Growth and the Development of Sexual Size Dimorphism in Lorises and Galagos

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KEY WORDS ontogeny; body mass; bimaturism; strepsirrhine; *Loris*; *Nycticebus*; *Galago*; *Otolemur*

ABSTRACT Three fundamental ontogenetic pathways lead to the development of size differences between males and females. Males and females may grow at the same rate for different durations (bimaturism), grow for the same duration at different rates, or grow at a mix of rate and duration differences. While patterns of growth and the development of adult body size are well established for many haplorhines, the extent to which rate and duration differences affect strepsirrhine growth trajectories remains unclear. Here, we present iterative piecewise regression models that describe the ontogeny of adult body mass for males and females of five lorisoid species (i.e., lorises and galagos) from the Duke Lemur Center. We test the hypotheses that, like most haplorhines, sexual size dimorphism (SSD) is a result of bimaturism, and males and females of monomorphic species grow at the same rate for a similar duration. We confirm that the galagos in this sample (*Galago moholi* and *Otolemur garnettii*) show significant SSD that is achieved through bimaturism. Unlike monomorphic lemurids, the lorises in this sample show a diversity of ontogenetic patterns. *Loris tardigradus* does follow a lemur-like trajectory to monomorphism but *Nycticebus coucang* and *Nycticebus pygmaeus* achieve larger adult female body sizes through a mixture of rate and duration differences. We show that contrary to previous assumptions, there are patterns of both similarity and difference in growth trajectories of comparably sized lorises and galagos. Furthermore, when ontogenetic profiles of lorisoid and lemurid growth are compared, it is evident that lorisoids grow faster for a shorter period of time. Am J Phys Anthropol 147:11–20, 2012.

Strepsirrhine primates show variable degrees of sexual size dimorphism (SSD), but the ontogenetic processes that generate this variation have only been explored in the monomorphic lemurids (Leigh and Terranova, 1998). Counter to the typical mammalian pattern of SSD (Rensch, 1959), the largest living strepsirrhine species (*Indri indri)* and the large, extinct subfossil lemurs show little to no SSD (Godfrey et al., 1993), likely as a result of identical male and female growth trajectories (Godfrey et al., 1993; Leigh and Terranova, 1998). However, it is in the smallest bodied strepsirrhine species that the greatest SSD is found. These species show both male and female biased SSD, as well as strong seasonal fluctuations in the degree to which dimorphism is expressed (Kappeler, 1990; Schmid and Kappeler, 1998), but the growth processes that produce these levels of SSD have not yet been described.

In this article, we explore the ontogeny of adult body mass and SSD in galagos and lorises. We use the Lorisoidea taxonomy of Grubb et al. (2003) wherein galago species are placed into a single family, the Galagidae, and the lorises and pottos are placed into the Lorisidae. We refer to these groups as galagos and lorises, respectively, and collectively as lorisoids. We test the hypotheses that: 1) like most anthropoids, SSD in galagos is a result of differences in the duration of growth (bimaturism); and that 2) as in the lemurids, loris monomorphism results from the lack of differences in both the rate and duration of growth between males and females.

BACKGROUND

Development of SSD

SSD in most primates results from a modification of the male growth trajectory, either through a pronounced growth spurt or through prolonged duration. This change in the male growth profile is likely a response to intense sexual selection that acts to increase male body size more than female body size, and thus increases dimorphism (Jarman, 1983; Plavcan and van Schaik, 1997; Plavcan, 2001; Lindenfors, 2002; Gordon, 2006a). Primate species may show low levels of dimorphism either due to low levels of intrasexual competition or as a result of selection on an increase in female body mass (Gordon, 2006b; Clutton-Brock, 2009). An ontogenetic approach can identify how natural and sexual selection shape SSD through changes in the duration and/or rate of growth (Shea, 1986; Leigh, 1992; Leigh and Terranova, 1998).

