RESEARCH ARTICLE

Estimates of life history parameters in a high latitude, arid-country vervet monkey population

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Abstract

We present data on life history parameters from a long-term study of vervet monkeys in the Eastern Cape, South Africa. Estimates are presented of age at first conception for females and age at natal dispersal for males, along with the probability of survival to adulthood for infants born during the study, female reproductive life-span, reproductive output (including lifetime reproductive success for a subset of females), and inter-birth interval (IBI) duration. We also assess the effect of maternal age and infant survival on length of IBI. We then go on to compare life history parameters for our population with those from two East African populations in Kenya (Amboseli and Laikipia). We find there is broad consensus across the three populations, although mean infant survival was considerably lower for the two East African sites. Such comparisons must be made cautiously, however, as local ecology across the duration of the studies obviously has an impact on the estimates obtained. With this caveat in place, we consider that the concordance between values is sufficient to enable the values reported here to be used in comparative studies of primate life history, although data from habitats with higher rainfall and lower levels of seasonality are needed, and the results presented here should not be seen as canonical.

KEYWORDS
fecundity, inter-birth intervals, lifespan, sexual maturity, survival

1 | INTRODUCTION

"Life histories lie at the heart of biology; no other field brings you closer to the underlying simplicities that unite and explain the diversity of living things and the complexities of their life cycles" (Stearns, 1992, p. 9).

Life history theory offers a robust evolutionary framework by which we can study reproductive and mortality schedules and make direct comparisons between species (the famous "mouse to elephant" graph; Burness, 2002). Although not uniquely so (Healy et al., 2014), primates are characterized by slow life histories and, in particular, by a prolonged period of juvenile development. The latter has often

been the focus of studies of primate life history and its evolution, which, as pointed out by Whitten and Turner (2009), obscures variation in the shape of timing and growth within and between both individuals and species. Perhaps as a result, understanding functional interactions between different life history components, and how this varies, remains rather poorly understood. In addition to a focus on prolonged development, this state of affairs no doubt reflects the difficulty and time investment required to obtain estimates of life history parameters, especially on wild populations. As such, any and all information on primate life cycles represents a valuable addition to the literature, and also increases our ability to understand primates' ability to adjust to environmental variation (whether in terms of resource availability, predator pressure, or any combination thereof). More specifically, information on life history parameters across and within populations of the same species—especially those that occupy a broad array of habitats—will allow us to investigate the likely scope and limits of evolved reaction norms, that ensure an appropriate trade-off between life history components (Stearns et al., 1986).

Here, we offer an assessment of the life history parameters of a population of vervet monkeys (*Chlorocebus pygerythrus*) in South Africa and compare these estimates with those from two other *Ch. pygerythrus* populations in East Africa (Cheney et al., 1988; Isbell et al., 2009). Vervets are a wide-spread African genus, second only to the *Papio* baboons, and encounter a wide variety of environmental conditions. They also show an accelerated life history compared to other primate species, which enables assessments of their life cycle to be obtained within a reasonable period, and also suggests that selection has acted in ways that promote faster reproduction. As such, determining whether and how different populations converge or vary in terms of their reproductive and mortality schedules can shed light on how ecology likely shapes life history, while pointing to whether norms of reaction are present, and the degree to which these extend or limit the animals' ability to respond to ecological variation, including the kinds of rapid environmental change that many species now face.

2 | METHODS

2.1 | Study species and research site

We collected data from two to three fully habituated groups of wild vervet monkeys over the period 2008 to 2019 (RBM, RST since 2008, and PT from 2012) at Samara Private Game Reserve, South Africa (32°22′ S, 24°52′ E). An overview of group sizes is provided in Blersch et al. (2023). The study area is semi-arid riverine woodland (Pasternak et al., 2013), with a declining annual average rainfall of 386 mm, and average minimum and maximum temperatures of 6.1°C and 21.2°C, respectively. While rainfall is generally low, the area is also characterized by periods of severe drought and very low food availability (Young, Bonnell, et al., 2019).

