# Growth trajectories of wild Assamese macaques (*Macaca assamensis*) determined from parallel laser photogrammetry

Simone Anzà[1,2,3] · Andreas Berghänel[4] · Julia Ostner[1,2,3] · Oliver Schülke[1,2,3]

## Abstract

Socioecological factors are associated with life-history patterns and growth trajectories among primates. Under certain conditions, selection may favor a temporal decoupling of growth and major life-history events such as sexual maturation or natal dispersal. Yet, empirical tests of these associations in wild populations remain scarce owing to the lack of non-invasive methods to capture growth trajectories. In this study, we first compared two non-invasive methods of digital photogrammetry. Then, we used parallel laser photogrammetry to investigate forearm growth of wild Assamese macaque males and females in their natural habitat at Phu Khieo Wildlife Sanctuary, Thailand to test life-history and socio-ecological hypotheses. Across 48 males and 44 females, we estimated growth trajectories and pseudo-velocity curves by applying quadratic plateau models and non-parametric LOESS regressions. We assessed the development of sexual dimorphism by comparing the sexes at five different ages. Females had completed 96% of their growth at the age at first birth (5.9 years) and ceased growing at 7.1 years of age. Males, in contrast, grew until well after their average age of natal dispersal: they reached 81% of their size at the age of natal dispersal (4.0 years), and ceased growing only at 9.0 years of age, much later than females. Sexual dimorphism in forearm length was driven by an extended growth period in males, which is expected for males dispersing between multimale and multifemale groups and not facing the risk of being ousted by other larger males. Our results contradict the *neonatal investment hypothesis* that predicts a desynchronization of investment in growth and reproduction only in female baboons, but not other papionins producing cheaper neonates. Furthermore, male Assamese macaques do not delay natal dispersal until they are fully grown, in accordance with predictions of the *male-career-framework* for species with low to medium level of direct competition.

**Keywords** Development · Digital photogrammetry · Life history · Male career framework · Neonatal investment hypothesis · Parallel lasers · Sexual dimorphism

## Introduction

Darwinian fitness can be enhanced by growing fast to mature early, reproducing at higher rates than others, producing higher quality offspring, and surviving better to enjoy a long reproductive life span (Stearns 1976). The central tenet of life-history theory is that resource allocation trade-offs keep individuals from realizing this life-history strategy (Stearns 1989). As a result, none of the fundamental processes in life

✉ Simone Anzà
   simone.anza@uni-goettingen.de

1  Behavioral Ecology Department, University of Goettingen, Kellnerweg 6, 37077 Göttingen, Germany

2  Primate Social Evolution Group, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

3  Leibniz ScienceCampus Primate Cognition, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

4  Domestication Lab, Department of Interdisciplinary Life Sciences, Konrad Lorenz Institute of Ethology, University of Veterinary Medicine Vienna, 1160 Vienna, Austria

history may always work at the species' maximum capacity (Law 1979). This is evident from the observation that growth velocity can change dramatically during species-typical age-related growth spurts or individualized catch-up growth after facing a period of resource restriction (Dmitriew 2011). Somatic growth is energetically costly and, therefore, predicted to be traded-off against other energy consuming processes, the most prominent being reproduction (Roff 1992). Such trade-offs are particularly important in primates, because of their low total energy expenditure compared to other placental mammals of similar mass which constrains available energy (Pontzer et al. 2014). As a consequence, according to the *neonatal investment hypothesis* proposed by Leigh and Bernstein (2006) female primates investing simultaneously in their own somatic growth and in offspring production may not be able to produce high-quality precocial neonates and, therefore, need to complete as much growth as possible before reproduction. Put the other way around, the more altricial the young of a species, the more overlap is predicted for late somatic growth and first reproduction (Leigh and Bernstein 2006).

This hypothesis on neonatal investment was supported by comparisons of olive baboons (*Papio hamadryas anubis*) with other primates of the tribe papionini (Disotell et al. 1992): rhesus macaques (*Macaca mulatta*), mandrills (*Mandrillus sphinx*), and mangabeys (*Lophocebus* spp., C*ercocebus* ssp., Leigh and Bernstein 2006). Baboon neonates are regarded as rather precocial because they exhibit a prenatal growth spurt in brain size during the last trimester of gestation and, therefore, are born with relatively larger and costlier to produce brains than other papionines including rhesus macaques (Leigh and Bernstein 2006). This maternal investment in fetal development is hypothesized to be responsible for a shift in onset of female reproduction that occurs relatively late in baboons when all teeth have erupted and somatic growth is much advanced and almost completed which effectively desynchronizes growth and reproduction. Based on pre- and postnatal brain growth, mangabeys, mandrills, and macaques are thought to produce cheaper offspring that allow for simultaneous investment in offspring and maternal growth (Leigh and Bernstein 2006).

A recent study provided comparative data on wild geladas (*Theropithecus gelada*) which produce cheap offspring: neonatal body and brain size are small perhaps resulting from energetic constraints from a herbivorous diet and mothers readily terminate pregnancies in face of increased infanticide risk (Roberts et al. 2012; Lu et al. 2016). Contradicting the neonatal investment hypothesis, gelada females completed 97% of their growth in body length at first birth, i.e., they desynchronize growth and reproduction just like baboons. Here, we follow analytical methods laid out in that study (Lu et al. 2016) and contribute another data set on growth and reproduction in a wild papionini primate, the Assamese macaques (*Macaca assamensis*).

We assess whether sexual size dimorphism develops over ontogeny via increased growth rates, extended growth periods, or their combination, and whether this pattern depends on the socio-ecology of the species that determines the type and strength of external mortality risks (Shea 1986; Leigh 1995). For species living in one-male-multifemale groups where male immatures face aggressive expulsion from their natal group upon breeder male replacement followed by a period of life outside of bisexual groups it is predicted that males exhibit increased growth rates relative to females early in development (Shea 1986; Leigh 1995). Conversely, males in multimale–multifemale societies like Assamese macaques are predicted to extend their growth period and either out-grow females after dispersal or delay dispersal until there are fully grown.

We further explore in our study species sexual dimorphism in growth of a linear dimension in relation to life history events. Several aspects of primate male life history have been described to co-vary and form a continuum of male career trajectories (*male-career-framework,* van Noordwijk and van Schaik 2004). Careers vary in the mode of acquiring social status (challenge for alpha position, cooperative strategies, or queuing), decisions about the mode of transfer between groups (individual or joint migration, targeting groups with weakest alpha or with most females or most female-biased sex ratio), and notably about the timing of natal dispersal in relation to competitive ability, i.e., body size. At the highest levels of contest competition and paternity concentration in the alpha male, males attain top social status by direct challenge and, therefore, migrate individually into the group with the weakest alpha male and time their natal dispersal with their maximum physical fighting ability (e.g., crested macaques, *Macaca nigra*, Marty et al. 2015, 2016). At the other extreme at low contest competition and low male reproductive skew, tenure in a social group may determine dominance rank. Males may queue but do not fight for status, they target groups with a maximum number of mating partners and often transfer jointly especially during natal dispersal that occurs well before males reach their full fighting ability (van Noordwijk and van Schaik 2004). In Assamese macaques, males migrate before reproducing and females are philopatric. The study population exhibits low to medium male contest competition at 29% alpha male paternity (Sukmak et al. 2014).

