>0.28</i> | <i>1.89</i> | <i>3.01</i> |
| <i>2013 Male</i> | <i>2.10</i> | <i>0.23</i> | <i>1.66</i> | <i>2.53</i> |
| <i>2013 Female</i> | <i>1.91</i> | <i>0.31</i> | <i>1.35</i> | <i>2.64</i> |
| <i>2014 Male</i> | <i>2.07</i> | <i>0.43</i> | <i>1.27</i> | <i>2.85</i> |
| <i>2014 Female</i> | <i>1.57</i> | <i>0.30</i> | <i>1.03</i> | <i>2.20</i> |
| <i>t₀</i> | | | | |
| <i>Standard Male</i> | <i>126.71</i> | <i>5.20</i> | <i>116.44</i> | <i>136.92</i> |
| <i>Standard Female</i> | <i>135.08</i> | <i>6.05</i> | <i>123.09</i> | <i>146.78</i> |
| <i>Intervention Male</i> | <i>158.54</i> | <i>9.01</i> | <i>141.44</i> | <i>176.48</i> |
| <i>Intervention Female</i> | <i>168.11</i> | <i>9.76</i> | <i>149.25</i> | <i>187.39</i> |
| <i>2013 Male</i> | <i>42.46</i> | <i>9.40</i> | <i>23.01</i> | <i>59.99</i> |
| <i>2013 Female</i> | <i>50.72</i> | <i>10.15</i> | <i>30.33</i> | <i>70.20</i> |
| <i>2014 Male</i> | <i>32.44</i> | <i>10.84</i> | <i>12.00</i> | <i>54.22</i> |
| <i>2014 Female</i> | <i>-15.50</i> | <i>16.82</i> | <i>-49.16</i> | <i>16.42</i> |

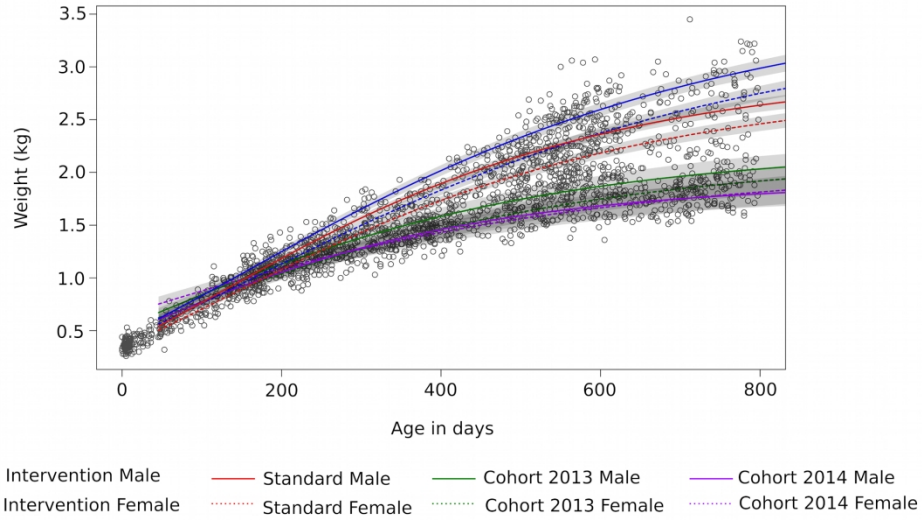


Figure 1. The von Bertalanffy growth curves for the wild and captive cohorts of vervet monkeys across the juvenile period. Open circles indicate raw body weight data.

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animals at the end of the juvenile period being those on the captive Intervention diet, while the lightest were those from the wild 2014 cohort (Supplementary material Table S2).

Growth in the wild cohorts

Whereas restricting growth curve comparisons to the Wake Forest animals reaffirmed that the von Bertalanffy curve continued to provide the best fit (Supplementary material Table S3), the best fit to the data for the wild population considered separately was given by the Logistic growth curve model (Table 3). The equation describing adjustments for cohort and sex, and interaction between sex and cohort, is provided in supplementary materials (Equation S2).

Did growth parameters vary across the wild cohorts?

Estimates indicate that, at the end of the juvenile period (800 days), the average member of the 2013 Cohort was 0.10kg heavier than its counterpart from the 2014 Cohort. The 2013 Cohort as a whole achieved a higher growth rate, with a maximum growth rate difference of 0.35g/day, which they reached 43.94 days later than juveniles from the 2014 Cohort. Posterior distributions of weight at 800 days are given in Table 4. Growth parameters estimated for the wild population by the Logistic growth curve model are provided in supplementary materials (Table S4).