2.2 | Births and deaths

Each study troop was followed by one to three fieldworkers for 5 days a week across the study period. Vervet females in our study population experienced a moderately circumscribed birth season with a peak centered on October (Blersch et al., 2023). We classified live births into cohorts based on the year of conception (e.g., 2008). Gestation in vervet monkeys has been estimated at ~163 days (Johnson et al., 1973 for *Ch. pygerythrus*), and infants in our population are considered to have completed weaning by the age of 217 days|7 months (Sashaw, 2012). Data were collected on individually recognizable animals. The dates of all live births were recorded from 2008 to 2018 (RBM, RST) or 2012−2018 (PT), as were indicators of terminated pregnancies, as well as the dates of adult deaths or departures. We were able to determine infant survival to weaning for the 2010−2017 cohorts (2012−2017 cohorts for PT; Blersch et al., 2023) but were only able to track infants to adulthood from the 2013 cohort onwards. The troops were censused on each observation day. Where births, deaths, or migrations occurred on a weekend, when the animals were not under observation, we allocated Saturday's date to the event. Daily fieldwork ended in early 2019 but frequent censuses were conducted subsequently until October 1, 2019.

2.3 | Statistical analyses

We used JMP (JMP, 2021) to generate survival curves and to estimate the probability of survival to indicator ages. We used inter-birth intervals (IBIs) as the dependent variable in a model to test for the possibility of age-specific fecundity (Fairbanks & McGuire, 1984; Isbell et al., 2009) and the effect of infant survival on IBI. We did so in a Bayesian framework using the "brms" package (Bürkner, 2017) in R4.2.2 (R-Core-Team, 2022). We entered infant survival to weaning (Y/N), the order of each female's births (as a proxy for increasing age), and whether she had been nulliparous or parous before her first recorded birth, as main effects, specifying an interaction between them. Troop identity was entered as a statistical control. As the distribution of IBIs was markedly right-skewed (Figure 3), we used the "skewnormal" distribution along with weakly informative priors to model the data, and entered female identity and birth cohort as crossed random effects. The model was run on the reduced data set for which we had infant survival data (see Blersch et al., 2023). Excluding infant survival to model age-specific fecundity alone did not change the outcomes and we only present the full model here.

We ran the model with four chains and 2000 iterations. Chain convergence was confirmed ($\hat{R}$ = 1.0), and model goodness-of-fit was assessed using the "pp_check()" function from the "bayesplot" package (Gabry & Mahr, 2017). R^2 values were estimated with "bayestest" (Makowski et al., 2019). We set the credible intervals at 95% because of their interpretive familiarity and used these, backed by "probability of direction" estimates (Makowski et al., 2019), to evaluate model outcomes. The distribution of IBIs was plotted with "ggplot 2" (Wickham, 2009).

3 | RESULTS

3.1 | Female age at first conception

A total of 46 female infants from the 2013–2017 cohorts survived beyond weaning. We obtained the age at the birth of her first infant for 13 of these females (mean: 1533 days|4.2 years; median: 1470 days|4.0 years; range: 1108–1820 days). Assuming a gestation period of 163 days, this indicated a mean age at first conception of 1370 days|3.7 years (median: 1307 days|3.6 years; range: 945–1657 days). It should be noted that 15.3% (7/46) of these females manifested signs of terminated pregnancies (heavy vaginal bleeding) in the breeding season before their first successful conception, which would place their first conception in the previous season. By the same token, however, seven females, for whom no possible terminations had been recorded, had not given birth by the last recorded birth dates for the 2018 cohort (05/12/2018). These females were of an age that fell within the range of days recorded for successful first births and matched the median age (mean: 1487 days; median days: 1493; range: 1476–1500 days). A survival analysis, therefore, incorporating censored data from females (N = 33) that had either died or not yet conceived by the last day of confirmed conception in the 2018 mating season, indicated an estimated mean age at first conception of 1537 days|4.2 years and a median age of 1657 days|4.5 years (Figure 1a).