Grant sponsor: National Science Foundation; Grant number: BCS- 0503988 to GTS. Grant sponsor: NSF Graduate Research Fellowship to MTO.

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Received 13 November 2010; accepted 18 July 2011

DOI 10.1002/ajpa.21600
Published online 12 October 2011 in Wiley Online Library (wileyonlinelibrary.com).

In sexually dimorphic mammals, males grow to a larger size than females through one of three developmental trajectories. The most common is bimaturism where males grow for a longer period of time than females, but at the same rate (Wiley, 1974; Alexander et al., 1979; Jarman, 1983; Leigh, 1992). For example, haplorhine males grow an average of 10% longer than females (Leigh, 1992). Bimaturism is a response to strong intrasexual (male) competition where access to mates is limited (Wiley, 1974; Jarman, 1983). In primates, however, intrasexual competition may not be the strong selection pressure on body mass that is typical of other vertebrates. Primate body mass is often constrained by arboreality, and canine size plays a prominent role in male-male competition (Plavcan and van Schaik, 1997; Plavcan, 2001). Bimaturism reflects selection on male body mass that keeps growth rates constant and simply extends the duration of growth. Because bimaturism is common across vertebrates, it may be the simplest path to produce dimorphic sexes.

Second, males and females can grow for the same duration, but males then grow at faster rates (Shea, 1986). Rate differences may be a response to sexual selection that increases overall body mass but holds constant the age at sexual maturity. Rate differences typically occur at the end of the growth period near the onset of sexual maturity that greatly accelerates body mass growth (Leigh, 1992; Gasser et al., 2001; Walker et al., 2006).

Finally, a rarer combination of rate and duration differences may produce sexual dimorphism in adults (Shea, 1985; Leigh, 1992, 1995). Rate and duration of growth may respond to selection independently of each another, and the combination of rate and timing differences of males and females may reflect complex interactions of both intrasexual and intersexual competition.

Growth in strepsirrhines

SSD in strepsirrhines is generally low, absent, or reversed (Kappeler, 1990, 1991; Leigh and Terranova, 1998). Low SSD has been attributed to low levels of gregariousness, to scramble competition and the retention of agility in males, to environmental constraints, and to evolutionary disequilibrium (van Schaik and Kappeler, 1996; Leigh and Terranova, 1998; Lindenfors, 2002). However, SSD levels in the small-bodied galagos are similar to those in many haplorhines, particularly colobine monkeys (Plavcan and van Schaik, 1997). Understanding the diversity of growth patterns within the strepsirrhines provides additional insight into the social and ecological diversity that characterizes these primates (Nekaris and Bearder, 2010) and how they relate to established haplorhine growth profiles.

Lemurid monomorphism is unusual when compared to other primates of similar group sizes and high levels of agonism, which often show significant SSD (Plavcan and van Schaik, 1997). Within these monomorphic lemur species, males and females possess identical ontogenetic trajectories, growing at the same rate for the same duration of time (Leigh and Terranova, 1998; King et al., 2011). Rate differences determine the interspecific variation in adult lemurid body sizes, with most species growing for similar lengths of time (Leigh and Terranova, 1998). This ontogenetic monomorphy is consistent with hypothetical models that link lemurid growth and dimorphism to evolutionary disequilibrium if extant lemurs lived until recently in socially bonded pairs (van Schaik and Kappeler, 1996), as well as to tight environmental regulation of life history that limits SSD (e.g., Wright 1999).

The underlying processes linking behavior, growth, and SSD are less understood in lorisoids (i.e., lorises and galagos). Lorises exhibit "slow" life histories with low basal metabolic rates (BMR), late ages at sexual maturity, and long gestation lengths, lactation periods, and interbirth intervals (Hildwein and Goffart, 1975; Müller, 1985; Rasmussen and Izard, 1988; Isler and van Schaik, 2006). It was shown previously that galagos grow faster and for a shorter duration of time than lorises and that BMR has a stronger influence on loris life history than does either brain size or body mass (Rasmussen and Izard, 1988). Kappeler (1996) discounted this explanation as a major influence on life history variation in strepsirrhines and instead favored more central roles of maternal investment and maternal body mass. Further explorations of brain size, BMR and growth in the lemurs have shown little independent influence of each of these factors on the ontogeny of body size (Barrickman and Lin, 2010).

