*Growth and Development in Wild Owl
Monkeys (Aotus azarai) of Argentina*

Maren Huck, Marcelo Rotundo &
Eduardo Fernandez-Duque

International Journal
of Primatology

Springer

Available
online
www.springerlink.com

🖄 Springer

Springer

Growth and Development in Wild Owl Monkeys (*Aotus azarai*) of Argentina

**Maren Huck · Marcelo Rotundo ·
Eduardo Fernandez-Duque**

Abstract Life history predicts that in sexually dimorphic species in which males are the larger sex, males should reach sexual maturity later than females (or vice versa if females are the larger sex). The corresponding prediction that in sexually monomorphic species maturational rates will differ little between the sexes has rarely been tested. We report here sex differences in growth and development to adulthood for 70 female and 69 male wild owl monkeys (*Aotus azarai*). In addition, using evidence from natal dispersal and first reproduction (mean: 74 mo) for 7 individuals of known age, we assigned ages to categories: infant, 0–6 mo; juvenile, 6.1–24 mo; subadult, 24.1–48 mo; adult >48 mo. We compared von Bertalanffy growth curves and growth rates derived from linear piecewise regressions for juvenile and subadult females and males. Growth rates did not differ between the sexes, although juvenile females were slightly longer than males. Females reached maximum maxillary canine height at *ca.* 2 yr, about a year earlier than males, and females' maxillary canines were shorter than males'. Thus apart from canine eruption and possibly crown–rump length, the development of Azara's owl monkeys conforms to the prediction by life history that in monomorphic species the sexes should develop at similar paces.

Keywords First reproduction · Growth rates · Ontogeny · Sexual monomorphism · von Bertalanffy growth model

M. Huck (✉) · E. Fernandez-Duque
Department of Anthropology, University of Pennsylvania, Philadelphia 19104 PA, USA
e-mail: maren_huck@gmx.net

M. Rotundo · E. Fernandez-Duque
Barrio Gen. J. de San Martín, casa 100, manzana 55, Formosa, CP 3600, Argentina

E. Fernandez-Duque
Consejo Nacional de Investigaciones Cientificas y Tecnicas (CONICET), Av Rivadavia 1917, C1033AAJ, Argentina

Introduction

In polygynous mammals, males often mature later than females, and it has been hypothesized that in sexually dimorphic species in which males are the larger sex, males should reach sexual maturity, as well as adult body size, at an older age than females (Bolter and Zihlman 2003; Rubenstein 1993; Shea 1986). Differing adult body sizes in the sexes are the result of differing growth strategies (Badyaev 2002a, b). Sexual size dimorphism can be achieved either by differing growth rates, by reaching maximal size at differing ages, or by a combination of both, and primates exhibit a multitude of different patterns (Leigh 1992; Shea 1986). Comparative analyses showed that species with multimale–multifemale social structures are more likely to diverge owing to bimaturism, whereas males often grow at a higher rate in species with harem-like social structures (Leigh 1995). For example, in mandrills (*Mandrillus sphinx*), females reach adult body mass 3 yr before their male age peers (Setchell *et al.* 2001), whereas spider monkey (*Ateles geoffroyi*) females decelerate growth rates more strongly than males (Fig. 5 in Leigh 1992). In monomorphic species, in contrast, life history theory predicts that growth and maturational rates will differ little between the sexes (Leigh and Terranova 1998). Indeed, Leigh (1995) showed that in monogamous monomorphic species sex differences in growth rate or time to maturity are usually minimal. However, in a comparative study of primates, Leigh (1992) found that in some monomorphic species males grow faster but for a slightly shorter time than females.

Although there are yet no solid explanations for bimaturism in monomorphic species, it could be, e.g., associated to sex differences in dispersal or differential parental investment. If there is sex-biased dispersal, then the dispersing sex may need to reach physical maturity at an earlier age to face the hardships of migration. Alternatively, if there is sex-biased "helpers at the nest" behavior, there may be associated sex-specific parental investment in the infants' growth and development, analogous to the concept of local resource enhancement leading to biased sex ratios (Silk and Brown 2008). Currently, these hypotheses cannot be tested but will require robust intertaxa comparisons and meta-analyses in the future, based on data from a large number of species, preferentially from wild populations, because captive individuals are often heavier and have faster developmental rates (Leigh 1994; Rowell 1977).

Owl monkeys (*Aotus* spp.) are among the few primates with a monogamous social system and intense involvement of males in the care of infants (Fernandez-Duque 2011; Fernandez-Duque *et al.* 2009; Wright 1981). The species vary widely in body mass, with the smallest species, *Aotus vociferans*, weighing *ca.* 0.70 kg, and the largest, our focal species Azara's owl monkey (*A. azarai*), *ca.* 1.25 kg (Fernandez-Duque 2011). Although social and behavioral patterns seem to be similar across species (Fernandez-Duque 2008, 2011), intensive behavioral observations of sexed and identified wild individuals have been conducted only for *Aotus azarai*, which is also the only species that is to some degree diurnal (Fernandez-Duque *et al.* 2010; Wright 1989). Owl monkeys show little sexual dimorphism as adults (Fernandez-Duque in press), thus presenting an excellent opportunity to evaluate the extent of sex differences in a monomorphic species during development and growth. In fact, the sexes are so similar in their external appearance that it is virtually

impossible for a human observer standing on the ground to tell the sexes of individuals only a few meters above in a tree. In captive owl monkeys from Colombia (*Aotus griseimembra*; in the original publication referred to as *A. trivirgatus griseimembra*, but later renamed) there is a link between the amount of subcaudal gland secretion visible below the tail and sexual development (Dixson 1994; Dixson *et al.* 1980). In females, the size and color of the nipples can change from very slight protrusion and pale skin-colored to noticeably protruding, dark pink-colored (M. Rotundo and E. Fernandez-Duque, *pers. obs.*). In several other primate species, the length or color of the nipple can roughly be related to reproductive status (Hayama *et al.* 1997; Mendes Pontes and Cruz 1995). Similarly, the development of the testes of owl monkeys is related to hormone production and thus to the onset of puberty (Dixson *et al.* 1980). Information on the behavioral development of wild owl monkeys is restricted to weaning age (at *ca.* 6 mo of age; Rotundo *et al.* 2005) and median age at dispersal (3.1 yr; Fernandez-Duque 2009).

We here present the first data on the development of various morphological and behavioral characteristics of wild owl monkeys of the Argentinean Chaco (*Aotus azarai azarai*). We test the prediction that maturation and growth are similar for males and females in this monogamous species. To test this prediction, we developed growth curves and growth rates for a variety of morphological measures. We then compared developmental rates of male and female owl monkeys for juvenile and subadult monkeys. A secondary aim of this study was to determine minimum age of dispersal and first reproduction to assign individuals to the juvenile and subadult age classes.

Methods

Area of Study, Population, and Capturing Procedures

The owl monkey subspecies *Aotus azarai azarai* inhabits the gallery forests of the Río Paraguay and its tributaries in the Argentinean provinces of Formosa and Chaco (Brown and Zunino 1994). Researchers of the Owl Monkey Project headed by E. Fernandez-Duque studied the population found along the Pilagá and Guaycolec rivers in the Province of Formosa (58° 11′W, 25° 58′S) regularly and intensively since 1997 (Fernandez-Duque 2009; Fernandez-Duque *et al.* 2001, 2010; Fernandez-Duque and Rotundo 2003; Rotundo *et al.* 2005).

Since 1999 we captured owl monkeys to mark and radio-collar individuals to facilitate behavioral and demographic data collection (Fernandez-Duque and Rotundo 2003; Juárez *et al.* 2011). We captured monkeys on 222 occasions, including 70 females and 69 males of known or estimated age, living in 37 different social groups or ranging solitarily. We never attempt to capture very young individuals given the possible risks associated with darting small-sized monkeys. We anesthetized subjects with a small dose of ketamine hydrochloride (25–50 mg/kg; Vetanarcol, Konig, Argentina) loaded on disposable 0.5-cc darts projected with a blowpipe between 1999 and 2001 or a CO_2-powered rifle starting in 2002 (for more details see Fernandez-Duque and Rotundo 2003). The National Wildlife Directorate in Argentina, the Institutional Animal Care and Use Committee of the University of

Pennsylvania, and the Zoological Society of San Diego approved these procedures. Further, capturing owl monkeys and fitting them with collars has no serious consequences for the welfare of the subjects (Juárez *et al.* 2011).