3.2 | Male age at natal emigration and first paternity

Forty-four males from the 2013–2017 cohorts survived beyond the mean age of weaning. Of these, 21 males emigrated from their natal groups (mean: 1474 days|4.03 years; median: 1621 days|4.4 years; range: 619–2178 days). The age of the oldest male not to have left his natal group by the end of the study—a male from the 2009 cohort—was 3640 days (9.9 years). We ran a survival analysis to account for censored data (N = 24), which indicated a mean age at first migration of 1574 days|4.3 years and a median age of 1721 days|4.7 years (Figure 1b).

Fortuitously, the transfer of natal males to adjacent study groups, together with a concurrent study of male paternity (Minkner et al., 2018), made it possible to identify the ages at which three males first sired offspring. Dates of birth were used to estimate the ages of the males at the time of their infants' conception. These were 2045 days|5.6 years, 2050 days|5.6 years, and 1972 days|5.4 years, respectively.

3.3 | Probability of survival to the commencement of reproductive careers

Of the 118 infants that were born during 2013–2017, 29 (24.6%) died before weaning, and before we could unambiguously sex them. A further 7 died before the end of their first year. While we consider weaning and consequent nutritional independence to be the biologically relevant threshold (Blersch et al., 2023), the estimate of the probability of death in the first year (36/118: 30.5%) allows comparison with other published studies.

There were 12 juveniles (N_{Female}: 6; N_{Male}: 6) that died after weaning but before reaching the estimated median ages at first conception (1657 days) or natal emigration (1721 days). Twelve females and 12 males were still younger than the relevant median age at the time of the last census (01/10/2019), leaving 27 females and 26 males that survived to their respective median ages at reproductive maturity. Accordingly, to set limits on the probability of surviving from birth to the age at which the median female and male
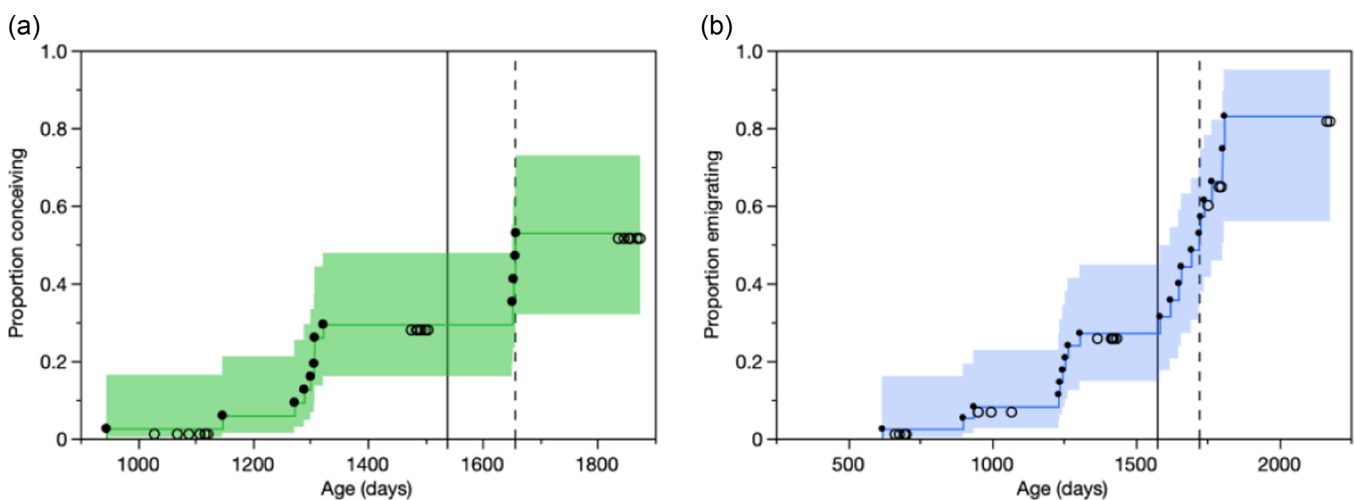
FIGURE 1 Kaplan–Meier failure plots for age at first conception (a) and age at natal emigration of males (b). Realized events indicated by solid circles, censored data by open circles. Solid line: mean age; dashed line median age. Shaded areas indicate 95% confidence intervals (green: females; blue: males).
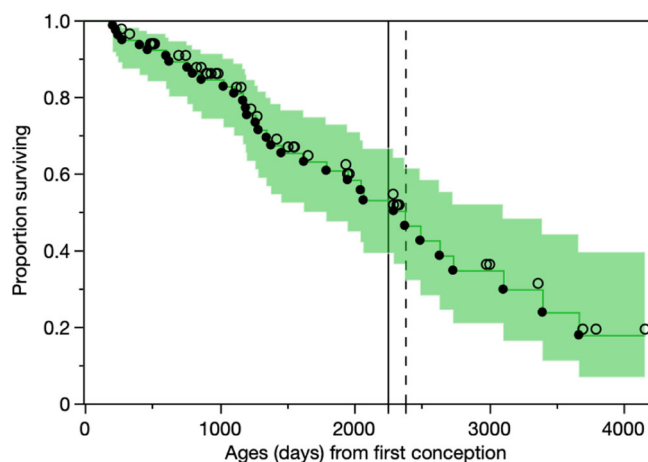
commenced their reproductive careers, we first assumed that preweaning deaths were equally divided between the sexes, arbitrarily allocating 15 to females and 14 to males. We then incorporated the 24 pre-median age females and males by assuming either that they had all died or had all survived. This generated minimum and maximum survival probability bounds of 0.45 (27/60) and 0.65 (39/60) for females. Corresponding values for males were 0.45 (26/58) and 0.66 (38/58).