With this study we aim to first establish parallel laser photogrammetry as a method of measuring size in wild Assamese macaques. We present sources of measurement error and their relationship to inter-individual differences in the dimension measured as well as a comparison with an alternative photogrammetric method. The second aim

is to test the *neonatal investment hypothesis.* Given that congeneric rhesus macaques produce cheap neonates and that the hypothesis is set up to explain differences between baboons and all other papionins, we predicted substantial overlap between maternal growth and reproduction, i.e., that females continue to grow long after they had their first infant. As our third aim, we test predictions about the ontogeny of sexual dimorphism and from the *male-career-framework*. We predicted that males grow longer but not faster than females and that due to their low-medium level of direct male competition, male Assamese macaques disperse from their natal group well before they are fully grown.

## Methods

### Study population and demography

Data have been collected on a population of Assamese macaques that has been studied since 2005 and lives in its natural habitat in Phu Khieo Wildlife Sanctuary (16° 5′–35′ N, 101° 20′–55′ E, part of a > 6500 km$^2$ system of connected protected forests) in Northeast Thailand. Phu Khieo Wildlife Sanctuary has the highest protection status Thailand offers for the conservation of plants and wildlife. The terrain at the local study site Huai Mai Sot Yai (16° 27′ N, 101° 38′ E) is hilly at 600–800 m a.s.l. and the habitat comprises mainly hill and dry evergreen forest (Borries et al. 2002). The study population is frugivorous with the main part of their plant diet comprising fruit, pulp, and seeds, and a considerable part of their feeding time budget devoted to slow and low intake foraging for animal matter (Schülke et al. 2011; Heesen et al. 2013; Touitou et al. 2021a). Individuals measured for this study lived in four neighboring social groups with overlapping home-ranges.

Age at weaning is approximately 12 months based on last observations of nipple contact (Ostner et al. 2013; Berghänel et al. 2016). For assessment of age at natal dispersal from the demographic records of the long-term project, we only used individuals that were born into our study groups after habituation to human observers was accomplished with birthdates often known to the day (median precision ± 1.2, mean 10.7, maximum 60 days). The first study group we followed since 2006 split in two in 2011 and the second one we followed since 2012 split in 2014; all four resulting groups have been followed since. These group splits were relevant when determining the average age at natal dispersal for males. We once calculated average age at natal dispersal very conservatively only across those males that did not experience a group split before their first dispersal. Since both groups split along matrilines (De Moor et al. 2020), if males left their mother in the course of a group split, they also left all of their maternal female kin. Therefore, we interpret a group split as a natal dispersal event if an immature ended up in another sub-group than its mother which we did for our second calculation. The mean age in years at natal dispersal was the same when calculated including (4.0 ± 1.2 years mean ± SD, N = 41) or excluding (4.0 ± 1.2) 11 males that experienced a group split the way described above.

Reproduction was seasonal with 79% of 201 births recorded between 2006 and 2019 occurring in the 3 months from April through June (Touitou et al. 2021a; unpubl. data). Female age at first reproduction was assessed from live birth events and averaged 5.9 ± 0.5 years (mean ± SD, range 5.0–7.0 years) in 40 first-time mothers born into the study groups after habituation with mother birth dates often known to the day (median 2.5, mean 13 days) and offspring birth dates estimated with a precision of 21 days on average, median 11 days. For some of the adults and first births in the sample, only the year of birth was known; for this analysis, their birth day was estimated at the middle of the birth season, i.e., May 15th, of the respective year with a precision of 60 days.

### Laser device setup and sampling regime

We took pictures with a Nikon D7100 camera and an AF-S Nikkor 18–200 G II EO lens with a resolution of 6000×4000 pixels at distances between 0.54 and 6.71 m (mean 2.20 m) from the object measured for 375 photos with a digital laser range finder (Bosch PLR 25, Bosch, Gerling, Germany). A custom-made laser box with three green lasers (DD532-1-3(16×60), Picotronic, Koblenz, Germany), situated in an aluminum block and powered by 6 AA rechargeable batteries was mounted under the camera and used to project a size standard onto the object to be measured. The three lasers were oriented in an L shape with 2 cm length on each arm and thus formed a right isosceles triangle (Galbany et al. 2016; Fig. 1). The idea was that if the object to measure was large enough, all three laser dots could be projected onto it and most deviations from the object dimension to be measured being perpendicular to the camera-object axis will result in relative distances between projected laser dots deviating from the right isosceles triangle formed by the lasers (Fig. A1). Yet, even if the object was too small to accommodate all three laser dots, as in infant Assamese macaques, the setup will allow measuring objects that were oriented roughly horizontally or vertically without turning the laser-mounted camera.

The choice of dimension used to measure body size was constrained by substrate use. Body length is best measured as head-rump-length or shoulder-rump length if the animal stands on a horizontal surface (Lu et al. 2016), typically on the ground (but see Rothman et al. 2008). Given that Assamese macaques are highly arboreal (Schülke et al. 2011) and rarely stand on horizontal surfaces, we chose to measure the length of the lower arm from wrist to elbow (Turnquist and Kessler 1989; Berghänel et al. 2015). As a result of that

**Fig. 1** Adult Assamese macaques (*Macaca assamensis*) and laser dots projected on their forearm in **a** horizontal and **b** vertical position. Panel **a** shows a male resting in a typical posture with flexed elbow and wrist. Panel **b** shows a female grooming a male with the elbow flexed. Reference distance $D = 2$ cm distance between lasers measured in the digital picture as pixel number. $L_{pxl}$ = forearm length measured as number of pixels in picture and transformed to length in cm ($L$) from reference distance ($D$). The photographs were taken by Simone Anzà at Phu Khieo Wildlife Sanctuary (Thailand)
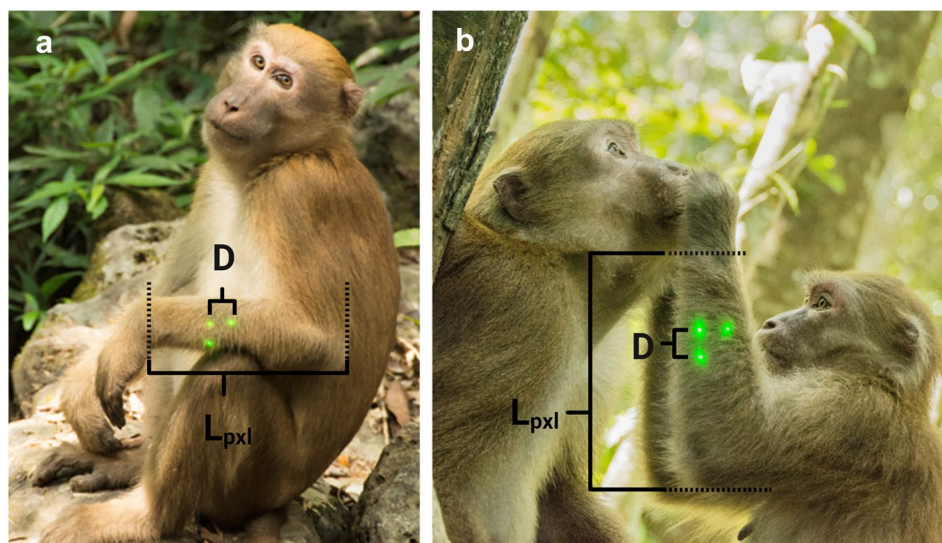


choice and because of our particular interest in immature growth, the distance between lasers had to be rather small (2 cm) to fit on the lower arm also of the youngest infants (see Fig. 1 for typical postures targeted by photographers). We ensured that the assumption of parallel orientation of lasers was not violated by controlling the 2 cm reference distance between lasers projected on photos of graph paper at different camera-object distances. These data are referred to as the parallel laser data set in the following.