Physical Examination and Body Measurements

While the monkeys were anesthetized we conducted a physical examination of various morphological traits (Fernandez-Duque in press). Two people, one of them always the same, took and read the measurements and if there was disagreement they checked again until agreement was reached. Differences between readings were low (<1.5%). We did not perform many of the measurements in non-adults, or when we did, sample sizes were too small for analyses (electronic supplementary material [ESM] Fig. SI). Thus, we present only the following measurements.

Body mass: We weighed each individual to the nearest 10 g using a 2000-g Pesola scale.

Crown–rump length: The distance (to the nearest 10 mm) from the crown between the eyes to the beginning of the tail, i.e., not including the tail, when the individual was stretched and the spine was roughly linear.

Mandibular and maxillary canine height and width: We measured height as the distance from the tip of the tooth to the cementum–enamel junction on the buccal face, whereas we measured the width (mesiodistal length) as the greatest dimension in the occlusal plane (Plavcan 1993). We recorded measurements to the nearest 0.1 mm using dial calipers with needle points and took the mean over the 2 canines of the mandible and maxilla, respectively, i.e., leading to one value of height and width each for the mandible, and one value each for the maxilla.

Dental attrition and staining: We evaluated the general level of attrition and stain of all teeth in the mandible and maxilla, i.e., incisors, canines, and cheek teeth, qualitatively and gave a score of no (= score value of 0), little (1), some (2), or very much (3) attrition or staining, respectively, with one score for attrition and one score for staining. We took the mean of values within each tooth class —canines, incisors, premolars, and molars— and finally calculated the mean across all classes to obtain an overall index for tooth attrition and stain, respectively.

Gland staining: We measured the length and the width of the stain produced by secretions from the subcaudal gland to the nearest 0.1 cm using a measuring tape.

Subcaudal gland development: We assessed qualitatively the general appearance of the gland secretion by coding the amount, smell, and color of the secretion in 4 categories: no (0), little/light (1), some/dark (2), and very much/very dark (3). To summarize general gland development we computed an overall gland index by taking the mean of the 3 values obtained for the amount of secretion, smell, and color.

Nipple color (females only): We coded the skin color of the nipples as skin-colored (0), pink (1), or red (2).

Nipple protrusion (females only): We coded the protrusion of the nipple as none (0), little (1), or very much (2) protruding.

Testis size (males only): We measured the length and width of the left and the right testes to the closest 0.1 mm.

Age Estimates

We classified individuals as of known (K) or estimated age (E) at the time of capture and measurement. We considered age as known for subjects for which the birth year was certain through observation of them as dependent infants or young juveniles. If a more exact date could not be established through intensive monitoring of groups, we assigned October 1 of the respective year as date of birth, because births are seasonally spread between September and December, with the peak in October (Fernandez-Duque 2002). For individuals born before intense demographic monitoring of the population began in 1997 (Fernandez-Duque *et al.* 2001), we estimated their birth years based on size, tooth wear, and gland development relative to individuals of known age (Fernandez-Duque and Rotundo 2003; Juárez *et al.* 2011). Two trained researchers or field assistants estimated ages independently, and we reevaluated estimates with every recapture of an individual. It is unlikely that we regularly under- or overestimated ages of adult individuals by >1 or 2 yr. For adults, the percentage of estimated ages was 90% (82/91). We therefore compared regression coefficients, intersects, and slopes of the correlations between age and body mass for individuals of known age and individuals of estimated age to decide whether the inclusion of data for individuals with estimated ages would be problematic. Neither regression coefficient ($z=0.8$, $p=0.78$), nor intersect ($t=1.0$, $p=0.31$), nor slope ($t=0.9$, $p=0.39$) differed between these 2 groups. Thus, we consider the inclusion of individuals with estimated ages to be of little concern given the questions being addressed (for similar reasoning see Strum 1991). Our study is concerned mainly with differentiating the younger age categories. Younger ages (2–3 yr) are reliably estimated owing to birth seasonality (Fernandez-Duque 2002) and birth intervals of ≥ 1 yr (Fernandez-Duque 2009). The estimated birth year for non-adults will therefore usually be quite precise. In fact, the birth year was known for 100% of individuals <2 yr and 80% of individuals <4 yr.

We captured several individuals (26 females, 22 males) multiple times. For those caught only when they were ≥ 4 yr old we computed the mean age (14 females, 13 males) to avoid pseudoreplication. For younger individuals caught more than once, we analyzed all values independently. Their repeated captures usually occurred at least a year apart. With a high degree of repeated measures, a mixed effect model would be appropriate if other assumptions regarding the nature of the data are generally met. In preliminary analyses, we used a nonlinear mixed effect model (package nlme for R; R Development Core Team 2008) first including and then excluding random effects. We compared the 2 models in a likelihood ratio test (Crawley 2007). Further, we tested using Durbin-Watson tests whether there was any indication of serial correlation in the residuals, which would indicate a problematic influence of individuals with multiple data points. The 2 models comparing linear mixed models including or excluding individual identity were not significantly different (likelihood ratio=6.4, $p=0.27$), and using the Akaike Information Criterium (AIC; Crawley 2007; Johnson and Omland 2004) the model without random effects was indicated to be the better, more parsimonious, model. Further, Durbin-Watson tests, done separately for each variable, showed that the influence of repeated measures of a few non-adult individuals was negligible (D-W statistics=2.6–2.9, $p=0.3$–0.9). We therefore did not include random effects in further analyses.

Three females (Eulogia, ID no. 67; Solita, ID no. 85; and Gaviota, ID no. 44) and 1 male (Dixson, ID no. 21) had been recently expelled from their social groups when they were caught. Two of them died within 4 mo and 2 disappeared, but their collars were found, suggesting they had also died. We excluded these individuals from the analyses of body mass, gland size and index, and testes size because they were in a poor body condition that might have affected these variables.

Age at Dispersal, First Reproduction, and Resulting Age Categories

We used information on 7 individuals (3 females, 4 males) of known age for which we documented the dispersal and subsequent immigration into a new group (Fernandez-Duque 2009) to define age categories. For 6 of these individuals we also know the birth dates of infants that were subsequently born in their new groups. We consider the dates of birth of those infants as the age at first reproduction of their mothers and putative fathers. For females, these births represent the true age at first reproduction (AFR). Lacking the genetic information on paternity, this is of course not as certain for males. Owl monkeys are socially monogamous and we have never witnessed extrapair copulations, but these cannot be excluded. Extrapair copulations could influence the AFR in 2 ways: The male could have already obtained successful fertilizations before his immigration to the current group while a solitary floater (overestimation of AFR), or an extragroup male could have sired the infant, so that the group male has in fact not yet sired any offspring (underestimation of AFR). These extragroup fertilizations could be obtained either by males that are themselves members of established groups or by solitary floaters. In the latter case, the probability of having sired an offspring before immigrating into a group, and having lost paternity through an extragroup male after immigration, would on average cancel out. Unless these extragroup fertilizations are consistently biased toward older males that are already established in other groups —and there are no indications supporting this assumption— the average age of a male at the birth of the first infant in his first non-natal group should be a good approximation of age at first reproduction for males.

The dates of those events were established by intense (weekly to monthly) monitoring of groups. When we did not know the exact date of an event we used the average date between the 2 known dates most closely around that event; e.g., the last time an individual was observed ranging solitarily and the first time it was observed in a new group (see Table I for ranges of estimates). Building on the already established age of weaning at an age of 6 mo (Rotundo et al. 2005), we used these developmental milestones to assign ages to the juvenile and subadult (and thus adult) age categories (Pereira and Altmann 1985; Pereira and Fairbanks 1993; Setchell and Lee 2004).