3.4 | Survival of reproductively mature females

We obtained the reproductive histories of 79 females over the period 2008–2018. Of these, we had the complete histories of 34 females who were nulliparous before their first recorded births. An additional 18 females, who were parous before their first recorded births, died during the study, while 27 females were still alive at the time of the last census (01/10/2019). We estimated female reproductive lifespan from the first recorded conception by adding 163 days to the estimates based on date of first recorded birth. The minimum recorded age at death after the date of known first conception was 186 days|0.5 years, while the maximum known age was 3666 days|10 years. The longest recorded duration, from a female alive at the end of the study, was 4160 days|11.4 years.

The 34 females for which the data were complete had a mean adult lifespan (i.e., from age at first conception until death) of 1454 ± 1034 days|3.98 years (median: 1143 days|3.13 years). The Weibull distribution (α: 1643 ± 184 SE; β: 1.61 ± 0.22 SE) provided the best fit to these data, with the β value indicating a slightly increasing likelihood of death—rather than earlier or constant failure—with increasing age.

Incorporating the censored data into a survival analysis (Figure 2), generated a mean adult lifespan estimate of 2245 ± 162 days|6.15 years (median: 2374 days|6.5 years). The probability of surviving to the oldest recorded reproductive lifespan (4160 days) was 0.16, while only 5% of females were predicted to have a reproductive career that spanned 5744 days|15.7 years. Adding the mean (1537 days) and median (1657 days) age at first conception provided estimates of a mean and median female total life expectancy of 3782 days|10.36 years and 4031 days|11.04 years, respectively.