Lower arm length was also measured for the data from Berghänel et al. (2015) who used a slightly different method. Instead of parallel lasers, we used a Nikon D5000 camera and a digital laser range finder (Bosch PLR 50) to synchronously take the picture and measure the distance between the camera and the object. Length of the lower arm was then calculated using the intercept theorem by multiplying the number of pixels in the picture (determined with ImageJ 1.44p, National Institutes of Health; version 1.52a; Schneider et al. 2012) with the distance. These data are referred to as the distance meter data set in the following.

The sampling regime was similar for both the parallel laser data set and the distance meter data set. To eventually generate one size estimate for an individual of a given age, several photos were taken within a 1–2-week period. Juvenile and adult individuals of different ages were measured during only one of these periods, whereas the 2011, 2012, and 2018 birth cohorts were each measured repeatedly in a longitudinal sampling design at several of these periods scattered across their first year of life. We excluded photos of poor quality (exposure, focus, obvious parallax) and with size estimates deviating more than two standard deviations from the mean across photos taken from the same individual within one period (between photograph error; see below). After quantifying different types of measurement error, we further excluded all repeated measurements of the same

individual at different ages. We used only one size estimate per individual (mean over a maximum of six photos) for estimating growth trajectories and sexual size differences from this cross-sectional sample. Because of these steps in excluding photos, sample size differs for different analyses and descriptive statistics across this paper.

With parallel lasers projected on the monkey, we collected a total of 1826 photos (1748 between 2016 and 2018 and 78 in 2021) from 48 males and 44 females. For descriptive purposes, we classified ages into infant (0–1 year, 16 males, 8 females), juvenile (1–6 years, 19 males, 15 females) and adult (> 6 years, 13 males, 21 females; intervals included the upper boundary value). Please note that we used one cutoff for adult males and females here although males mature more slowly and reach adulthood only with 7.4 years of age on average ($N = 18$) and are, therefore, classified differently in our other publications. Error estimates were derived from 782 pictures ($5.35 \pm 0.72$ per subject; mean ± SE) remaining after excluding low quality and outlier pictures.

The full distance meter data set comprised 1571 photos from 30 males and 31 females. We classified ages with the same criteria (infants: 6 males, 6 females; juveniles: 14 males, 16 females; adults: 10 males, 9 females).

### Estimating size from photographs

We used ImageJ software to measure: (i) the 2 cm reference distance between two lasers in pixel number ($D$), (ii) the subjects' forearm length in pixel number ($L_{pxl}$) from the elbow to the wrist, and then (iii) we used the 2 cm reference distance to transform the forearm length from pixel to centimeters ($L$) with the following formula: $L = \frac{2*L_{pxl}}{D}$. The

multiplier of $L_{pxl}$ value (here 2) is derived from the reference distance in centimeters (Fig. 1).

Remote measuring with parallel laser has been shown to be highly accurate (Bergeron 2007; Rothman et al. 2008; Deakos 2010; Barrickman et al. 2015; Galbany et al. 2016, 2017), yet potential error sources associated with human measurement of digital photographs can affect precision (Barrickman et al. 2015; Lu et al. 2016; Galbany et al. 2016, 2017). To test the quality of our method, we assessed three types of error in measurement repeatability: (i) *Repeated measurement error,* (ii) *Between photograph error*, and (iii) *Between measurer error*. Two observers, or measurers (S. Anzà and an assistant, Pearl Väth), performed all digital measurements. Error was expressed as the coefficient of variation (CV) in % of the absolute differences. We calculated the *Repeated measurement error* from 555 pictures each measured twice by the same observer (Pearl Väth). We estimated the *Between photograph error* from different photographs of the same animal shot at different days. We calculated this error twice, once per each measurer (709 and 627 pictures from a total of 782) and also report the average for those pictures measured by both observers (*Between photograph error mean*: 585 pictures). We estimated the *Between measurer error* by comparing measurements from the same photograph between the two observers (*N* = 555). We excluded from further analyses all pictures with a *Between photograph error* larger than 2 standard deviations. We compared our results with the *Between photograph error* (*N* = 1571) and the *Between measurer error* (*N* = 179) estimated from the distance meter data set; Table A4). We provide detailed information on types of error and specific age-related tables in the results section.

## Growth trajectories and pseudo-velocity curves

We estimated growth trajectories separately for 48 males and 44 females. Date of birth was known (40 males, 38 females) or estimated to the year of birth with the middle of the birth season set as birth date (8 males, 6 females). We built quadratic plateau models and ran local polynomial regressions (Locally Estimated Scatterplot Smoothing—LOESS) using the software RStudio 1.3.1093 (RStudio Team 2021; with R 4.0.4—R Core Development Team 2021) and packages *stats* (version 4.0.3), *easynls* (version 5.0), *nlstools* (version 1.0–2; Baty et al. 2015), *rcompanion* (version 2.4.0; Mangiafico 2016). While LOESS fits consecutive segments using subsets of data and, therefore, does not require any specified function, quadratic plateau models assume the data follow a quadratic curve up to a critical value, and then settle into a plateau. The critical value can be interpreted as age at growth cessation (Leigh 1994; Leigh and Terranova 1998; O'Mara et al. 2012; Lu et al. 2016):

$$Y = ax^2 + bx + c \ \text{ for } \ x \leq -\frac{b}{2a}$$

$$Y = -\frac{b^2}{4a} + c \ \text{ for } \ x > -\frac{b}{2a}$$

where $c$ is the neonatal size, $-b^2/4a + c$ is the adult body size and $-b/2a$ is the critical value (age at reaching adult body size). Next, we estimated 2.5–97.5% confidence intervals around the four parameters ($a$, $b$, $c$, critical value) with 999 bootstrap iterations, and used the predicted values as estimates of the percentage of growth at specific life-history milestones. We compared the quadratic plateau models built from the parallel laser data set with models built in the same way from the distance meter data set using only cross-sectional data (each individual only contributing one data point; 323 photos from 61 individuals; Males: 6 infants, 14 juveniles, 10 adults; Females: 6 infants, 16 juveniles, 9 adults; Berghänel et al. 2015). Previous work on growth trajectories in geladas showed that the quadratic plateau model performs well on a global level but poorly fits neonatal size (Lu et al. 2016). We, therefore, excluded the information on predicted size at birth.

We estimated pseudo-velocity curves of growth in forearm length (Coelho 1985; Lu et al. 2016; Galbany et al. 2017) by dividing the difference in successive predicted values by the difference in successive age values, and smoothing the resulting values using LOESS curve fitting (Setchell et al. 2001) for both sexes separately. The degree of smoothing can be set by adjusting the time span over which it is applied. We chose 0.6 as a compromise between precision and confidence. The effects of smoothing on pseudo-velocity curves are demonstrated in Fig. A2. Then, we estimated sex-related differences in growth by comparing residual differences in size for age.

To assess sexual dimorphism in body size, we compared forearm lengths between males and females at different ages (0–1, 1–3, 3–5, 5–7, and > 7 years old, intervals including the upper boundary value). Two-year blocks were chosen arbitrarily starting at weaning. We performed Mann–Whitney-U-tests using the function *wilcox.test* of the R base package *stats*, and Benjamini–Hochberg correction for multiple testing.