The growth patterns of lorisoids are thus unresolved. These strepsirrhines (70–1,200gm) are distributed throughout Africa and Asia and across a variety of habitat types: the galagos (*Galagoides, Galago, Euoticus, Sciurocheirus*, and *Otolemur*) and pottos (*Perodicticus* and *Arctocebus*) are confined to mainland Africa, with the lorises (*Loris* and *Nycticebus*) distributed throughout Asia (Nekaris and Bearder, 2010). Using an iterative piecewise regression growth model, we characterize growth in body mass and the ontogeny of SSD in *Galago moholi, Otolemur garnettii, Loris tardigradus, Nycticebus coucang*, and *N. pygmaeus*. We test the hypotheses that sexual dimorphism in galagos is a result of differences in the duration of growth (bimaturism) and that the monomorphic lorises show lemur-like growth trajectories with no sex differences in either the rate or duration of growth. In documenting the pathways that produce sexual dimorphism in the lorisoids (or lack thereof) we can begin to evaluate how different selective pressures are at work throughout ontogeny in these two lorisoid groups. We then compare the growth profiles of lorises and galagos to published data on lemurid growth to evaluate trends in strepsirrhine growth and examine clade level differences in the duration and rate of growth to adult body mass. An ontogenetic approach allows us to examine how selection has shaped variation in strepsirrhine growth, adult SSD, and how this relates to social and environmental constraints.

MATERIALS AND METHODS

Longitudinal data on body mass were transcribed from Duke Lemur Center records (1979–2007) for 256 captive individuals (7,000 individual data points) of *Galago moholi* (southern lesser galago), *Otolemur garnettii* (thick-tailed greater galago), *Loris tardigradus* (slender loris), *Nycticebus coucang* (slow loris), and *Nycticebus pygmaeus* (pygmy slow loris; Table 1). All animals used in this study were assumed healthy at the time when body mass was recorded. When noted by caretakers, obese, sick, or pregnant individuals were excluded. Obese individuals were defined as those animals with adult body mass greater than two standard deviations

TABLE 1. Comparative measures for each species ± standard error

	Galago moholi (n = 57/37)	*Otolemur garnettii* (n = 37/34)	*Loris tardigradus* (n = 17/17)	*Nycticebus coucang* (n = 17/18)	*Nycticebus pygmaeus* (n = 12/10)
Birth Mass (gm) ± SE	**M: 13.95 ± 0.55 (6)**	**M: 53.2 ± 3.989 (5)**	**M: 10 (1)**	**M: 51.5 ± 3.58(5)**	**M: 22.75 ± 0.65 (6)**
	F: 13.1 ± 3.10 (2)	**F: 48.3 ± 2.05 (5)**	**F: 10.94 ± 1.04 (5)**	**F: 50.96 ± 2.80 (5)**	**F: 22.59 ± 1.86 (4)**
Female Adult Mass (gm) ± SE	**158.6 ± 0.85**	**983.1 ± 5.60**	**179.5 ± 1.38**	**1199.3 ± 9.19**	**525.1 ± 4.60**
	155.1 ± 3.9 (20)[a]	1027.5 ± 28.1 (19)[a]	192.8 ± 7.6 (8)[a]	1194.7 ± 235.48 (15)[a]	363.5 ± 16.5 (4)[a]
	162.8 ± 3.64 (20)[b]	805 [604 – 985, (11)][b]	181 ± 9.35 (12)[c]	637 ± 18.39 (11)[b]	422 ± 8.83 (97)[b]
Male Adult Mass (gm) ± SE	**184.3 ± 1.05**	**1166.2 ±9.57**	**183.0 ± 1.05**	**1138.7 ± 9.39**	**496.3 ± 3.91**
	180.6 ± 4.4 (25)[a]	1212.2 ± 48.0 (17)[a]	191.8 ± 6.7 (10)[a]	1207.0 ± 201.3 (14)[a]	440.8 ± 14.8 (5)[a]
	186 ± 3.643 (20)[b]	846 [690 – 1060][b]	205 ± 5.22 (22)[c]	737 ± 39.24 (8)[b]	418 ± 11.71 (70)[b]
ISD (M/F)	**1.16**	**1.19**	**1.02**	**0.95**	**0.95**
	1.16[a]	1.18[a]	1.00[a]	1.01[a]	1.21[a]
	1.14[c]	1.05[c]	1.13[c]	1.15[c]	0.99[d]
Basal Metabolic Rate (VO_2 ml/h)[e]	198.0	412.3	107.4	272.6	171.9