3.5 | Reproductive output

Over the period 2008–2018, the 79 females generated 212 live births. The 34 females for which we have complete reproductive histories had, on average, 2.97 live births (N; 104; median: 3; range: 1–7). These 104 births were produced over 144 female-birth seasons, across which 11 stillbirths/terminated pregnancies were also recorded. The 44 females whose complete reproductive histories were not known were associated with a similar average of 2.45 live births (N: 108; median: 2; range: 1–8) produced across 166 female-birth seasons and incorporating 10 terminated pregnancies.
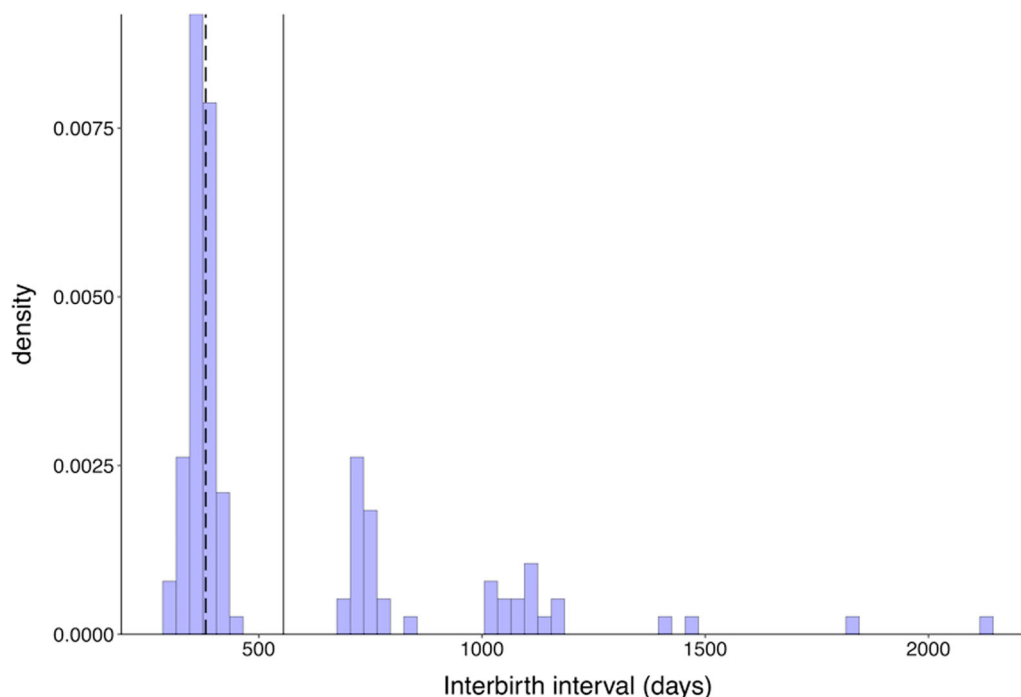
3.6 | IBI

We were able to extract 134 IBIs from the 55 females for which we had multiple birth records. The mean IBI was 545 days|1.49 years (median: 380 days|1.04 years; range: 288–2121 days). The distribution was very strongly right-skewed, with the peak centered on the median IBI, and subsequently indicating seasonally defined and diminishing peaks (Figure 3).

3.7 | The effect of maternal age and infant survival on IBI

We found no meaningful evidence to support the expectation that IBI would increase with age, using either birth order or relative age (primiparous/multiparous) at first recorded birth, or their interaction, as predictors. Nor was there any effect of infant survival to weaning on IBI (Table 1). Neither the main effects ($R^2_{Marginal}$: 0.0.22), nor the model as a whole ($R^2_{Conditional}$: 0.032), accounted for much variance.

4 | DISCUSSION

Using median values to address skew in the distributions, and survival analyses to accommodate censored data, we estimate that the median female at our study site, having had a ~55% probability of surviving to adulthood, first conceived at 4.5 years of age and subsequently gave birth when approximately 5 years old. Before dying at the age of 11, she would have given birth to three infants, attempting to do so every year, with no effect of relative age on effort. Nevertheless, factoring in the 55% probability of survival to

FIGURE 2 Kaplan–Meier survival plot for female survival from first conception. Realized events indicated by solid circles, censored data by open circles. Solid line: mean age; dashed line median age.

FIGURE 3 Histogram of inter-birth interval frequencies (bin size: 30 days) Solid line: mean age; dashed line median age.

TABLE 1 Posterior density estimates of the effects of relative age (parity), birth order (order), and infant survival (survive) on inter-birth interval.