## Results

### Precision of photogrammetry

Several sources of error in the measurement of forearm length were assessed (Table 1). The error from the same person repeatedly measuring size from the same photo

**Table 1** Repeatability of photogrammetric measurements of forearm size

| Source of error | N (photos) | Mean CV (%) | Range CV (%) |
|---|---|---|---|
| Repeated measurement[a] | 555 | 2.67 | 0.00–14.99 |
| Between photograph error—1[b] | 627 | 4.66 | 0.93–10.74 |
| Between photograph error—2 | 709 | 3.26 | 0.49–9.99 |
| Between photograph error (mean 1, 2) | | 3.96 | |
| Between measurer error (1–2)[c] | 585 | 5.29 | 0.02–17.56 |

CV refers to coefficient of variation; 1, 2 are observers 1 and 2

[a]Comparison of two measurements taken by the same person from the same photo

[b]Averaged across two measurements rounds

[c]Comparison of measurements of the same photo assessed by two observers

**Table 2** Development of sexual dimorphism in body size estimated from forearm length. Data suggest that females tend to be larger than males at 1–3 years of age, and males are larger than females from age 5 onwards

| Age category | Inter-individual variation (CV %) | Sex | Forearm length (mean ± SD) | N | U | P-value | Adjusted P-value |
|---|---|---|---|---|---|---|---|
| 0–1 | 16.61 | F | 8.24 ± 0.77 | 7 | 67 | 0.332 | 0.335 |
| | | M | 8.12 ± 0.83 | 15 | | | |
| 1–3 | 13.20 | F | 11.66 ± 1.03 | 6 | 51 | 0.070 | 0.117 |
| | | M | 10.83 ± 0.92 | 11 | | | |
| 3–5 | 7.32 | F | 14.19 ± 0.39 | 7 | 19 | 0.336 | 0.336 |
| | | M | 14.25 ± 0.69 | 8 | | | |
| 5–7 | 6.40 | F | 15.28 ± 0.23 | 6 | 0 | 0.024 | 0.060 |
| | | M | 16.05 ± 0.14 | 3 | | | |
| 7+ | 7.71 | F | 16.04 ± 0.35 | 18 | 2 | <0.001 | <0.001 |
| | | M | 17.43 ± 0.35 | 11 | | | |

Size measured by laser photogrammetry compared between males and females for five different age windows (0–1, 1–3, 3–5, 5–7, and >7 years old) and tested with Mann–Whitney-$U$ tests. Raw $P$-values and $P$-values adjusted for multiple testing with the Benjamini–Hochberg method are reported

**Table 3** Quadratic plateau model of growth in forearm length of females and males with best fit value of (a) quadratic term, (b) linear term, and (c) intercept. Confidences and $P$-values were estimated with 999 bootstrap iterations. $R^2$ refers to adjusted-$R^2$

| Parameter | Best fit value | 2.5% C.I | 97.5% C.I | P-value |
|---|---|---|---|---|
| **Females** | | | | |
| a | −0.17 | −0.26 | −0.11 | <0.001 |
| b | 2.40 | 1.96 | 3.03 | <0.001 |
| c | 7.26 | 6.46 | 8.00 | <0.001 |
| Critical value (age at growth cessation) | 7.07 | 5.86 | 8.39 | |
| $R^2$ | 0.89 | | | |
| **Males** | | | | |
| a | −0.13 | −0.16 | −0.11 | <0.001 |
| b | 2.33 | 2.11 | 2.59 | <0.001 |
| c | 6.81 | 6.47 | 7.17 | <0.001 |
| Critical value (age at growth cessation) | 8.93 | 8.02 | 9.82 | |
| $R^2$ | 0.97 | | | |

(*Repeated measurement error*) was rather small with 2.67%. The error from measuring the same individual from several different photos taken within a 2-week window (*Between photograph error*) was 3.26–4.66% depending on how information from different observers were integrated. Two observers measuring the same photo (*Between measurer error*) disagreed by 5.29%. All these sources of error were sensitive to the size of the object as evident from errors declining from estimates for adult monkeys only (e.g., mean across observers of *Between photograph error* 2.90%), via juveniles (3.51%) to infants where the absolute forearm length was the smallest and the measurement error the largest (5.30%, Tables A1, A2, A3).

In the distance meter data set, measurement errors were similar both the *Between measurer error* (mean across age classes = 4.44%) and the *Between photograph error* (mean across age classes = 3.67%). The *Between photograph error* also decreased with age (infants = 4.37%, juveniles 3.58%, adults 3.06%, Table A4) showing the same sensitivity to object size.
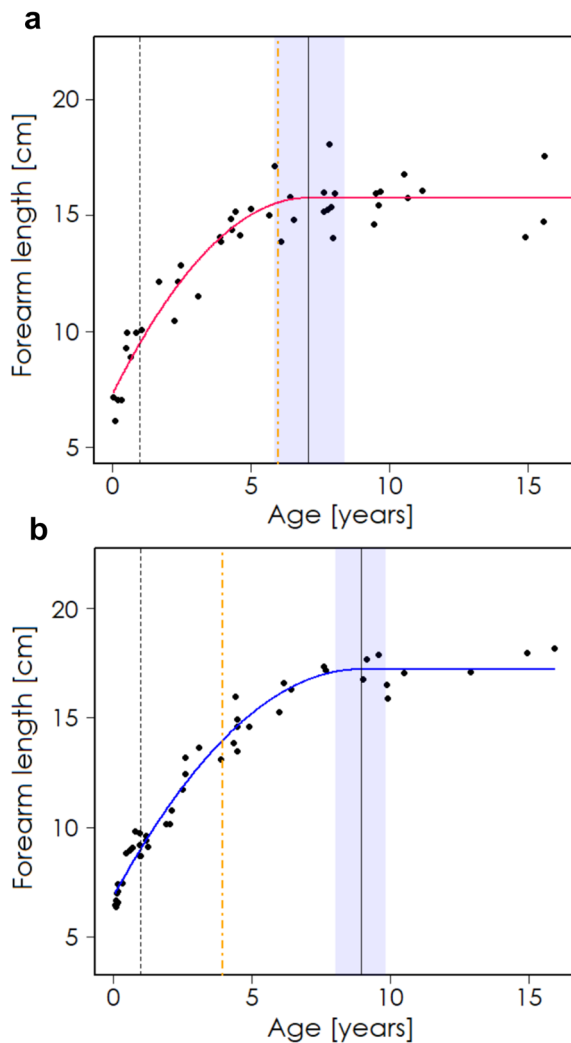
**Fig. 2** Growth curves for **a** females and **b** males estimated with separate quadratic plateau models. Dashed black line indicates age at weaning (1.0 year), orange dash-dotted line indicates mean age (**a**) at first birth (5.9 years) in females (**b**) at natal dispersal (4.0 years) in males. Solid black line indicates the model estimated age at cessation of growth with the 95% confidence interval shown as the shaded area. First birth coincides with growth cessation whereas natal dispersal occurs years before males stop growing

The inter-individual variation in the dimension of interest was at its maximum in infants (16.61%), decreased with age but stabilized at around 7% from age 4 onwards (Table 2, parallel laser photogrammetry). Thus, inter-individual variation in lower arm length was much larger than any of the measurement errors.