Mean values obtained from the growth models in this study are in bold, and sources for comparative data are referenced below. Study sample sizes are provided below the species name (M/F) and for comparative data in parentheses after the sex-specific value.
ISD = Index of Sexual Dimorphism (Male mass/Female mass).
[a] Kappeler (1991).
[b] Compiled in Nekaris and Bearder (2010) (wild-caught body mass).
[c] Kar Gupta (2007).
[d] Streicher (2004).
[e] Compiled in Isler and van Schaik (2006).

above the mean (Terranova and Coffman, 1997), and those data points were removed from analysis.

The use of captive body masses has the advantage of known exact ages and health histories within a controlled environment. It is assumed that captivity affects males and females, as well as all species, equally (Leigh, 1992). Captivity can accelerate life history parameters such as the age at first reproduction; however, body masses of captive animals reflect those of wild populations (Leigh, 1994a; Terranova and Coffman, 1997). While captive data may not demonstrate the absolute velocity of growth in wild counterparts, comparisons between sexes and between species within captive populations are expected to exhibit the same relative patterns of growth that would be seen in comparisons of wild populations.

Mass is presented in grams and age in days. As complete ontogenetic sequences of body mass are not available for each individual in this study, our data represent a mixed longitudinal dataset. Data were separated by sex for each species and analyzed cross-sectionally (Gasser et al., 1984; Eubank, 1999). Treating the data cross-sectionally obscures information regarding individual variation in growth; however, it provides sufficiently large sample sizes to allow the comparison of ontogenetic patterns both between sexes and between species, both of which are goals of this study.

Average sex-specific adult body masses were calculated from the iterative regression model (described below) and an index of sexual dimorphism (ISD) was created by dividing the average adult male body mass by the average adult female body mass for each species. Sex-specific average birth mass was calculated as the average mass of individuals that were weighed within the first four days since birth (day zero through to day three). No individual was included in this average more than once.

The ontogeny of adult body mass was modeled in two steps. First, nonparametric cubic spline regressions (Eubank, 1999) were fit to the data in R 2.6.2 (R Core Development Team, 2011) to identify growth spurts or changes in velocity and acceleration that were inconsistent with a linear growth model during the first phase of life (Gasser et al., 1984; Müller, 1988). Nonparametric regression or smoothing techniques (including spline models and loess regression) are commonly used to describe growth and development (Gasser et al., 1984; Shea, 1985; Müller, 1988; Leigh, 1994b; Leigh and Shea, 1995; Leigh and Terranova, 1998). Cubic spline smoothing offers a simplified goodness of fit, a more global fit, and direct derivative calculation. The first derivative was then used to generate pseudo-velocity curves to evaluate timing and velocity of growth. The cubic spline regressions indicated that a simple two-phase growth model would fit these data. Growth in these species could subsequently be modeled as: 1) as a period of rapid but decelerating growth until and 2) the final asymptotic adult body mass is reached.