	β	SE	l-95% CI	u-95% CI	Bulk_ESS	Tail_ESS	PD (%)
Intercept	0.09	0.17	−0.28	0.42	3958	1978	71.47
Parity (ref: primiparous)	−0.09	0.4	−0.92	0.73	3678	2678	59.50
Order	−0.02	0.03	−0.09	0.04	5463	2852	72.65
Parity*order	0.16	0.26	−0.37	0.67	3407	2508	74.60
Infant survive? (ref: no)	0.05	0.1	−0.15	0.27	6015	3017	67.70
Troop (ref: PT) RBM	0.03	0.15	−0.24	0.34	3608	2354	56.38
Troop (ref: PT) RST	0.12	0.14	−0.13	0.42	3031	1907	81.23

Note: Mother ID and birth cohort were entered as crossed random effects. Troop was entered as a statistical control.

Abbreviations: β, slope of the predictor; CI, credible interval; ESS, effective sample size; PD, probability of direction; SE, standard error of the estimate of β.

adulthood suggests that, under the conditions prevailing during our study, she would not be able to replace herself. Having said this, we should also note the existence of wide variation in certain parameters (e.g., age at first conception, female adult lifespan, number of offspring produced), which could represent either a response to ecological variation across years (i.e., could be indicative of cohort effects) and/or to variation across individual females in their ability to cope with, and adjust to, local ecological variation.

While we were not able to track male careers over the lifespan with the same precision, their trajectory to adulthood was, despite differences in size and growth rates (Jarrett et al., 2020), remarkably similar to that of females, with the probability of surviving to natal

emigration also ~55% and a median age at natal emigration of 4.7 years, followed by the possibility that their first offspring could be conceived when they were ~5.5 years, making them ~6 years when the infant was born. Unlike species such as chacma baboons, *Papio ursinus*, where male reproduction is contingent on attaining alpha status soon after immigration (Henzi et al., 2010), the reproductive success of vervet males, by being tied to dominance rank (Minkner et al., 2018), increases over time and is contingent on socio-spatial integration with females in the new troop (Young et al., 2017; Young, McFarland, et al., 2019). The departure of natal males, typically during the mating season (Young, McFarland, et al., 2019) and before they have completed somatic growth (Turner et al., 2018), suggests

that the first year in the new group offers them the prospect of developing advantageous relationships in advance of the inevitable reproductive competition.

Generally, despite differences in sample size and analytical approach, our results cohere broadly with those from Amboseli (AMB) and Laikipia (LAI), both in Kenya, for which reasonably comparable data are available (Cheney et al., 1988; Isbell et al., 2009). Expressed life history values, not surprisingly, reflect the intersection of selection for optimal trajectories with the specific environmental conditions experienced at the time of the study. This needs to be acknowledged when evaluating the implications of detectable inter-site differences. More specifically, both Kenyan study populations declined to the point of local group extinction in response to environmental stochasticity (Isbell et al., 2009; Lee & Hauser, 1998), while this was not the case for our study population. Together with the fact that annual rainfall (AMB: 300 mm; LAI: 720 mm) was low, and its interannual variability high (Isbell et al., 2009; Lee & Hauser, 1998; Young, Bonnell, et al., 2019) at all three sites, the observation that female reproduction at Samara was below replacement indicates extirpation as a possible outcome of an even slightly extended downturn in environmental conditions, as we have seen in groups outside of our study area (Pasternak et al., 2013). By the same token, however, the high potential reproductive rate and early onset of reproductive careers offers the prospect of rapid recovery when conditions improve. There is support for this both in our earlier finding that infant survival varied principally across cohorts in response to resource availability (Blersch et al., 2023), and that Laikipia IBIs were markedly lower during a period of unusually high rainfall (Isbell et al., 2009).

This broad consensus glosses over the fact that these data by their very nature are skewed, and it will be the variation that will be important when translating life history parameters into the context of individual action and group-level processes, and other social outcomes. That is, we need to consider more deeply aspects of life history trade-offs (i.e., between growth, maintenance, and reproduction) and the likely expression of reaction norms, both across and within populations, and within populations in relation to climatic extremes (as we see very clearly at Samara).