## Growth trajectories

Estimates of age at growth cessation from the best fit quadratic plateau models of growth in females and males (Table 3 and Fig. 2) suggested that females stopped growing earlier than males (non-overlapping confidence intervals of
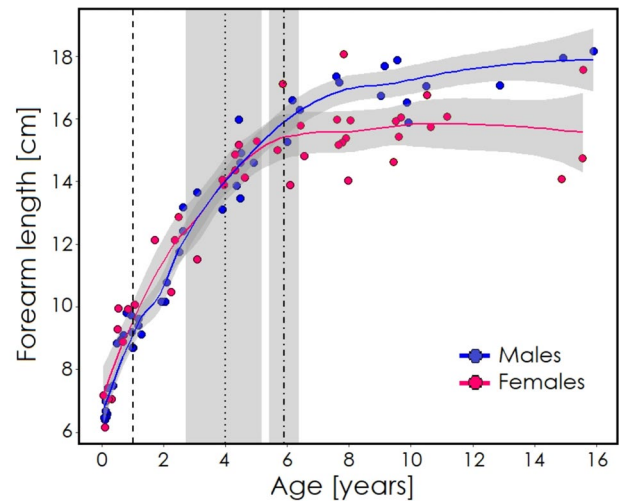


**Fig. 3** Growth curves of females and males fitted with non-parametric LOESS regression method, and developmental milestones. Dashed line indicates age at weaning (1.0 year), dotted line indicates mean age at natal dispersal (4.0 years) in males, and dash-dotted line indicates mean age at first birth in females (5.9 years). The grey-shaded area around the vertical lines depicts the standard deviation around the age at natal dispersal (SD = 1.23) and the age at first birth (SD = 0.48), respectively. Confidence intervals around the LOESS curve are larger for females (yellow) than males (blue) from age 2 through 10. We selected a span value of 0.60 by visually identifying more conservative curves with less "noise" produced by the local regression method

critical values). More precisely, females grew until they were 7.1 years of age whereas males continued to grow for two more years until they were 8.9 years old. As a consequence, females had completed 96% of growth at 5.9 years, the age at first birth (compared to 91% for males at this age). At 4.0 years, the average age of male natal dispersal, males had finished 80% of growth (females 88%). Males went through 96% of their growth until they reached adulthood at the average age of full canine size development and full testicular enlargement (7.2 years, $N = 18$ unpubl.data). Very similar patterns were seen when using the distance meter data set from 2011 to 2012 (Berghänel et al. 2015; Fig. A3).

Non-parametric LOESS regressions of growth (Fig. 3) and pseudo-velocity curves (Fig. 4) suggested that female growth rate declined rather steadily from birth (2.8 cm/year) until 6 years of age (0.3 cm/year) with a reduction in speed of −0.4 cm/year per year. From 6 years onwards, the change in growth velocity was much smaller at −0.1 cm/year per year. The pseudo-velocity curve fitted to size data from males has similarities and differences with the one for females. Both sexes show a similarly steep decline in growth rate during the first year of life down to 2.1 cm/year in males and 2.3 cm/year in females at age 1. The estimated speed of growth for males in their second year of life is associated with considerable
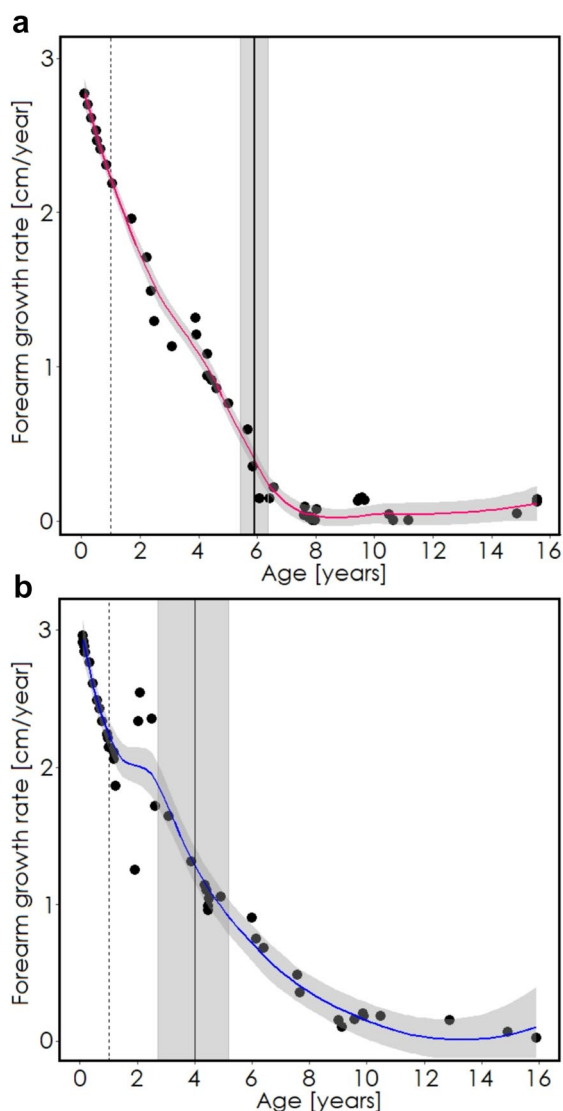
**a**



**b**

**Fig. 4** Pseudo-velocity curve for (**a**) females and (**b**) males estimated by non-parametric LOESS regression method, and developmental milestones. Dashed line indicates age at weaning (1.0 year). Solid black line indicates age at first birth for females (5.9 years) and age at natal dispersal for males (4.0 years) with gray shades indicating standard deviation around those measures (0.48 for age at first birth and 1.23 for age at natal dispersal). We selected a span value of 0.60 by visually identifying more conservative curves with less "noise" produced by the local regression method (Fig. A2)

uncertainty and appears slightly faster than females. However, the same delay in male growth rate decline is not found in the distance meter data set for males aged 1–2 years (Fig. A4) and inspection of the overlaid LOESS curves (Fig. 3) also suggests that growth trajectories of males and females did not differ strongly from birth until age 4–4.5 years. After that, male growth rate declined more slowly than that of females which bottomed out soon after age 6.

As a consequence of these growth trajectories, sexual dimorphism in forearm length was not detected until age

5–7 (Table 2) when males tended to be larger than females ($F = 15.3$ cm, $M = 16.1$ cm; adjusted $P = 0.060$). From 7 years of age onwards, males had clearly outgrown the females ($F = 16.0$ cm, $M = 17.4$ cm, adjusted $P < 0.001$).

## Discussion

### Photogrammetry

Assamese macaques are highly arboreal in the study population and spend 60% of time away from the ground and low story of the forest, which makes it difficult to weigh them on a balance (Schülke et al. 2011), especially if the balance cannot be baited with food. Therefore, in this study we used non-invasive parallel laser photogrammetry to measure growth trajectories from skeletal dimensions (Galbany et al. 2016). In a previous project, we had used distance to object measured with a digital laser range finder to convert pixel number in digital photos to actual size in centimeters (Berghänel et al. 2015, Berghänel et al. 2016). With the box holding the parallel lasers being mounted under the camera, the new method was less demanding in the field and should eventually allow for computer guided automation of measurements in digital photographs (see Richardson et al. 2022 in this Special Issue).

The repeatability of single measurements was not ideal which partly is owed to the small size of the body part measured (the forearm) which also forced us to use a rather small between-laser distance of 2 cm (25% of body part in infants, 15% in juveniles, 12% in adults). Repeatability increased with increasing size of the animal from infants via juveniles to adults. Other primate studies have used 4 cm laser spacing, measured larger body parts of larger animals, and achieved lower measurement errors around 2 cm (Rothman et al. 2008; Barrickman et al. 2015; Lu et al. 2016). With a laser spacing of 4 cm used to measure a trait of 2–8 cm size Bergeron (2007) produced an intermediate error of 3.7%. As a further point in case, in a study using 50 cm laser spacing for morphometrics of whale sharks, measurement error increased the smaller the somatic structure that was measured (Jeffreys et al. 2013). The error in the arm length estimate was similar in the parallel laser data set and the distance meter data set, but we were unable to properly propagate errors for both methods in similar ways; the parallel laser method holds errors from counting pixels between-laser dots and from counting pixels on the forearm, whereas with the distance meter method error from counting pixels on forearm have to be considered along with unknown error from camera-object distance measurement (for a more direct comparison between these methods see Galbany et al. 2016). Repeatability of photogrammetric studies will be enhanced when automated computer assisted methods become available for identifying locations of and distances (a) between projected laser dots and (b) surface landmarks of interest (see Richardson et al. 2022 in this Special Issue).