Data Analyses

Growth Curves To obtain growth curves, we used the scores of the physical measurements recorded during the examination for all continuous variables. For gland stain, we calculated the area of the subcaudal gland stain from the 2 measures of length and width, assuming a triangular shape (Aquino and Encarnación 1986).

Table I Age (in mo) at natal dispersal, immigration, and birth of first offspring for 2 female and 3 male owl monkeys of known age

Name (sex)	Age at natal dispersal	Age at immigration	Age at birth of first offspring
Mony (F)	43 (±0.1)	44 (±0.2)	58 (±0.1)
Diosa (F)	35 (±0.1)	35 (±0.2)	—
Diuresis (F)	59 (±0.2)	74 (±0.3)	88 (±1.3)
Dardo (M)	43 (±2.3)	49 (±2.4)	72 (±2.4)
Anibal (M)	37 (±1.5)	41 (±2.0)	72 (+3.0 /–1.0)[a]
Dionisio (M)	36 (±0.4)	36 (±0.2)	71 (±0.6)
Felix (M)	27 (±2.2)	37 (±6.1)	85 (±1.6)
Mean (F/M/total)	46/43/44	51/41/45	73/75/74

After each age, the potential error for the age is given between parentheses (range of error for birth date plus range of error for event/2).

[a] The exact birth date of this infant was not known. Assuming a birth date of October 1, it can be assumed that the infant was not born >1 mo before or 3 mo after this date.

We calculated the volume of each testis assuming an ellipsoid form, i.e., $(\pi/6)$ * length * width^2 (Dixson *et al.* 1980). We then took the mean of the left and right testis volumes to obtain a mean volume. Occasionally, it was difficult to feel both testes during the examination, and in 2 cases we were able to measure only 1 of them. In these cases, we used the value of this single testis as the mean value for both, given that these males were fully reproductive and it is unlikely that they showed true monorchism. Unilateral cryptorchidism can result in striking differences in body size of yellow baboons (Altmann *et al.* 1992), but this was not the case for these 2 owl monkeys.

We evaluated 6 growth models —2-, 3-, and 4-parameter logistic, Weibull, asymptotic exponential, von Bertalanffy— using likelihood-ratio tests and comparing AIC values. Of these models, the von Bertalanffy model represented all of the continuous variables best, with the exception of canine sizes. The von Bertalanffy model can be expressed in several parameterizations, all of which are functionally similar. We chose the Mooij parameterization (Mooij *et al.* 1999). The 3 parameters used in this model are $L\infty$, L_0, and ω; wherein $L\infty$ is the asymptote, L_0 is the size at birth, and ω can be understood as the growth rate near L_0. We checked whether the data conformed satisfactorily to the assumption of normality using the Anderson-Darling normality test and visually checking residual plots (Crawley 2007). Only the data for the size of the subcaudal gland excretion indicated heteroscedasticity (the variance increased with increasing age), so we log-transformed this variable, after which the normality of the data was acceptable.

The data for canines did not conform to normality either transformed or untransformed, and we could therefore not use any of the parametric growth models. Instead we fitted LOESS curves with 1 polynomial degree to the data (Cleveland and Devlin 1988; Crawley 2007) similarly to the approach used by Leigh and Terranova (1998) and Whitten and Turner (2009).

We plotted the values of the categorical variables as box plots with notches against age. The notches are a visual aid to better assess the extent of differences between medians. Only categories for which notches do not overlap are likely to be

statistically different (Crawley 2007; for further details on the calculation see the legend to Fig. 1).

The parameter ω refers to an estimated growth rate around the time of birth and is not comparable to growth rates obtained for other ages. To allow comparison to published data of growth rates, where the growth rate was determined as (body mass at weaning minus body mass at birth)/age at weaning, i.e., a linear relationship, we calculated growth rates separately for juveniles and subadults (see Results for the ages associated with each age category). To calculate growth rates, we used piecewise regression, after checking that the inclusion of a quadratic term would not improve the fit. Because the likelihood ratio test indicated no improvement by including the quadratic term ($F=1.4$, $p=0.25$), we used a linear piecewise regression.

Sex Differences in Growth To test the prediction that female and male owl monkeys do not differ in their development, we compared first the parameters of the von
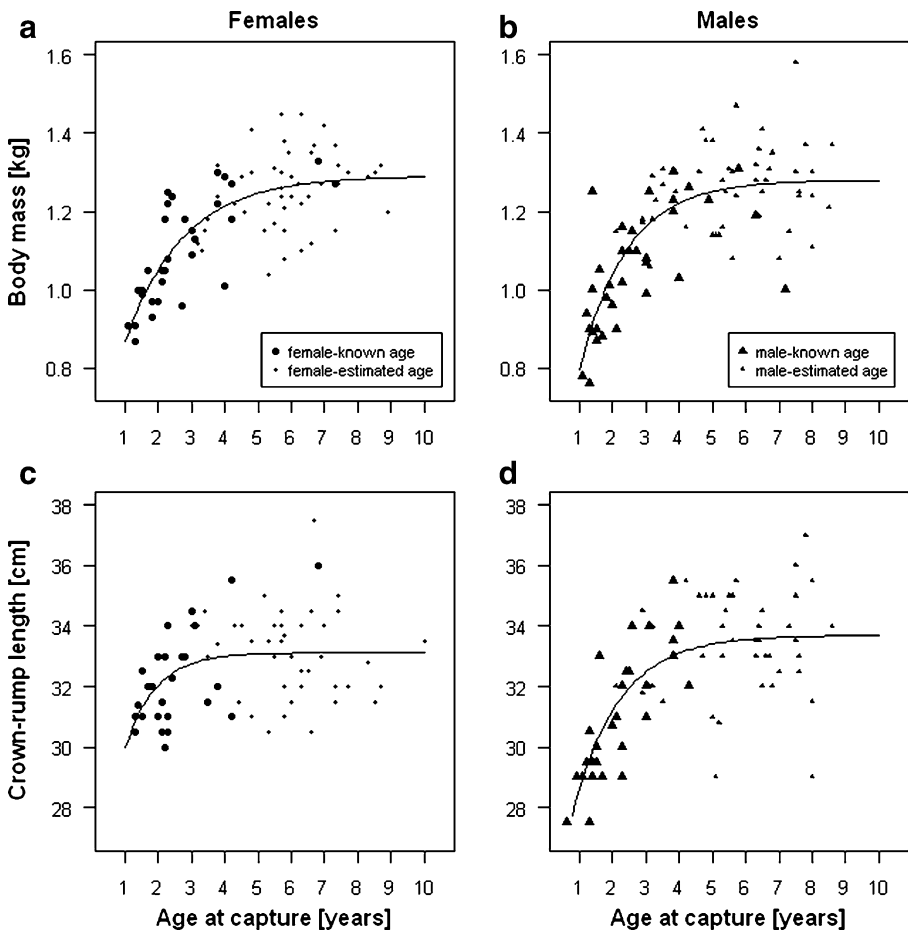
Fig. 1 Changes in body mass and crown–rump length of owl monkeys with age. Von Bertalanffy curves fitted through scatterplots for body mass vs. age in (a) females and (b) males and for crown–rump length vs. age in (c) females and (d) males.

Bertalanffy growth curves. To compare groups, i.e., males and females, using this model, we tested if there were differences between the groups by examining whether a model that included different values for males and females for each of the 3 parameters generated a better fit than models that had 1 parameter in common for both sexes. Statistically nonsignificant results of these likelihood ratio tests indicated that the simpler model, i.e., 1 parameter in common for both sexes, explained the data as well as the others. We then compared the best (lowest AIC) of the 1-parameter-in-common models to the three 2-parameters-in-common models. If all these were statistically nonsignificant, we compared the best of these to the common model, a model that assumed the same parameters for both males and females. If none of the comparisons produced statistically significant differences, the von Bertalanffy models for males and females did not differ (Holst and Stirling 2002; Ogle 2010; Ritz and Streibig 2008).