MODEL FITTING

To understand how rate and duration differences affect the development of body mass and SSD, an iterative piecewise regression model was fit to the data in R 2.6.2 based on the assumption of a two-phase growth model from the cubic splines. This model allows for the direct and quantitative parameterization of development including growth rate, time to asymptotic adult body

TABLE 2. Growth curve parameters from the iterative growth model used in this study

Species	Sex	Duration of growth (days)	Growth rate-mean method (gm/day)	Growth rate-regression method (gm/day)	Adult mass (gm)	R^2
Galago moholi	F	**262.0 (238.5–303.1)**	0.557 (0.483–0.610)	0.512 (0.424–0.580)	**158.6 (156.9–160.2)**	0.851
	M	**319.0 (296.0–348.0)**	0.526 (0.485–0.567)	0.479 (0.431–0.525)	**184.3 (182.3–186.4)**	0.834
Otolemur garnettii	F	**444.5 (418.1–466.0)**	2.10 (2.00–2.23)	1.96 (1.83–2.12)	**983.1 (972.0–994.2)**	0.880
	M	**529.0 (472.0–620.0)**	2.10 (1.79–2.31)	1.96 (1.63–2.19)	**1166 (1150–1187)**	0.877
Loris tardigradus	F	279.2 (253.0–427.0)	0.603 (0.393–0.666)	0.599 (0.385–0.661)	179.5 (177.0–182.4)	0.769
	M	302.0 (234.8–386.2)	0.573 (0.449–0.735)	0.595 (0.458–0.745)	183.0 (181.0–185.1)	0.764
Nycticebus coucang	F	**436.7 (380.0–523.4)**	2.62 (2.21–3.00)	2.64 (2.14–3.10)	**1199 (1181–1217)**	0.597
	M	**366.0 (265.0–410.7)**	2.97 (2.66–4.11)	3.06 (2.70–4.24)	**1139 (1121–1158)**	0.683
Nycticebus pygmaeus	F	**418.4 (376.0–448.8)**	**1.20 (1.12–1.33)**	**1.20 (1.10–1.34)**	**525.1 (515.3–533.4)**	0.939
	M	**294.1 (265.2–392.9)**	**1.61 (1.20–1.77)**	**1.64 (1.25–1.80)**	**496.3 (488.6–503.9)**	0.928

Values in parentheses are bootstrapped 95% confidence intervals. Bold type indicates a significant difference between males and females at $\alpha = 0.05$.

mass, asymptotic body mass, etc. Similar to the piecewise regression models used by Leigh (1994b) and Leigh and Terranova (1998), the first segment of the regression models growth prior to age at growth cessation and the second portion of the regression equation models asymptotic adult body mass.

The model is fit as follows. An arbitrarily selected age is used to divide the dataset into a growth portion (all data points younger than that age) and an adult portion (all data points that age and older). The mean of all masses in the adult portion is calculated to represent asymptotic adult body size. A quadratic model is then fit to all data points in the growth portion of the data set. The quadratic model is constrained to intersect the arbitrarily selected age at adult body size at the calculated mean body size. It is further constrained such that only the ascending portion of a quadratic may be modeled; that is, the model does not allow for a decrease in body size to follow the initial increase. The sum of squared residuals (SSR) from the two-piece model is then calculated for all data points as a measure of goodness of fit.

An iterative procedure recalculates the model by incrementally increasing the arbitrarily selected age at adulthood from just after birth until the oldest datum represented in the sample in increments of tenths of a day. The cutoff age with the lowest SSR is identified, and the corresponding model parameters identify that model, which minimizes error about the two portions of the model. The SSR is then used to calculate the corresponding R^2 value for the two-piece model.