Comparison of the sexes within cohorts indicate considerable overlap between males and females from the 2013 Cohort in terms of maximum growth rate and predicted weight at 800

Table 3. Comparison of the best fitting growth curve functions for the Samara dataset alone. The table represents a WAIC value for each model (smaller WAIC indicate better estimated out-of-sample deviance). The pWAIC value is the estimated effective number of parameters. The dWAIC value is the difference between each WAIC and the lowest WAIC. The dSE value is the standard error of the differences in WAIC between each model and the top-ranked model (i.e. smallest WAIC). Lastly, the w is the Akaike weight for each model.

| <i>Model</i> | <i>WAIC</i> | <i>pWAIC</i> | <i>dWAIC</i> | <i>dSE</i> | <i>w</i> |
|------------------------|----------------|--------------|--------------|-------------|----------|
| <i>Logistic</i> | <i>-3688.6</i> | <i>107.2</i> | <i>0</i> | <i>NA</i> | <i>1</i> |
| <i>Gompertz</i> | <i>-3677.1</i> | <i>104.4</i> | <i>11.5</i> | <i>4.79</i> | <i>0</i> |
| <i>von Bertalanffy</i> | <i>-3672.6</i> | <i>102.4</i> | <i>16</i> | <i>6.33</i> | <i>0</i> |

Table 4. Posterior distributions of weight at 800 days for each specified group in the within-wild population model.

| | <i>Mean (kg)</i> | <i>SE.</i> | <i>L95%</i> | <i>U95%</i> |
|--------------------|------------------|-------------|-------------|-------------|
| <i>2013 Male</i> | <i>2.02</i> | <i>0.05</i> | <i>1.93</i> | <i>2.13</i> |
| <i>2013 Female</i> | <i>1.91</i> | <i>0.05</i> | <i>1.82</i> | <i>2.01</i> |
| <i>2014 Male</i> | <i>1.79</i> | <i>0.05</i> | <i>1.68</i> | <i>1.88</i> |
| <i>2014 Female</i> | <i>1.81</i> | <i>0.05</i> | <i>1.71</i> | <i>1.91</i> |

days (Fig. 2, Table 4). However, while the shape of the growth curves of the males and females of the 2013 cohort were qualitatively similar, the 2013 males were heavier than the 2013 females, and also heavier than both sexes of the 2014 cohort. In contrast, there was a much greater difference between the sexes in the 2014 cohort with respect to maximum growth rate, with the 2014 males growing 0.97g per day faster than the 2014 females. Within the sexes, our results also show differences across cohorts: the 2014 females had lower maximum growth rates and reached a lower weight at 800 days. While males of both cohorts attained similar maximum growth rates, the 2014 males were predicted to be lighter at 800 days, suggesting that they grew more slowly overall and/or they were lighter at birth than the 2013 cohort. We found no evidence that parity was influential in the growth parameters of a , *maximum growth rate*, and t_0 (see Table 5).

Did ecological conditions (NDVI) vary between the wild cohorts?

We used a Bayesian t-test (Kruschke, 2013) to model the mean and standard deviation sigma of differences in NDVI in order to determine whether there was a difference in experienced resource availability across the juvenile period of the two cohorts (Table 6). The 2013 cohort encountered generally higher NDVIs (0.54 ± 0.01 SE) than did the 2014 cohort (0.49 ± 0.01 SE). For both cohorts, the standard deviation sigma, – i.e. the variability around the NDVI value – was small, (2013: 0.08 ± 0.01 SE; 2014: 0.10 ± 0.01 SE. Fig. 2), indicating that the estimated NDVI values for each cohort were highly predictable.

Table 5. Model output for the Logistic growth curve function, where a is the asymptotic weight, k is the growth rate constant, and t_0 is the age at inflexion in the growth curve (the point at which the acceleration in growth changes from positive to negative), together with the subsequent adjustments of sex, parity, and cohort on a , k , and t_0 . The estimate refers to the posterior distributional mean; standard error (SE) is the error around the estimate, and the uncertainty around estimates is expressed with 95% credible intervals (CI). The males of the 2013 cohort were the reference group for cohort comparisons.