Growth models describe the development over the entire range of ages. Thus, a comparison of von Bertalanffy models will indicate whether the final asymptotic value of a variable, the growth rate around birth, or the size at birth differ between sexes. However, nonparametric models, as the LOESS curve describing maxillar canine height or categorical variables, cannot be compared this way. Further, slight differences that may show only at specific ages might not be detected in this manner. It was not possible to compare median values for a large number of age categories, as has been done, e.g., in sifakas (*Propithecus edwardsi*: King *et al.* 2011), because sample sizes were too small. Instead, we compared data for male and female juvenile and subadult owl monkeys, respectively. Effect sizes and confidence intervals are more informative than test statistics (Colegrave and Ruxton 2003; Nakagawa and Cuthill 2007). Therefore, we calculated as effect sizes the difference between medians or means of males and females of the 2 age categories and determined the confidence intervals for all effect sizes. We tested for statistical significant differences between medians using Mann-Whitney U and Student's t-tests. We compared growth rates b of males and females, i.e., slopes from the 2 subsections of the piecewise regression, for juveniles and subadults using t-tests.

The variances for estimates of testes volume and gland stain area were quite high. In some species, testes and scent glands undergo seasonal changes. We did not have sufficient data to examine the influence of season on the growth trajectories of the gland stains or testes, e.g., by including season as a fixed term in the models. To evaluate how much season might have influenced our results, we compared median testis volume and gland stain area (the latter separately for males and females) for adult individuals caught during the mating season (May–August), birth season (September–December), and nonreproductive season (January–April) using Mann-Whitney U and Kruskal-Wallis tests. We did not compare statistically tooth variables because of small sample sizes.

We conducted most statistical analyses using R 2.10.1 (R Development Core Team 2008). For the von Bertalanffy models we used the FSA package by Derek H. Ogle for R (http://www.ncfaculty.net/fishR/). We calculated confidence intervals for median values using a program written by R. Hoekstra and H. Kiers, University of Groningen (www.ppsw.rug.nl/~sda/software/CIs%20for%20medians.xls; accessed March 26, 2010) that follows the method described by Bonett and Price (2002).

Results

Age at Dispersal, First Reproduction, and Resulting Age Categories

We never witnessed a dispersing or solitary individual <27 mo old (Table I). This suggests that individuals <2 yr of age would not be able to survive on their own outside the group. We therefore consider juveniles to be between 6.1 (after weaning; Rotundo *et al.* 2005) and 24 mo of age. After dispersal, an individual usually lives as a floater for some months and immigration into another group occurs around 4 yr of age (Table I; Fernandez-Duque 2009). Data of age at first reproduction of individuals of known age (Table I) indicate that reproduction does not start before an age of 4 yr. We therefore consider subadults to be between 24.1 mo and 48 mo of age. Individuals >48 mo of age are termed adults.

Growth Curves

Male and female owl monkeys showed pronounced increases in body mass until *ca.* 4 yr of age, when the rate of increase slowed down (Fig. 1a). Likewise, crown–rump length, gland stain size, and testis size, but not canine size, reached their asymptotic value, i.e., adult size, around 4 yr of age (Figs. 1b, 2, 3, and 4). However, the variances for these variables were generally much larger than for body mass (ESM Table SI). The asymptotic values estimated using the von Bertalanffy models compared well to the median values for adults (Table II; ESM Table SI). For both sexes, the width of the maxillary and mandibular canines increased until *ca.* 3.5 yr of age (ESM Fig. 2c–f). Maximum mandibular canine height was reached at *ca.* 3 yr of age in both sexes (ESM Fig. 2a,b). In contrast, females reached maximum maxillary canine height at *ca.* 2 yr of age, whereas males reached it when they were almost 3 yr old (Fig. 2a,b). At older ages (>4–5 yr), canine height declined again, partly through attrition, partly due to broken teeth. Given that comparatively few measures of canines were available, particularly for younger ages, the canine results should be regarded as preliminary. The largest sample sizes were available for maxillary canine height. Therefore we present the data for the other canines only as supplementary figures (ESM Fig. 2a–f).

Tooth attrition and gland stain area are strongly related to age in both sexes (Figs. 2c,d and 3a,b). Only 2 of 20 monkeys <2 yr of age showed any signs of attrition, whereas approximately a third of the individuals between 2 and 4 yr old had little to heavily worn teeth (36%, 18/50). The teeth staining showed a similar pattern, but was more variable (ESM Fig. 2g,h).

The size of the stain produced by the subcaudal gland secretions is also positively associated to age in both males and females. There was no staining of the tail with gland secretions for individuals <12 mo, and several individuals still had relatively small stained areas until they reached 24 mo of age (median: 0.2 cm^2, range: 0.0–2.5 cm^2, compared to adults (median: 6.5 cm^2, range 1.6–9.5 cm^2; Fig. 3). From *ca.* 2–4 yr the stained area became increasingly larger until *ca.* 4 yr of age. Likewise, the overall gland index also increased with age (Fig. 3c, d). Gland stains did not differ statistically between mating season (MS), birth
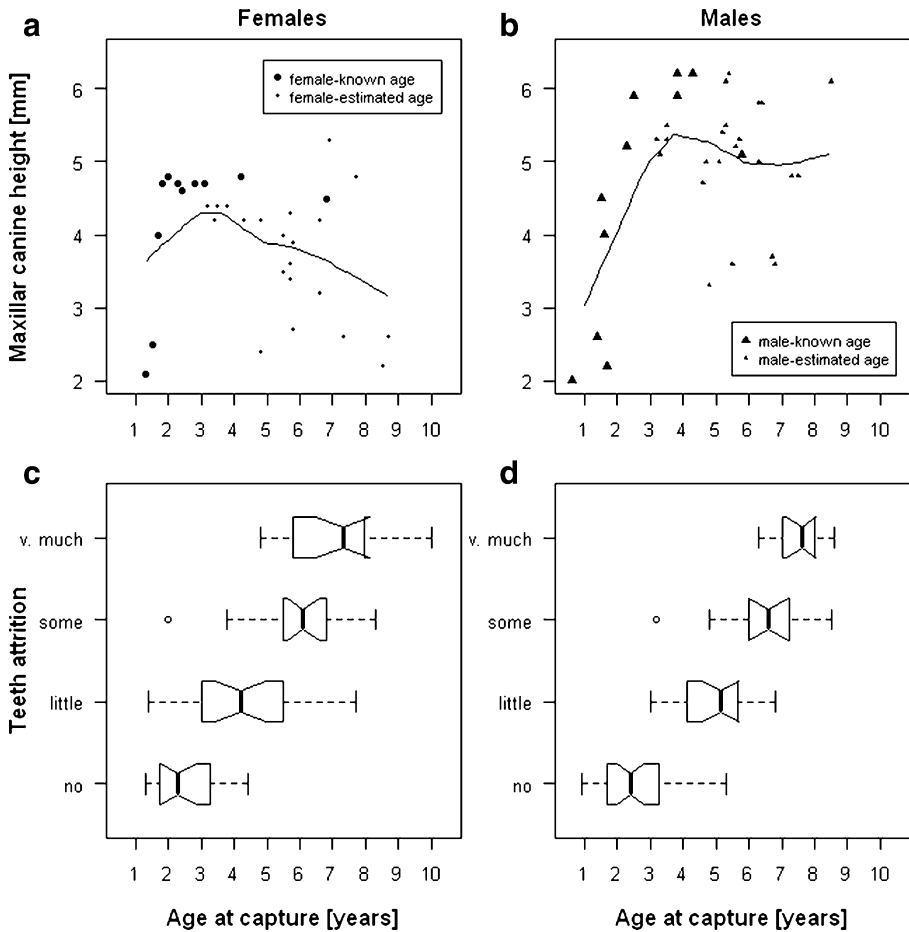
Fig. 2 Changes in condition and height of tooth of owl monkeys with age. Maxillary canine height vs. age in (**a**) females and (**b**) males. Box plot for tooth attrition at different ages in (**c**) females and (**d**) males. LOESS curves are fitted through scatterplots (refer also to the legend of Fig. 1). Box plots represent medians, interquartile ranges (IQRs), and ranges (excluding only values larger than ±1.5 times the IQR; outliers beyond this range are represented as open circles). The notches in the boxes indicate values ±1.58 times IQR/√n, which corresponds roughly to a 95% confidence interval (R Development Core Team 2008).

season (BS), and nonreproductive (NR) season (females: median$_{MS}$=7.3 cm^2, N=24; median$_{BS}$=6.0 cm^2, N=13; median$_{NR}$=5.5 cm^2, N=23; males: median$_{MS}$= 8.5 cm^2, N=18; median$_{BS}$=8.0 cm^2, N=15; median$_{NR}$=8.0 cm^2, N=19; Kruskal-Wallis test, females: χ^2=3.8, df=2, p=0.15; males: χ^2=0.2, df=2, p=0.92).