One important source of error (parallax) results from the camera-object axis not being perfectly perpendicular to the dimension to be measured (Deakos 2010). Possible issues with parallax distortion can be identified, but not easily corrected, if more than two lasers of known position are used and if all points can be projected on a rather plane surface.

## Life history

The data presented here suggest that female Assamese macaques living in their natural habitat completed the vast majority of their growth in forearm length before they started to reproduce. With 96% of growth finished at first birth, wild Assamese macaques were more similar to captive olive baboons (~ 100%) than to captive mangabeys (90%, Leigh and Bernstein 2006). Together with evidence on the rather close coincidence of growth cessation and first birth in wild geladas (Lu et al. 2016), these results contradict the *neonatal investment hypothesis* (Leigh and Bernstein 2006) which suggests that the production of rather costly offspring selected for a desynchronization of growth and reproduction in the genus *Papio*, but not in other papionins.

Discrepancy between original work and recent tests of the hypothesis concern (i) the choice of body size metric, (ii) methods to determine age at growth cessation, and (iii) food provisioning, and (iv) assumptions about the costs of producing neonates. Body size was measured by body mass or crown-rump length by Leigh and Bernstein (2006), yet the gelada study (Lu et al. 2016) used shoulder-rump length and the current study is based on forearm length. The latter two studies are non-contact, photogrammetric studies using parallel lasers which require taking measurements at highly repeatable body postures. The arboreal Assamese macaques studied here are rarely found standing on a rather horizontal surface to be measured. Gelada head position when standing is variable and affects crown-rump length, making the metric less reliable. The shoulder is a more tangible landmark (Lu et al. 2016). If the metrics chosen for the photogrammetric studies followed different growth trajectories than crown-rump length as measured by Leigh and Bernstein (2006), age at growth cessation would be affected and the conclusions regarding the neonatal investment hypothesis would be invalid. Evaluation of this argument is hampered by the lack of repeatable objective metrics of growth cessation (e.g., estimation from a quadratic plateau model) in earlier studies. Comparative growth data are available for provisioned rhesus macaques and wild toque macaques (*Macaca sinica*) and our visual inspection of tabulated (Turnquist and Kessler 1989) and plotted data (Cheverud et al. 1992) suggest forearm growth in rhesus and arm growth in toque macaques to cease at the same age as crown-rump growth in the respective data sets. We conclude that our growth trajectories for forearm length of a third macaque species is comparable to trajectories of crown-rump length of other papionins and note that body arm length follow

slightly different age trajectories in a large great ape species (*Gorilla gorilla berengei*, Galbany et al. 2017). It remains to be shown whether comparative data on body mass growth in wild baboons and other papionins supports the *neonatal investment hypothesis.*

The second predictor from the neonatal investment hypothesis is age at first reproduction which may be systematically different in the recent studies on wild populations experiencing natural fluctuations in food availability compared to the captive and food provisioned groups studied by Leigh and Bernstein (2006). Female cercopithecid primates experiencing food enhancement show marked shifts towards earlier maturation and onset of reproduction (Strum and Western 1982; Sugiyama and Ohsawa 1982; Borries et al. 2001, 2013; Altmann and Alberts 2005). Females in the study population are under food stress evident from the observation that females have to skip a mating season if they gave birth late in the same year (Heesen et al. 2013). Considerable food stress is suggested also by correlations between food availability and (a) the probability to conceive (Heesen et al. 2013) and (b) female fecal glucocorticoid levels during gestation with effects on offspring phenotype (Berghänel et al. 2016, Touitou et al. 2021b). At 5.9 years, wild Assamese macaque females reproduce considerably later than congeneric provisioned rhesus macaques (4.0 years; Leigh and Bernstein 2006) which contributes to the separation of somatic growth and reproduction in rhesus macaques. The restricted data available to date suggest an important role of energy allocation in the scheduling of growth and reproduction in female primates, but conclusive tests of the *neonatal investment hypothesis* have to await the collection of more comparative data, ideally from wild populations.

Our test of the neonatal investment hypothesis rest on the assumption that Assamese macaques are more similar to rhesus macaques and mangabeys than to baboons in pre- and postnatal brain development. Baboons are born with more developed brains which makes gestation particularly costly to females. Comparative data on brain development are not available for Assamese macaques and neither are data on feeding behavior of immatures that could indicate how skilled and constrained they are compared to baboons (Altmann 1998). However, the relationship between ecological seasonality and female reproduction may inform the question how costly reproduction is to female Assamese macaques in the study population. Assamese macaques are mainly frugivorous: the feeding time budget comprises of 59% fruit and seeds, 24% insects, spiders, reptiles, and other animal matter, 13% leaves, and 4% other food items; Heesen et al. 2013). Timing of reproduction relative to seasonal fluctuations in food availability follows a relaxed income breeder strategy (Brockman and van Schaik 2005): females accumulate fat before conception and the birth season includes the peak of food availability. Gestating females trade-off feeding time at the expense of resting, do not conserve energy, and use up their fat stores during gestation (Touitou et al. 2021a). Females have to be in good physical condition to conceive (Heesen et al. 2013), food

availability affects conception rate (Richter et al. 2016), and infant mortality is very low (5%; Ostner and Schülke unpubl. data) all of which suggests that females face considerable costs during gestation and invest prenatally in high-quality offspring. It remains unclear how these demonstrated investments of Assamese macaque females in offspring quality compare to those of baboons and other papionins. Even if Assamese macaques were more similar to baboons than to rhesus macaques and mangabeys, the desynchronization of growth and reproduction found in geladas still does not fit predictions of the neonatal investment hypothesis.

Sexual dimorphism in body size may develop from sex differences in growth speed, growth duration, or both (Shea 1986; Leigh 1995) and variation in these patterns has been associated with male reproductive strategies and resulting differences in social organization (Leigh 1995). The data set presented here is too sparse to conclusively determine the intricacies of ontogeny of sexual size dimorphism. The pseudo-velocity curves suggest that males may maintain a higher growth rate than females between age 1 and 2 for this new data set or between age 1 and 3 in the older distance meter data set. Yet, this difference in rate is associated with considerable measurement uncertainty and the 1-year shift between the two data sets further suggests these results to be spurious; since both curves were based on cross-sectional data, size differences between age cohorts (Berghänel et al. 2016) may have produced these patterns. The most parsimonious interpretation is that this study provides no evidence of adolescent growth spurts in forearm length of females or males. Instead, sexual dimorphism in forearm size among adult Assamese macaques seems to be owed to an extended growth period following natal dispersal, rather than increased growth rate in males (Leigh 1996; Badyaev 2002). Extended growth periods in males have been described for several dimensions of skeletal growth in wild toque macaques (Cheverud et al. 1992), crown-rump length in free-ranging mandrills (Setchell et al. 2001), and shoulder-rump length in wild geladas where both sexes go through a small growth spurt around the age of 4 years before females give birth for the first time (Lu et al. 2016). Male growth spurts have been associated with particular risks for males growing up in a one-male–multi-female social organization where males can expect to be ousted from their natal group upon take-over by another male (Leigh 1995). Males living in multimale–multifemale groups do not face similar risks and may either delay dispersal until they are fully grown or disperse at young age and small size when they do not face much resistance from residents. Thus, multimale societies are conducive to prolonged male growth periods driving sexual size dimorphism. Notably, the analyses listed above all concern skeletal growth and neglect possible changes in muscle mass. In one-male–multifemale groups, sexual dimorphism in body mass is more pronounced than in one-dimensional size metrics (Leigh 1996). Sexual mass dimorphism results from both increased growth rate and extended growth period in males compared to females in wild and food-enhanced yellow baboons (Altmann and Alberts 2005), food-enhanced rhesus (Turnquist and Kessler 1989) and long-tailed macaques (Schillaci et al. 2007), but not wild toque macaques (Cheverud et al. 1992) and thus contradict the explanation based on social organization alone.