| | <i>Mean</i> | <i>SE</i> | <i>L95% CI</i> | <i>U95% CI</i> |
|-------------------------------|--------------|-------------|----------------|----------------|
| <i>a</i> | <i>1.38</i> | <i>0.04</i> | <i>1.31</i> | <i>1.46</i> |
| <i>k</i> | <i>2.22</i> | <i>0.13</i> | <i>1.96</i> | <i>2.47</i> |
| <i>t₀</i> | <i>0.35</i> | <i>0.03</i> | <i>0.30</i> | <i>0.40</i> |
| <i>Sex X a</i> | <i>-0.07</i> | <i>0.05</i> | <i>-0.17</i> | <i>0.03</i> |
| <i>Sex X k</i> | <i>-0.04</i> | <i>0.16</i> | <i>-0.35</i> | <i>0.29</i> |
| <i>Sex X t₀</i> | <i>0.04</i> | <i>0.04</i> | <i>-0.03</i> | <i>0.11</i> |
| <i>Parity X a</i> | <i>-0.03</i> | <i>0.04</i> | <i>-0.11</i> | <i>0.06</i> |
| <i>Parity X k</i> | <i>0.09</i> | <i>0.15</i> | <i>-0.21</i> | <i>0.38</i> |
| <i>Parity X t₀</i> | <i>0.02</i> | <i>0.03</i> | <i>-0.04</i> | <i>0.08</i> |
| <i>Cohort (2014) male X a</i> | <i>-0.19</i> | <i>0.05</i> | <i>-0.29</i> | <i>-0.09</i> |
| <i>Cohort (2014) male X k</i> | <i>0.33</i> | <i>0.19</i> | <i>-0.03</i> | <i>0.70</i> |

| | | | | |
|---|--------------|-------------|--------------|--------------|
| <i>Cohort (2014) male X t₀</i> | <i>-0.05</i> | <i>0.04</i> | <i>-0.12</i> | <i>0.02</i> |
| <i>Cohort (2014) female X a</i> | <i>0.13</i> | <i>0.08</i> | <i>-0.02</i> | <i>0.29</i> |
| <i>Cohort (2014) female X k</i> | <i>-0.59</i> | <i>0.29</i> | <i>-1.19</i> | <i>-0.06</i> |
| <i>Cohort (2014) female X t₀</i> | <i>-0.06</i> | <i>0.06</i> | <i>-0.17</i> | <i>0.05</i> |
| <i>sigma</i> | <i>0.04</i> | <i>0.00</i> | <i>0.04</i> | <i>0.04</i> |

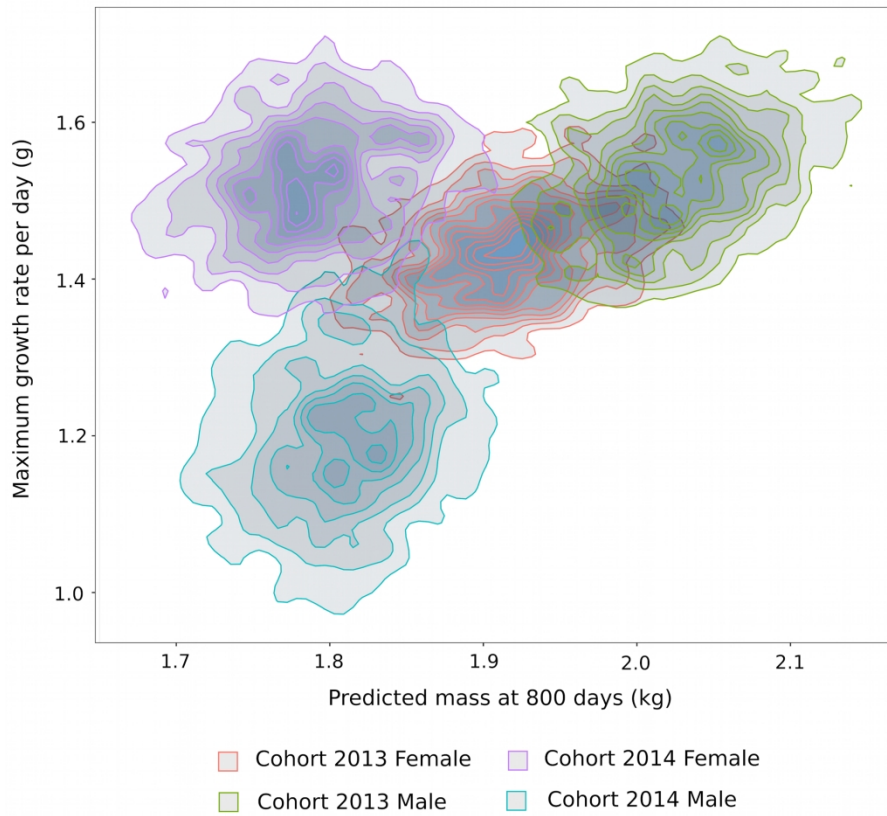


Figure 2. Density plots of estimated growth parameters for males and females in the 2013 and 2014 cohorts. Contour lines are provided to aid visualisation of the shape of each density plot.