Among females, nipple protrusion and color changed with age, but showed large variation (Fig. 3e and ESM Fig. 3). No female <18 mo of age had even slightly protruding nipples, and only two 18- to 24-mo-old females did. Only females of ≥5 yr of age had strongly protruding nipples. The median age of females with nonprotruding nipples was slightly greater than 2 yr, but females as old as 5 yr of age also regularly had inconspicuous nipples. Overlap of categories was much higher for nipple color than for nipple protrusion (ESM Fig. 3 and Fig. 4a).
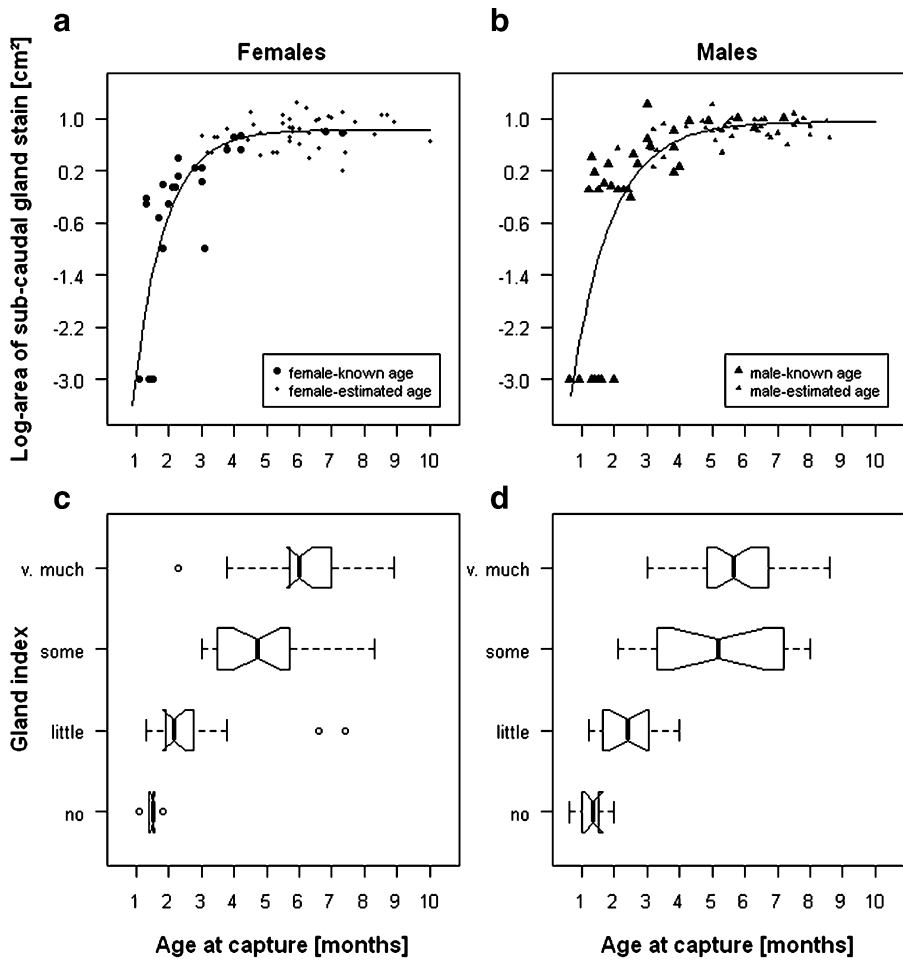
Fig. 3 Subcaudal development of owl monkeys in relation to age in **(a)** females and **(b)** males. Box plot for subcaudal gland index at different ages in **(c)** females and **(d)** males. Von Bertalanffy curves are fitted through scatterplots. Female data points are represented by circles, those of males by triangles. Large circles or triangles represent data for individuals of known age, smaller symbols data for individuals with estimated ages. Box plots represent medians, interquartile ranges (IQRs), and ranges (excluding only values larger than ±1.5 times the IQR; outliers beyond this range are represented as open circles). The notches in the boxes indicate values ±1.58 times IQR/√n, which corresponds roughly to a 95% confidence interval (R Development Core Team 2008).

Some males had relatively large testes volumes, i.e., adult-sized, before reaching 48 mo of age, when the von Bertalanffy curve first started to level off (Fig. 4b). The variance of testes volumes was very high (ESM Table SI). For example, one male had fairly undeveloped testes at the age of 31 mo, and 5 males <2 yr old had testes volumes that were as large as testes volumes measured for some adult males (Fig. 4b). The median volumes of testes of adult males caught in the mating season and the nonreproductive season did not differ significantly (Mann-Whitney U test, $W=28$, $p=0.76$, $N_{NR}=9$, median$_{NR}=$ 184 mm^3, $N_{MA}=7$, median$_{Ma}=197$ mm^3). We had data on testes size during the birth season for only 1 adult male (113 mm^3).

a

Females

b
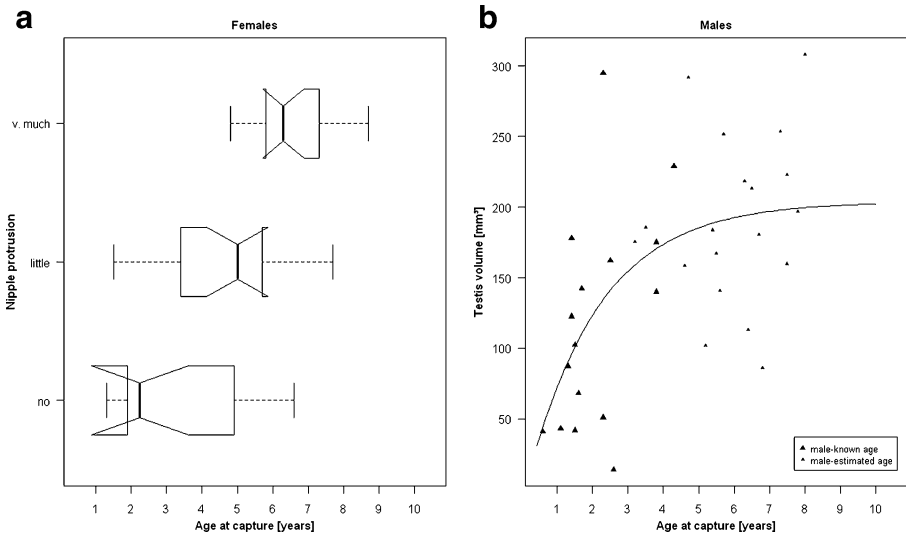
Males

Fig. 4 Nipple protrusion and mean testis size in owl monkeys in relation to age. **(a)** Box plot for nipple protrusion in females. Box plots represent medians, interquartile ranges (IQRs), and ranges (excluding only values larger than ±1.5 times the IQR; outliers beyond this range are represented as open circles). The notches in the boxes indicate values ±1.58 times IQR/√n, which corresponds roughly to a 95% confidence interval (R Development Core Team 2008). **(b)** Testes volume vs. age. A von Bertalanffy curve is fitted through the scatterplot.