The *male-career-framework* offers another socio-ecological explanation for the timing of dispersal relative to growth. As expected for a species with medium to low levels of reproductive skew, male Assamese macaques did not delay natal dispersal until they were fully grown and at their maximum fighting ability. This latter life-history strategy is seen for example in male crested macaques, where natal migrants challenge the current alpha of another multimale group and replace him, if successful, immediately after immigration, and sire the vast majority of offspring for about 1 year until they are replaced themselves (Marty et al. 2015, 2016). Male Assamese macaques leave their natal group at a much younger age and much smaller size. Male dominance rank attainment has a cooperative component (Schülke et al. 2010) and some alpha males were clearly not the largest males in the group (see discussion in Schülke et al. 2014). Thus, body size may be less decisive for dominance rank attainment and reproductive success. Further studies will have to elucidate whether small size facilitates integration into a new group, whether males migrate together with others to further reduce risks, and exactly how they acquire their adult dominance rank in relation to immigration status as predicted from the *male careers framework* (van Noordwijk and van Schaik 2004).

# Appendix

See Figs. A1, A2, A3, A4 and Tables A1, A2, A3, A4.
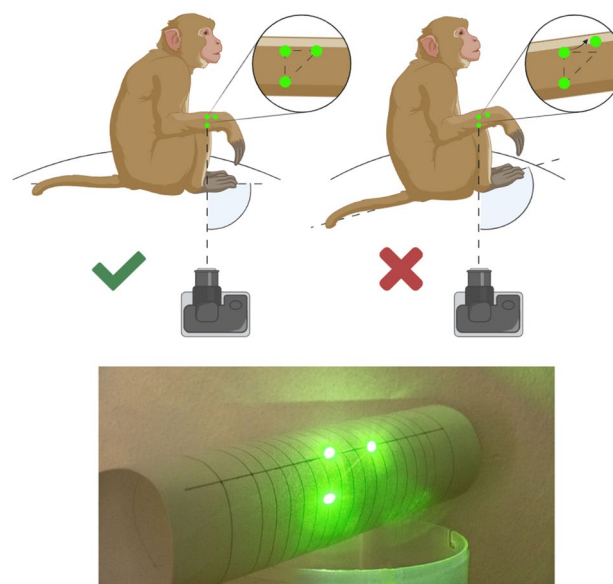


**Fig. A1** Illustration of how deviation from a perpendicular orientation camera-object axis can be detected with a 3-laser set-up. In most cases such deviation leads to the projected laser dots not forming a right isosceles triangle, either because the triangle is not right or not isosceles or both
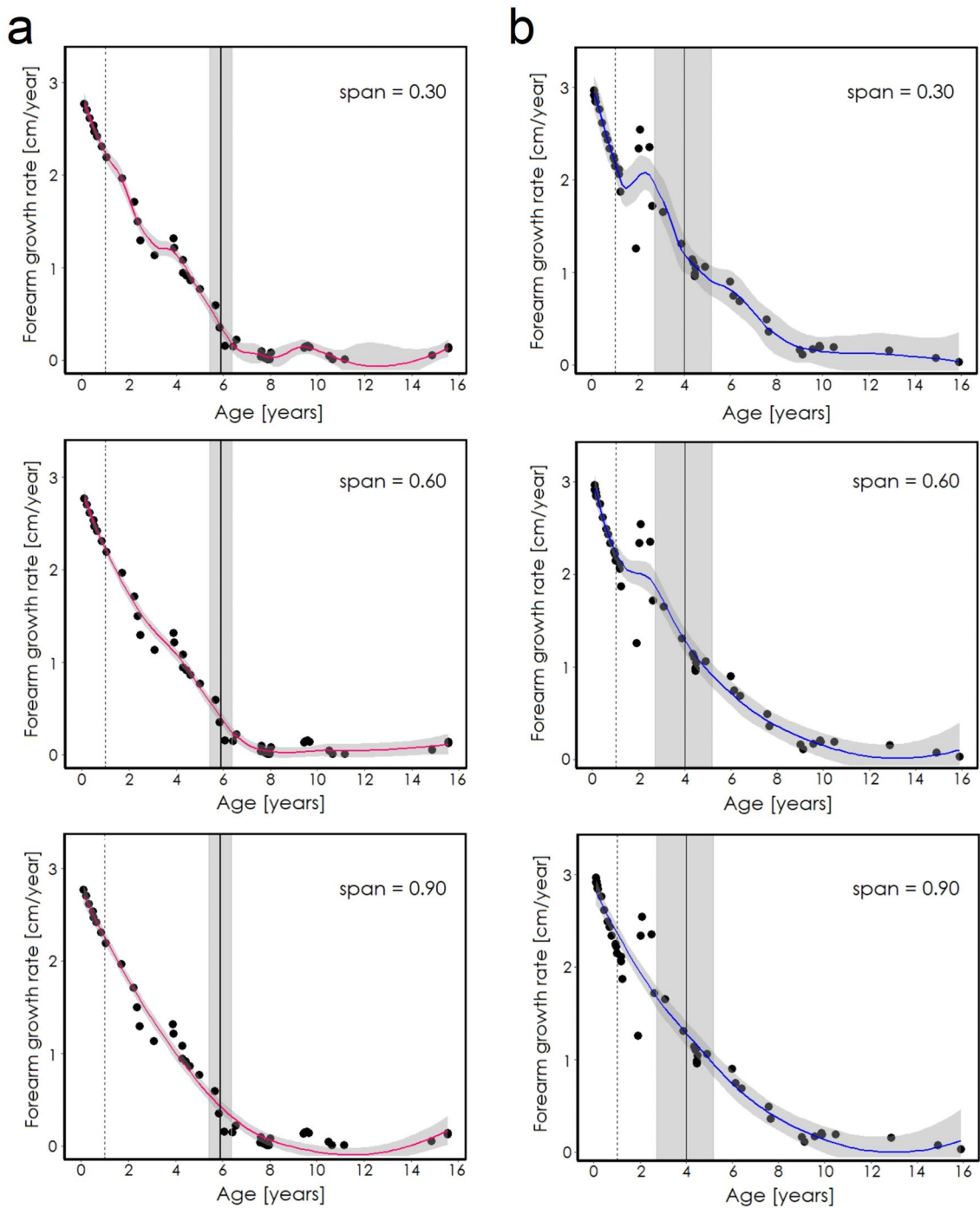
**Fig. A2** Example of visual inspection of LOESS curves for **a** females and **b** males of wild Assamese macaques plotted with a span value of 0.30, 0.60, and 0.90. The most conservative curves with less "noise" produced by the local regression are the one with span = 0.6 (central plots)
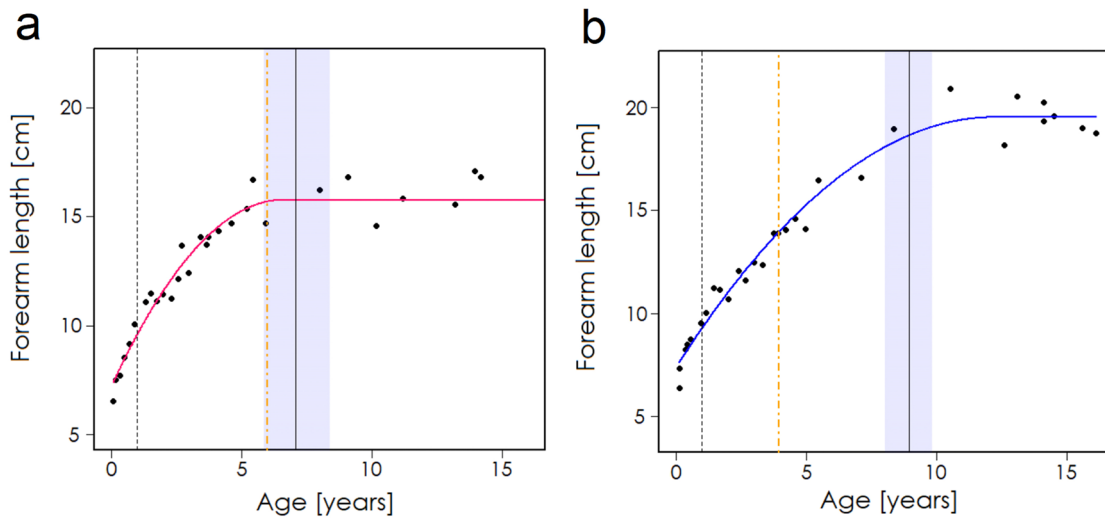
**Fig. A3** Growth curves for females (**a**) and males (**b**) estimated from distance meter data set (Berghänel et al. 2015) with separate quadratic plateau models. Age at weaning and age at first birth are estimated using data from this study. Dashed line indicates age at weaning (1.0 year), orange dash-dotted line indicates mean age at first birth (5.9 years) in females (**a**) and mean age at natal dispersal (4.0 years) in males (**b**). Solid line indicates the model estimated age at cessation of growth with the 95% confidence intervals shown as a grey bar. Consistently with this study, also in Berghänel et al. (2015) the first birth coincides with growth cessation whereas natal dispersal occurs years before males stop growing