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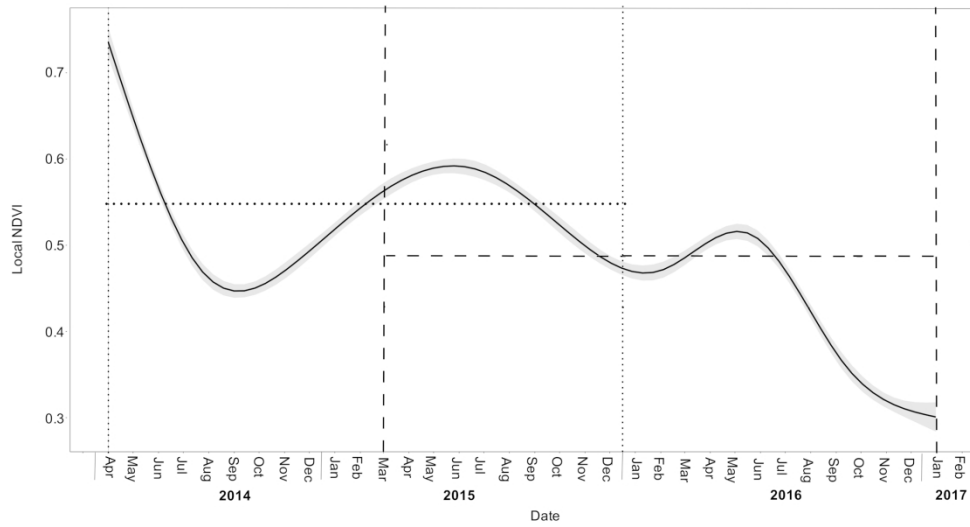


Figure 3. Local Normalized Difference Vegetation Index (NDVI) values (\pm 95% CI) from April 2014 to December 2016. The two blocks indicate the range of NDVI values experienced by each cohort during the juvenile period.

199x106mm (300 x 300 DPI)

Discussion

In keeping with work on other taxa, our results indicate that juveniles in our wild population grew more slowly and reached lower weights at the end of the juvenile period than did their captive counterparts, with males in both captive cohorts, and the 2013 wild cohort, reaching heavier weights than females. While differences in dietary quality and their consistency over time may make this an obvious conclusion, the value of the comparison stems from the fact that the growth curves of the two captive cohorts are likely to lie at or near the maximum realistically attainable by juvenile vervets. In much the same way, then, that Altmann (1991) was able to use the extent of the shortfall in the dietary optima of juvenile baboons to model lifetime fitness, it may be helpful to include deviations from these captive growth rates when assessing the consequences of early nutritional environments for the later behavior and reproductive performance of wild vervet monkeys.

We should also be careful not to over-simplify here, as there are other influences on growth besides nutrition. One prominent influence is likely to be disease which affects the trade-off between growth and maintenance: mounting an immune response increases metabolic energy requirements and diverts energy that otherwise could be placed into growth. Disease can also prevent nutrient intake, and adversely affect nutrient absorption, which can also lead to reduced growth rates (see Stulp and Barrett (2016), and Urlacher et al. (2016) for human examples). In addition, any factors that acutely increase the mortality risk of particular age classes can affect the life-history trade-off between growth and reproduction: as mortality on juveniles increases,

and the chance of reaching adulthood decreases, the postponement of reproduction becomes more costly, and growth rates should thus increase, giving rise to an earlier age at sexual maturity (Stearns 2000; see Stulp and Barrett 2016, Walker et al. 2016 for human examples). Wild populations thus face additional constraints on growth and will show norms of reaction that differ from their captive counterparts (especially as captive colonies receive high levels of veterinary care and treatment that ameliorate immune costs and influence survival probabilities). A fully comprehensive comparison of wild and captive groups would need to take these influences into account.

While not quite as clear cut, captive studies may also benefit from comparison with wild reference groups. Although it is very likely that juveniles at Samara, even those from the 2013 cohort, are not growing at the rates possible for wild vervets, they do at least present realistic trajectories against which to examine the sequelae of experimentally-manipulated diets (see, for example, Schmitt et al., 2018). It is noteworthy, for example, that captive animals on the Intervention diet – introduced as a reduced calorie, weight-loss diet – were predicted to be heavier at both the end of the juvenile period and across the lifespan (Schmitt et al., 2018) than animals on the Standard diet. Although it is possible that these changes in adult weight are due to a diet-related shift in body composition (i.e., altered ratio of fat to lean muscle tissue), rather than fat alone, we are unable to assess this with our current dataset. Future work in the VRC focusing on dual energy X-ray absorptiometry scans across dietary interventions may be able to shed light on this question (i.e., Kundu et al., 2013). In our wild cohorts, however, reductions in dietary quality seemed to have the opposite effect (Table 2), with our two cohorts encountering the same declining food availability (Figure 3) but at different stages of development. Clearly, this reflects, at least in part, the consequences of consistent food availability and absolute nutritional