Sex Differences

Male and female juveniles did not differ markedly in body mass (Table II; ESM Table SI). Although females tended to have a slightly larger median body mass (70 g higher), a

Table II Parameter estimates (and 95% confidence intervals) of von Bertalanffy growth models for female and male body mass, crown–rump length, area of gland stain, and testis size

	Parameters	Females	Males	Significance[+]
Body mass	$L\infty$ (conf. int.)	1.29 (1.24–1.34)	1.28 (1.24–1.32)	n.s.
	L_0 (conf. int.)	0.55 (0.20–0.89)	0.31 (−0.01 to 0.63)	n.s.
	ω (conf. int.)	0.73 (0.38–1.08)	0.89 (0.59–1.19)	n.s.
Crown–rump length	$L\infty$ (conf. int.)	33.1 (32.6–33.6)	33.7 (33.0–34.4)	*
	L_0 (conf. int.)	23.9 (3.9–43.8)	23.3 (18.2–28.4)	n.s.
	ω (conf. int.)	35.7 (−9.3 to 80.7)	24.1 (11.5–36.7)	*
Gland secretion	$L\infty$ (conf. int.)	0.83 (0.65–1.0)	0.95 (0.68–1.23)	n.s.
(log transformed)	L_0 (conf. int.)	−9.9 (−15.8 to −4.1)	−6.3 (−9.05 to −3.51)	n.s.
	ω (conf. int.)	0.87 (0.62–1.13)	0.78 (0.56–1.00)	n.s.
Testis size	$L\infty$ (conf. int.)	—	203.9 (142.4–265.3)	—
	L_0 (conf. int.)	—	−10.6 (−206.4 to 185.3)	—
	ω (conf. int.)	—	99.9 (−29.0 to 228.8)	—

[a] Determined in likelihood ratio tests. Crown–rump length: $F=5.5$, $p=0.02$. Statistics for all other likelihood ratio tests can be found in ESM Table SII.

common von Bertalanffy model, assuming the same growth rate, asymptotic value, and mass at birth, explained the development more parsimoniously than models assuming different parameter values for the sexes (Table II). Median body mass did not differ significantly between males and females for either juveniles or subadult individuals (ESM Table SI). Regarding crown–rump length, both the asymptotic value, as estimated by the model, and the actual medians differed between males and females (Table II; ESM Table SI), although the slopes from the linear piecewise regressions did not (*b*, ESM Table SI). This showed particularly in juveniles, where females were longer than their male age-peers. These differences were no longer apparent in subadult monkeys. The model produced a statistically significant difference in growth rate around birth (ω) for crown–rump length (Table II); but this result is meaningless given the estimated values for crown–rump length at birth. Maxillary canines were nearly 1 mm longer in subadult males than in same-age females, and females reached maximum canine height earlier than males (Fig. 2a,b; ESM Table SI).

The growth rates ω for the log-transformed gland stain area are not statistically significant different between females and males (Fig. 3a,b; Table II). There is no pronounced difference between males and females in the overall gland index, either (Fig. 3c,d; ESM Table SI).

Discussion

Growth Rates and Development

In most aspects, the development of male and female Azara's owl monkeys is very similar, as expected for a monomorphic species. The growth parameter at birth ω, as estimated from the von Bertalanffy models, was 0.81 kg/yr (mean of female and male value), or 2.2 g/d around the time of birth. This is very similar to the growth rate of 2.6 g/d reported for 36 captive *Aotus "trivirgatus"* (proper species identification is not possible because the genus nomenclature has changed since then), in their first month (Hall *et al.* 1979) and a rate of 2.1 g/d that we computed using information in Lee *et al.* (1991). Hall *et al.* (1979) and Lee *et al.* (1991) obtained their estimates with a traditional (linear) estimate, whereas we derived our estimate from a von Bertalanffy growth model based on data for individuals that were ≥13 mo old. Our estimates of slopes *b* for juveniles and subadults (maximum value 0.7 g/mo; see ESM Table SI) are much lower than those reported by Hall *et al.* (1979), who report growth rates of 1.4 g/d for infants between the age of 1 and 4 mo. The growth curves depicted in Fig. 1a,b indicate that the growth rate is steadily declining, i.e., there is no obvious growth spurt detectable, so that a smaller value for subadults than for juveniles, for juveniles than for infants, and the largest for ω are to be expected. Unfortunately the data of Hall *et al.* (1979) stop at 1 yr, whereas our data start after this age. Although these data suggest very similar patterns for the studied populations, much more data from various owl monkey species are needed before we know whether, within specific age categories, growth rates are similar among owl monkey species, in particular because all other species are substantially smaller than *Aotus azarai* (Fernandez-Duque 2011).

The von Bertalanffy models provide also an estimate of size at birth (L_0, Table II), but we regard these estimates with extreme caution. A body mass at birth of 300 (males) or even 500 g (females) is nonsensical, given that the birth mass reported for other, albeit smaller species ranges between 88 and 99 g (Gálvez-Durand *et al.* 2004; Hall *et al.* 1979; Smith and Leigh 1998). Because we did not capture very young individuals, we do not have data for monkeys <1 yr but two 1-yr-old individuals we captured had body masses of *ca.* 600 g. Forcing the von Bertalanffy model through, for example, a body mass at birth of 100 or 200 g produced fits that substantially underestimated sizes, i.e., lay under the scatter; data not presented. This gives some indication that the true fit will be noncontinuous, e.g., rapid growth in early infancy, followed by a lower growth rate, followed by an increase again. However, this remains speculative until body mass data at birth for *Aotus azarai* are available. For the ages for which we have data, models resulting in sigmoid curves did not provide a better fit, so that some discontinuity in growth rates can be expected before 1 yr of age. For example, Hall *et al.* (1979) found some indication for an interrupted growth or even transient weight loss soon after the eruption of the last deciduous teeth that could be related to the weaning process.

Our results regarding sexual maturation differ to some degree from findings in captive individuals of other owl monkey species. Data for captive *Aotus griseimembra,* a significantly smaller species (average female body mass, 0.86 kg; average male body mass, 0.92 kg vs. 1.25 kg in both female and male *Aotus azarai azarai*; Fernandez-Duque in press), may indicate differences in subcaudal gland development. In *Aotus griseimembra*, the stiffening of subcaudal hairs, which apparently begins while the gland is still growing, occurs on average at 316 d of age and is complete between 336 and 442 d of age (Dixson 1994; Dixson *et al.* 1980). Although it is unclear how the stiffening of the hairs relates to the overall development of the subcaudal gland, in our population, the majority of individuals did not show a significant onset of glandular function, based on either size of the stain produced by the gland or gland index, before 2 yr of age, and full development did not appear to be complete until they reached 4 yr of age. Dixson and co-workers (Dixson 1994; Dixson *et al.* 1980) found that plasma testosterone first increased when males were 211–337 d old (median=313 d), with larger rises at 300–400 d. Although not explicitly stated, it appears that testes size in adult *Aotus griseimembra* is reached between 1.5 and 2 yr (Fig. 3 in Dixson 1994), which is similar to some of our individuals. In the same study, the volume of adult testes size is reported to be 514 mm^3 (Dixson *et al.* 1980). Even if we assume that Dixson used the combined volumes of both testes (not clearly stated in the Methods) instead of the means as we did, 514 mm^3 is far larger than the volumes we estimated. As Dixson (1994) noted, the exact measurement of testes is very difficult and measurement errors are likely to be large. This most likely influenced the variance in our testes volume data (Fig. 4b; ESM Table SI). Further, there might also be a bias introduced by the fact that very small testes or gland stains were not measurable at all, generating a higher proportion of missing data for younger ages that might lead to a lower than real median age at the onset of testicular or gland development.

Seasonal effects might also contribute to the variance for testes and gland stain sizes. At least in females, there is a solid trend for gland stains to be larger during the mating season, although differences between seasons were not statistically

significant. However, this lack of statistical significance might be due partly to small sample sizes or interannual variation. Olfactory inspection of the female's anogenital region decreased in male *Aotus griseimembra* that had been reversibly rendered anosmic (Dixson 1983), indicating that the glands convey information on the sexual status of monkeys, making seasonal effects likely. For testes volume, the sample sizes, and thus power of the test, were low, and with only 1 male in the nonreproductive season no solid conclusions can be drawn. However, given the apparently low effect size —testes during the mating season were on average 13 mm^3 larger than during the nonreproductive season— and that only 1 juvenile and subadult male were caught in the nonreproductive season, we do not think that seasonality affected the interpretation of the results, i.e., the growth curve, too strongly.