To calculate a measure corresponding to growth rate, Leigh and Terranova (1998) used the first principal component in a multivariate analysis of the intercept, linear coefficient, and quadratic coefficient of a quadratic growth curve. Here we use a slightly different approach, calculating mean growth rate as follows:

$$\text{mean growth rate} = \frac{(\text{asymptotic adult mass} - \text{birth mass})}{\text{duration of growth}}$$

Because data points are scarcer at the beginning of the growth portion of the model than in the asymptotic adult mass portion of the model, model-based estimates of birth mass (i.e., the *y*-intercept of the growth portion of the model) are subject to greater error than estimates of asymptotic adult mass. Consequently, we calculate mean growth rate in two ways based on two separate estimates of birth mass. The first measure uses the *y*-intercept of the growth model as birth mass, and the second method calculates birth mass as mean body mass in all individuals weighed within the first four days after birth. Results are compared and yield similar overall patterns.

These models were run independently for each sex for each species. Ninety-five percent confidence intervals for model parameters and for differences in model parameters between sexes and taxa were calculated by bootstrapping each sex- and species-specific model 5,000 times. This approach allowed for tests of differences in the rate of growth, duration of growth, and adult body mass between sexes, as well as for tests of interspecific differences in the rates and duration of growth.

This iterative model was also fit to the lemurid body mass data from Leigh and Terranova (1998) for comparisons of growth among strepsirrhines. Because relatively fewer data points are available for the growth portion of the curves in these taxa as compared to the lorisoids, model-based estimates of birth mass are poorly constrained. Thus, inclusion in this analysis was limited to lemurid species that had at least one mass measurement within the first four days after birth for at least one sex, or published neonatal body mass. When birth mass was available for only one sex, that birth mass was applied to both sexes for calculating mean growth rates.

RESULTS

Intraspecific ontogenetic variation

Descriptive statistics for birth mass, adult mass, indices of sexual dimorphism, and BMR are presented in Table 1. Consistent with previous work (Smith and Leigh, 1998), no significant SSD is present at birth; therefore, all subsequent differences in SSD are the result of postnatal growth (Table 1). Significant SSD is present in *Galago*, *Otolemur*, and *Nycticebus* while *Loris* displays monomorphic adult body mass.

The growth parameters from the iterative model are reported in Table 2. Dimorphism in *G. moholi* and *O. garnettii* is a result of bimaturism: males and females grow at the same rate, however, females grow for only 82–84% of the duration of time that males grow (Table 1; Fig. 1). In *G. moholi*, the growth phase is completed at an average of 262 days for females, while males continue to grow until, on average, they reach 319 days and a mean body mass that is 16% larger (Table 1). *Otolemur garnettii* males grow for an average of 84.5 days longer than females to a mass that is 19% larger.