quality on the ability to respond to maternal nutritional constraints through catch-up or compensatory growth (Boersma and Wit, 1997). Although there is evidence for compensatory adjustment in other wild cercopithecines (Berghänel et al., 2016), this did not appear to be a strategy available to our wild juveniles. It seems possible that the early age at which the 2014 cohort confronted declining resources may have contributed to their inability to rebound, at least during the juvenile period. Here, it would be helpful to have comparative data from other vervet populations, a possibility facilitated by our demonstration of the feasibility of longitudinal data collection from the species under natural conditions.

Although all members of the genus *Chlorocebus* have at various times been considered members of a single species (see Turner et al., 2019a), and all members of the genus have been considered comparable in evolutionary history, morphology, and behavior, more recent research suggests that we must consider potential phylogenetic constraints in how we interpret our results. Turner et al. (2018; 2019b), for example, found significantly higher sexual dimorphism in both body mass and length in West African and Caribbean *Ch. sabaesus* than in their sample of South African *Ch. pygerythrus*, with these differences being in female rather than in male body size variation. They also found that the cross-sectional growth patterns between these taxa, albeit based on dental age categories, showed qualitative differences in rates of growth between age categories: *Ch. pygerythrus* showed more gradual increases in body mass across age categories compared to *Ch. sabaesus*, which appeared to show a sharp increase in size at puberty. Although it is difficult to translate these results to meaningful chronological differences in growth patterns (Turner et al., 2018), the genetic component demonstrated for growth parameters (Schmitt et al., 2018) suggests the possibility that factors other than, or in addition to, captive diet may underlie

differences in growth between different vervet taxa. A fuller comparison would require comparable longitudinal wild data on weight from Caribbean or West African *Ch. sabaesus*.

The comparison of the wild and captive juveniles confirms that there is utility in both comparing different growth curve models for goodness-of-fit to particular data sets, and an appreciation that the best models may well differ for different populations. In other words, the choice of mechanistic growth model can be empirically justified, rather than theoretically predetermined. The fact that the von Bertalanffy model provided the best fit to both the combined captive-wild data, as well as to the captive data fitted separately, while the Logistic model best described the wild data, suggests that the captive cohorts are driving the fit of the comparative data. This can be seen, for example, in the estimates of the age at inflexion for the wild cohorts (t_0 : -15.5 days - 1.72 days; Table 2), which are unrealistically early and for which better absolute values are generated by the Logistic model (128.4 days - 186.9 days; see Table S4). Qualitatively, however, the outcomes from the two-population von Bertalanffy model do not differ from those produced by the Logistic model and do enable a direct comparison of relative growth trajectories in relation to resource availability.

Restricting analysis to the wild cohorts revealed that, in accordance with the difference in resource availability (indexed by NDVI) experienced by the two groups as well as, perhaps, differences in maternal physiological and nutritional stress, males and females in the 2014 cohort ended the juvenile growth period at lower weights than those in the 2013 cohort. More interestingly, perhaps, the maximum growth rate of the 2014 females was distinctively lower than those of the other three sex/cohort groups (Fig. 2), suggesting that females are more sensitive to a downturn in nutrient availability but are better able to minimize the deficit by adjusting growth rate. By the same token, juvenile males appear less able to compensate for

adverse ecological conditions, a constraint that may have downstream consequences for survival and mating success, unless they are able to compensate during the adolescent growth spurt characteristic of sexually dimorphic cercopithecines (Leigh, 1996). Although we included maternal parity in our model as a statistical control, it is worth noting that it had little effect on growth rates, a finding that echoes the results of Nuñez et al. (2015) on captive rhesus monkeys (*Macaca mulatta*), and suggests a fruitful line of comparative enquiry into the extent to which – and reasons why – this might differ across species and rearing conditions. We hope that ongoing data collection on these and later cohorts will allow us to address in more detail, not only this issue, but also questions concerned with catch-up growth, pubertal growth spurts, and other short-term shifts in rate within and across cohorts, and the social and ecological factors that underpin them.

In this regard, it is important to reiterate that individual differences in growth, and the consequences for adult size, are likely to underpin differences in fitness (Lindström, 1999). If growth is influenced by ecological conditions, it also offers a valuable means by which to understand a taxon's response to climate change and the larger differences observed across widespread taxa such as *Chlorocebus*.

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