Owl monkeys in captivity reproduced at earlier ages than at our study site (Table I). *Aotus nancymaae* from Perú have successfully reproduced in captivity as young as 25 mo old (mean age: 41 mo for females, 42 mo for males; Gozalo and Montoya 1990). Similarly, data on hormonal and gland development from captive *Aotus griseimembra* indicate that owl monkeys are sexually mature by *ca.* 3 yr of age (Dixson 1994). The average age of both males and females when their first infant was born was *ca.* 6 yr and the youngest female to conceive was *ca.* 4.5 yr old at conception, assuming a 4-mo gestation period like in *Aotus griseimembra* (Dixson 1983). In Azara's owl monkeys, individuals start to successfully enter new groups and to reproduce at 4 yr (Table I). A relative delay in the reproduction of wild individuals may be in part due to birth seasonality because it might be necessary to form a stable pair bond before reproductive activity starts. It may in part be explained by the larger body size of *Aotus azarai* vs. other owl monkey species (Fernandez-Duque in press).

Given that *Aotus azarai* is the largest owl monkey species (Fernandez-Duque 2011), living in a more seasonal habitat than other *Aotus* spp., it is also possible that developmental rates differ among species because of different ecological or phylogenetic constraints. Currently, no data on other species are available, and little information on the sexual development of female owl monkeys is available even in captivity. Thus, it is difficult to determine without more data from wild populations whether younger ages at first reproduction reported in other studies are a captivity artifact, i.e., adaptation to a food-enriched, predator-free environment, or due to intrinsic species differences.

Sex Differences

Our data also support the prediction from life history that developmental rates for males and females should be similar in monomorphic species (Leigh and Terranova 1998). The parameter estimates of the von Bertalanffy curves for body mass and size of the stain of subcaudal gland secretions did not differ statistically between the sexes, in strong contrast to sexually dimorphic species like the mandrill (*Mandrillus sphinx*), in which males grow for a much longer time and growth rates also differ between the sexes (Setchell *et al.* 2001). Similarly, none of the slopes (growth rates *b*) differed much between the sexes for either juvenile or subadult age categories. However, further investigation is necessary because the power of the statistical tests

was relatively low, and ≥3 effect sizes (difference in length of juvenile females and males, differences between the slopes for juvenile male and female body mass, and superior canine length) warrant further investigation. Thus, although juvenile females tend to be heavier and longer than males, the gain in body mass per month during this period tends to be lower in females. Likewise, Figs. 1c,d seem to suggest a lower increase of crown–rump length for females than for males. The biological significance of these differences remains unclear, and data from newborn infants will be necessary to decide whether females are born slightly larger and males make up the difference after the first 2 yr of life, or whether the difference appears at a later stage. There is some indication from captive data that females might indeed be born slightly larger (94 g vs. 90 g, for females and males, respectively) but the difference is not very large and is not statistically significant (Hall et al. 1979). Overall, our findings are in good agreement with other examinations of 9 monomorphic lemurid taxa that showed little sex differences in development (Leigh and Terranova 1998; see also King *et al.* 2011, for *Propithecus edwardsi*).

Conversely, although the maxillary canines were significantly longer in subadult males than in subadult females, female canines may emerge faster initially and reach the final length earlier than do those of males. The difference in canine size is also found for adult owl monkeys (Fernandez-Duque in press). It is not clear whether there is still actual selection for canine size dimorphism, or if it could be a retained character because canine size dimorphism has been proposed for a fossil *Aotus* species (Takai *et al.* 2009). However, this does not explain why the canines of young females should emerge faster.

Further data with less variance in the measurement are needed to investigate the described patterns for crown–rump length and canine height in more detail. For example, although body mass should be more variable than crown–rump length given that it is strongly dependent on environmental conditions, nutritional status, and health, crown–rump length was more variable in our data. It is quite likely that this result can be explained because body mass can be measured more reliably than crown–rump length, which depends to some degree on the posture of the subject and the proper and consistent identification of the 2 points used for measurement. The higher variance for crown–rump length vs. body mass also suggests that age evaluations in the field should rely on mass, with the additional help of gland development and tooth development and attrition, instead of length.

The patterns we found are similar to those described for sex–age categories in *Aotus nancimaae* (Aquino and Encarnación 1986). In these Peruvian owl monkeys, infant and juvenile females were slightly, albeit not statistically significantly, heavier than males, whereas adults of both sexes had similar masses. Thus, it seems possible that females start with a higher mass and then grow more slowly than do males. Also in accordance with our findings, juvenile female *Aotus nancimaae* had slightly longer maxillary canines, whereas subadult males had significantly longer canines than females.

Although the general similarity between male and female juvenile and subadult owl monkeys are in agreement with predictions from life-history theory (Leigh and Terranova 1998), our data also suggest that much more detailed data on sexually monomorphic species are needed to determine what factors might lead to apparent albeit slight differences between the sexes. Relatively small differences in the

development between the sexes of monomorphic species, like the development of the maxillary canines in owl monkeys, might still have profound biological implications.

References

Altmann, J., Alberts, S., & Sapolsky, R. M. (1992). Endocrine and developmental correlates of unilateral cryptorchidism in a wild baboon. *American Journal of Primatology, 26*(4), 309–314.

Aquino, R., & Encarnación, F. (1986). Population structure of *Aotus nancymai* (Cebidae: Primates) in Peruvian Amazon lowland forest. *American Journal of Primatology, 11*, 1–7.

Badyaev, A. V. (2002a). Growing apart: An ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology & Evolution, 17*(8), 369–378.

Badyaev, A. V. (2002b). Male and female growth in sexually dimorphic species: Harmony, conflict, or both? *Comments on Theoretical Biology, 7*, 11–33.

Bolter, D. R., & Zihlman, A. L. (2003). Morphometric analysis of growth and development in wild-collected vervet monkeys (*Cercopithecus aethiops*), with implications for growth patterns in Old World monkeys, apes and humans. *Journal of Zoology (London), 260*(1), 99–110.

Bonett, D. G., & Price, R. M. (2002). Statistical inference for a linear function of medians: Confidence intervals, hypothesis testing, and sample size requirements. *Psychological Methods, 7*(3), 370–383.

Brown, A. D., & Zunino, G. E. (1994). Hábitat, densidad y problemas de conservación de los primates en Argentina. *Vida Silvestre Neotropical, 3*(1), 30–40.

Cleveland, W. S., & Devlin, S. J. (1988). Locally weighted regression: An approach to regression analysis by local fitting. *Journal of the American Statistical Association, 83*(403), 596–610.

Colegrave, N., & Ruxton, G. D. (2003). Confidence intervals are a more useful complement to nonsignificant tests than are power calculations. *Behavioral Ecology, 14*(3), 446–450.

Crawley, M. J. (2007). *The R Book*. Chichester: John Wiley & Sons.

Dixson, A. F. (1983). The owl monkey (*Aotus trivirgatus*). In J. P. Hearn (Ed.), *Reproduction in New World primates: New models in medical sciences* (pp. 69–113). Lancaster: International Medical Publishers.

Dixson, A. F. (1994). Reproductive biology of the owl monkey. In J. F. Baer, R. E. Weller, & I. Kakoma (Eds.), *Aotus: The owl monkey* (pp. 113–132). San Diego: Academic Press.

Dixson, A. F., Gardner, J. S., & Bonney, R. C. (1980). Puberty in the male owl monkeys (*Aotus trivirgatus griseimembra*): A study of physical and hormonal development. *International Journal of Primatology, 1*(2), 129–139.

Fernandez-Duque, E. (2002). Environmental determinants of birth seasonality in night monkeys (*Aotus azarai*) of the Argentinian Chaco. *International Journal of Primatology, 23*(3), 639–656.

Fernandez-Duque, E. (2008). Behavior, ecology, and demography of *Aotus vociferans* in Yasuní National Park, Ecuador. *International Journal of Primatology, 29*(2), 421–431.