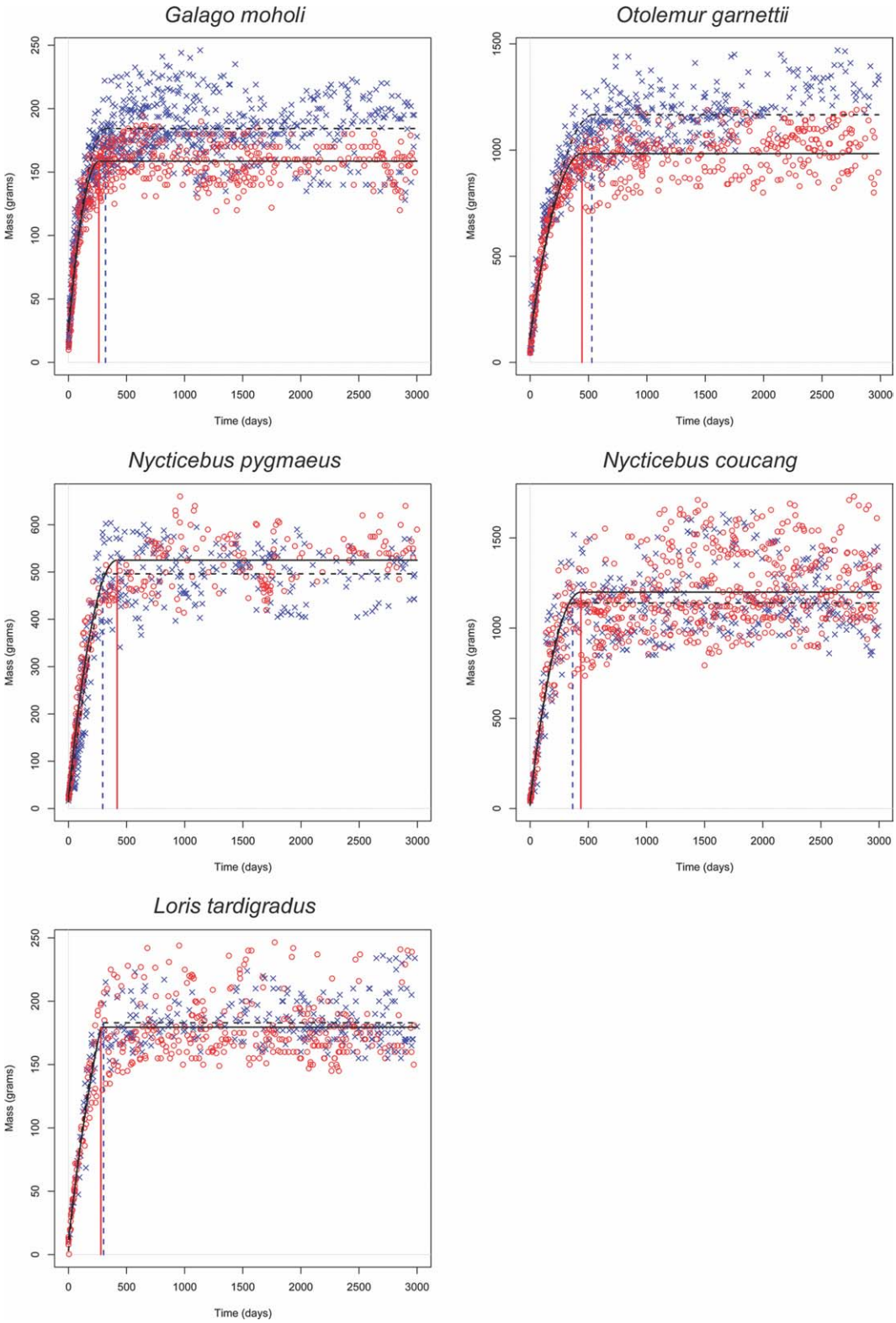

Fig. 1. Composite growth curves for *Galago moholi*, *Otolemur garnettii*, *Loris tardigradus*, *Nycticebus coucang*, and *Nycticebus pygmaeus*. Females are indicated by an open red circle and a solid line; males by a blue x and a dashed line. Vertical lines indicate the end of the growth period and the point at which asymptotic adult body mass is reached. Note that y-axes of the bivariate plots vary among species.

TABLE 3. Comparisons of rate and duration of growth for similarly sized galagos and lorises with summarized patterns for growth duration and growth rate

	Growth Duration	Growth Rate
Galago moholi and *Loris tardigradus* males (smaller-bodied)	No significant difference	No significant difference
Otolemur garnettii and *Nycticebus coucang* males (larger-bodied)	*Otolemur* males grow significantly longer	*Nycticebus* males grow significantly faster

Interspecific differences in growth parameters are assessed using bootstrapped 95% confidence intervals.