**Fig. A4** Pseudo-velocity curve of males estimated by non-parametric LOESS regression method, and developmental milestones. Dashed line indicates age at weaning (1.0 year). Solid black line indicates the age at natal dispersal (4.0 years) with gray shades indicating standard deviation (1.23) around the measure. We selected a span value of 0.60 by visually identifying more conservative curves with less "noise" produced by the local regression method
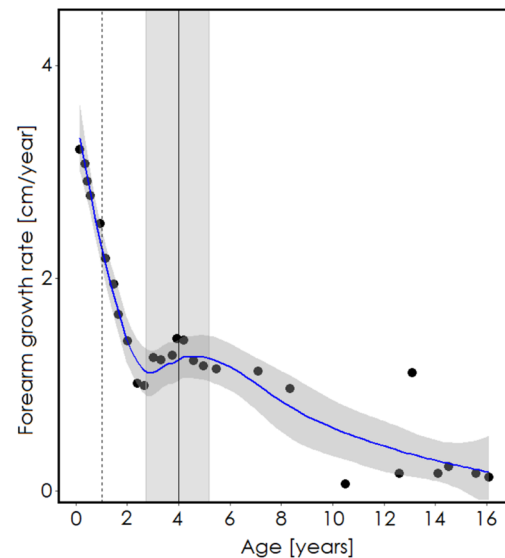


**Table A1** Repeatability of photogrammetric measurements of forearm size of adult individuals only (> 6 years old)

| Source of error | N (photos) | Mean CV % | Range CV % |
| --- | --- | --- | --- |
| Repeated measurement[a] | 127 | 2.37 | 0.00–10.49 |
| Between photograph error—1[b] | 163 | 3.18 | 1.15–5.76 |
| Between photograph error—2 | 169 | 2.63 | 0.73–9.98 |
| Between photograph error (mean 1, 2) | | 2.90 | |
| Between measurer error (1–2)[c] | 144 | 5.39 | 0.04–16.96 |

CV, coefficient of variation; 1, 2 observers 1 and 2

[a]Comparison of two measurements taken by the same person from the same photo

[b]Averaged across two measurements rounds

[c]Comparison of measurements of the same photo assessed by two observers

**Table A2** Repeatability of photogrammetric measurements of forearm size of juvenile individuals only (1–6 years old)

| Source of error | N (photos) | Mean CV % | Range CV % |
|---|---|---|---|
| Repeated measurement[a] | 69 | 2.25 | 0.01–12.07 |
| Between photograph error—1[b] | 79 | 3.99 | 1.05–12.35 |
| Between photograph error—2 | 152 | 3.02 | 0.49–12.11 |
| Between photograph error (mean 1, 2) | | 3.51 | |
| Between measurer error (1–2)[c] | 73 | 6.31 | 0.12–18.74 |

CV, coefficient of variation; 1, 2 observers 1 and 2

[a]Comparison of two measurements taken by the same person from the same photo

[b]Averaged across two measurements rounds

[c]Comparison of measurements of the same photo assessed by two observers

**Table A3** Repeatability of photogrammetric measurements of forearm size of infant individuals only (0–1 year old)

| Source of error | N (photos) | Mean CV % | Range CV % |
|---|---|---|---|
| Repeated measurement[a] | 359 | 2.86 | 0.00–21.62 |
| Between photograph error—1[b] | 385 | 5.59 | 1.53–17.20 |
| Between photograph error—2 | 388 | 5.01 | 0.49–14.99 |
| Between photograph error (mean 1, 2) | | 5.30 | |
| Between measurer error (1–2)[c] | 368 | 5.29 | 0.02–25.16 |

CV, coefficient of variation; 1, 2 observers 1 and 2

[a]Comparison of two measurements taken by the same person from the same photo

[b]Averaged across two measurements rounds

[c]Comparison of measurements of the same photo assessed by two observers

**Table A4** Between photograph error and between measurer error of forearm size estimated from distance meter data set in Berghänel et al. (2015)

| Age class | Between photograph error | | | Between measurer error | | |
|---|---|---|---|---|---|---|
| | N (photos) | Mean CV % | Range CV % | N (photos) | Mean CV % | Range CV % |
| Infant | 1111 | 4.37 | 0.99–25.28 | 63 | 3.89 | 0.24–19.91 |
| Juvenile | 370 | 3.58 | 0.14–19.55 | 116 | 4.99 | 0.16–16.08 |
| Adult | 90 | 3.06 | 1.04–7.37 | | | |

Infants: 0–1 year old; juveniles: 1–6 years old; adults > 6 years old. CV refers to coefficient of variation

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare that are relevant to the content of this article.

**Ethics approval** The study was observational and has been approved by the Thai National Research Council and the Department of National Parks, Wildlife and Plant Conservation Thailand (permits 0002/470 January 26 2016, 0002/4139 June 9th 2017, 0002/2747 May 4th 2018, 0402/2798 October 4th 2019, 402/4707 October 2nd 2020).

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