Fernandez-Duque, E. (2009). Natal dispersal in monogamous owl monkeys (*Aotus azarai*) of the Argentinean Chaco. *Behaviour, 146*(4–5), 583–606.

Fernandez-Duque, E. (2011). Aotinae: Social monogamy in the only nocturnal anthropoid. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. Stumpf (Eds.), *Primates in perspective* (2nd ed., pp. 139–154). Oxford: Oxford University Press.

Fernandez-Duque, E. (in press). Rensch's rule, Bergman's effect and adult sexual dimorphism in wild monogamous owl monkeys (*Aotus azarai*) of Argentina. *American Journal of Physical Anthropology.* doi:10.1002/ajpa.21541.

Fernandez-Duque, E., de la Iglesia, H., & Erkert, H. G. (2010). Moonstruck primates: Owl monkeys (*Aotus*) need moonlight for nocturnal activity in their natural environment. *PLoS ONE, 5*(9), e12572.

Fernandez-Duque, E., & Rotundo, M. (2003). Field methods for capturing and marking azarai night monkeys. *International Journal of Primatology, 24*(5), 1113–1120.

Fernandez-Duque, E., Rotundo, M., & Sloan, C. (2001). Density and population structure of owl monkeys (*Aotus azarai*) in the Argentinean Chaco. *American Journal of Primatology, 53*(3), 99–108.

Fernandez-Duque, E., Valeggia, C. R., & Mendoza, S. P. (2009). The biology of paternal care in human and nonhuman primates. *Annual Review of Anthropology, 38*, 115–130.

Gálvez-Durand, J., Montoya, E., Gálvez, H., & Ique, C. (2004). Desarrollo biométrico en *Aotus Nancymae* nacidos en cautiverio. In R. Bodmer (Ed.), *VI Congreso Internacional sobre Manejo de Fauna Silvestre en la Amazonia y Latinoamérica* (pp. 6–11). September 5–10, 2004; Iquitos, Perú.

Gozalo, A., & Montoya, E. (1990). Reproduction of the owl monkey (*Aotus nancymai*) (primates: Cebidae) in captivity. *American Journal of Primatology, 21*(1), 61–68.

Hall, R. D., Beattie, R. J., & Wyckoff, G. H. (1979). Weight gains and sequence of dental eruptions in infant owl monkeys (*Aotus trivirgatus*). In G. C. Ruppenthal (Ed.), *Nursery care of nonhuman primates* (pp. 321–329). New York: Plenum Press.

Hayama, S-I, Kamiya, S., & Nigi, H. (1997). Morphological changes of female reproductive organs of Japanese monkeys with reproductive conditions. *Primates, 38*(4), 359–367.

Holst, M., & Stirling, I. (2002). A comparison of ringed seal (*Phoca hispida*) biology on the east and west sides of the North Water Polynya, Baffin Bay. *Aquatic Mammals, 28*(3), 221–230.

Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology and Evolution, 19*(2), 101–108.

Juárez, C. P., Rotundo, M. A., Berg, W., & Fernández-Duque, E. (2011). Costs and benefits of radio-collaring on the behavior, demography and conservation of owl monkeys (*Aotus azarai*) in Formosa, Argentina. *International Journal of Primatology, 32*(1), 69–82.

King, S. J., Morelli, T. L., Arrigo-Nelson, S., Ratelolahy, F. J., Godfrey, L. R., Wyatt, J., et al. (2011). Morphometrics and pattern of growth in wild sifakas (*Propithecus edwardsi*) at Ranomafana National Park, Madagascar. *American Journal of Primatology, 73*(1), 155–172.

Lee, P. C., Majluf, P., Gordon, I. J. (1991). Growth, weaning and maternal investment from a comparative perspective. *Journal of Zoology (London), 225*, 99–114.

Leigh, S. R. (1992). Patterns of variation in the ontogeny of primate body size dimorphism. *Journal of Human Evolution, 23*, 27–50.

Leigh, S. R. (1994). Relations between captive and noncaptive weights in anthropoid primates. *Zoo Biology, 13*, 21–43.

Leigh, S. R. (1995). Socioecology and the ontogeny of sexual size dimorphism in anthropoid primates. *American Journal of Physical Anthropology, 97*(4), 339–356.

Leigh, S. R., & Terranova, C. J. (1998). Comparative perspectives on bimaturism, ontogeny, and dimorphism in lemurid primates. *International Journal of Primatology, 19*(4), 723–749.

Mendes Pontes, A. R., & Cruz, M. A. O. Md. (1995). Home range, intergroup transfers, and reproductive status of common marmosets *Callithrix jacchus* in a forest fragment in northeastern Brazil. *Primates, 26*, 335–347.

Mooij, W. M., Rooij, J. M. V., & Wijnhoven, S. (1999). Analysis and comparison of growth from small samples of length-at-age data: Detection of sequal dimorphism in Eurasian perch as an example. *Transactions of the American Fisheries Society, 128*, 483–490.

Nakagawa, S., & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: A practical guide for biologists. *Biological Reviews, 82*, 591–605.

Ogle, D. H. (2010). Accompanying documentation to the FSA package: http://www.ncfaculty.net/dogle/fishR/gnrlex/VonBertalanffyCompare/VonBertalanffyCompare.pdf (Accessed January 14, 2011).

Pereira, M. E., & Altmann, J. (1985). Development of social behavior in free-living nonhuman primates. In E. S. Watts (Ed.), *Nonhuman primate models for human growth and development* (pp. 217–309). New York: Alan R. Liss.

Pereira, M. E., & Fairbanks, L. A. (1993). *Juvenile primates: Life history, development, and behavior.* Oxford: Oxford University Press.

Plavcan, M. J. (1993). Canine size and shape in male anthropoid primates. *American Journal of Physical Anthropology, 92*, 201–216.

R Development Core Team. (2008). *R: A language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing.

Ritz, C., & Streibig, J. C. (2008). *Nonlinear regression with R* (p. 144). Heidelberg: Springer.

Rotundo, M., Fernandez-Duque, E., & Dixon, A. F. (2005). Infant development and parental care in free-ranging *Aotus azarai azarai* in Argentina. *International Journal of Primatology, 26*(6), 1459–1473.

Rowell, T. E. (1977). Variation in age at puberty in monkeys. *Folia Primatologica, 27*, 284–296.

Rubenstein, D. I. (1993). On the evolution of juvenile life-styles in mammals. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: Life history, development, and behavior* (pp. 38–56). Oxford: Oxford University Press.

Setchell, J. M., & Lee, P. C. (2004). Development and sexual selection in primates. In P. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: Causes, mechanisms and consequences* (pp. 175–195). Cambridge: Cambridge University Press.

Setchell, J. M., Lee, P. C., Wickings, E. J., & Dixson, A. F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *American Journal of Physical Anthropology, 115*, 349–360.

Shea, B. T. (1986). Ontogenetic approaches to sexual dimorphism in anthropoids. *Human Evolution, 1*, 97–110.

Silk, J. B., & Brown, G. R. (2008). Local resource competition and local resource enhancement shape primate birth sex ratios. *Proceedings of the Royal Society of London B: Biological Sciences, 275*, 1761–1765.

Smith, R. J., & Leigh, S. R. (1998). Sexual dimorphism in primate neonatal body mass. *Journal of Human Evolution, 34*, 173–201.

Strum, S. C. (1991). Weight and age in wild olive baboons. *American Journal of Primatology, 25*(4), 219–237.

Takai, M., Nishimura, T., Shigehara, N., & Setoguchi, T. (2009). Meaning of the canine sexual dimorphism in fossil owl monkey, *Aotus dindensis* from the middle Miocene of La Venta, Colombia. *Comparative Dental Morphology, 13*, 55–59.

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

Wright, P. C. (1981). The night monkeys, genus *Aotus*. In A. Coimbra-Filho & R. A. Mittermeier (Eds.), *Ecology and behavior of Neotropical primates* (pp. 211–240). Rio de Janeiro: Academia Brasileira de Ciencias.

Wright, P. C. (1989). The nocturnal primate niche in the New World. *Journal of Human Evolution, 18*, 635–658.