With that in mind, then, we can note that mean infant survival to 12 months was lower (AMB: ~40%; LAI: 52%), than the 70% recorded at Samara. The difference in survival to weaning at Samara in this study (75%) to that estimated in our earlier analysis (70%; Blersch et al., 2023), which folded in data from earlier, more challenging years, simply confirms, however, that estimates are contingent on immediate environmental conditions. All three sites concurred that preadult mortality was largely confined to the first year although, unlike Samara, male juvenile mortality at AMB (0.11) was higher than that of females (0.06). Estimates of age at first birth were similar (AMB: 4.4−5.6 years; LAI: 3.5−6.1 years), as was the single available estimate of the age at male sexual maturity (AMB: +5 years). The range of mean troop-level IBIs at AMB (1.13−1.75 years), and the mean estimate for LAI (1.09 years) were adjacent to the values for Samara. Interestingly, and unlike the data presented for captive

vervets (Fairbanks & McGuire, 1984), the data from Samara corroborate the earlier finding from Amboseli of an absence of age-related fecundity. Despite general expectation (Borries et al., 2013), and the observation that AMB females with non-surviving infants were less likely to skip a breeding season, a Samara infant's survival had no detectable effect on maternal reproductive rate. Finally, while estimates of female lifespan were less precise (AMB: 10−13 years; LAI: 9.3 years from already multiparous females, oldest - ~12 years), they were close to the values from Samara.

All-in-all, then, summary estimates from the three sites appear to be sufficiently coherent to contribute a taxon datum—either singly or in concert—to comparative analyses that need to fold in life history variables (see, for example, Powell et al., 2019). At the same time, despite the large latitudinal difference in location, the outcomes clearly reflect the animals' engagement with similarly harsh environmental conditions (Turner et al., 2018), and should not be considered to be canonical for the taxon group. Long-term captive data for *Ch. sabaeus*—vis., survival beyond 12 months: 80%; female survival to adulthood: 69%, with 5% surviving to ~25 years; IBI: mean: 10.7 months, median: 10.2 months (Fairbanks & McGuire, 1984; M. J. Jorgensen, unpublished data)—confirm the life historical benefits of abundant food and environmental stability, and should probably be taken to represent the upper bounds of what is possible for *Chlorocebus*. As the survey in Turner et al. (2018) makes clear, however, vervets occur in many areas where rainfall is far more abundant, and seasonality less evident than at Samara, Amboseli, and Laikipia. In encouraging the collection of life historical data at such localities, we would expect to see values that are to a greater or lesser degree intermediate between ours and those from captivity, as we would from sites where free-ranging groups have access to supplemental resources (e.g., Thatcher et al., 2020).

AUTHOR CONTRIBUTIONS

S. Peter Henzi: Conceptualization (equal); formal analysis (lead); methodology (equal); supervision (equal); writing—original draft (equal); writing—review and editing (lead); funding acquisition (equal); project administration (equal). **Rosemary A. Blersch**: Investigation (equal); data curation (equal); writing—review and editing (equal). **Tyler R. Bonnell**: Formal analysis (equal); supervision (equal); writing—review and editing (equal). **Madison Clarke**: Data curation (equal); writing—review and editing (equal). **Marcus J. Dostie**: Investigation (equal); writing—review and editing (equal). **Miranda Lucas**: Investigation (equal); writing—review and editing (equal). **Jonathan Jarrett**: Investigation (equal); data curation (equal). **Richard McFarland**: Investigation (equal); supervision (equal); Investigation (equal); writing—review and editing (equal). **Christina Nord**: Investigation (equal); writing—review and editing (equal). **April Takahashi**: Investigation (equal). **Chloé Vilette**: Investigation (equal); data curation (equal); writing—review and editing (equal). **Chris Young**: Investigation (equal); supervision (equal); investigation (equal); writing—review and editing (equal). **Mirjam M. Young**: Investigation (equal); methodology (equal). **Louise Barrett**: Conceptualization (equal); methodology (equal); supervision (equal); writing—original draft (equal); writing—

review and editing (lead); funding acquisition (equal); project administration (equal).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study have been uploaded to Figshare. https://doi.org/10.6084/m9.figshare.22814312

ETHICS STATEMENT

All protocols were noninvasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505).

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