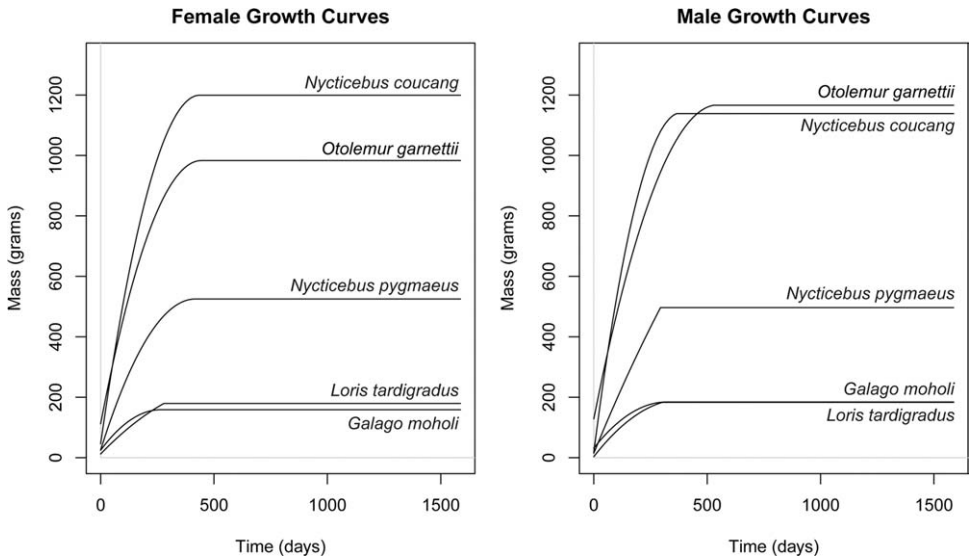

Fig. 2. Interspecific comparisons of lorisoid growth curves.

The growth model also shows that, contrary to our prediction of lemurid-like growth for all lorises, only *L. tardigradus* follows a growth trajectory typical of monomorphic lemurids, with males and females growing at the same rate (0.57–0.60 gm/day) for the same period of time (279–302 days; Table 2; Fig. 1). Note that growth rates calculated using the two methods in this study are highly similar (Table 2). The 5–6% larger females in the *Nycticebus* species are a result of reversed bimaturism (*N. coucang*), and a combination of rate and duration differences (*N. pygmaeus*). *Nycticebus coucang* females grow 83 days longer than males at the same rate to attain an adult body mass of 1,200 grams (cf. 1,139 grams for males; Table 2; Fig. 1). Interestingly, contrary to previous studies from the same captive colony that report marked SSD in *N. pygmaeus* with males over 20% larger than females (Kappeler, 1990, 1991), our *N. pygmaeus* sample shows low female-biased SSD that is consistent with wild body masses (Streicher, 2004). Larger female size is due to sex differences in both duration and rate of growth (Table 2, Fig. 1). *Nycticebus pygmaeus* females grow for a longer period of time than do males, finishing growth 113 days later, although they do so at a slower rate than males.

Interspecific ontogenetic variation

Comparisons within Lorisoidea. Males of *G. moholi* and *L. tardigradus* grow to similar adult masses, as do *O. garnettii* and *N. coucang*. For both pairs of similarly sized species, the galagid has a BMR substantially higher than that of the lorisid (BMR of *G. moholi* 84.5% greater than that of *L. tardigradus*, BMR of *O. garnetti* 51.2% greater than that of *N. coucang*, Table 1). Despite these differences in BMR, the comparisons show that loris species do not grow at slower rates or for longer durations than do galagos (Table 3; Fig. 2). *Galago moholi* and *L. tardigradus* males grow at similar rates and for similar lengths of time to reach adult mass, with no significant difference in either parameter (Fig. 2; Tables 2 and 3). For the larger species in this sample (*O. garnettii* and *N. coucang*), male *N. coucang* grow at significantly faster rates than *O. garnettii* males, while *O. garnettii* males grow over a significantly longer time than *N. coucang* males (Tables 2 and 3).

The size difference between *Nycticebus* species is a result of the differences in the rate of growth (Table 2): *N. coucang* grows twice as fast as *N. pygmaeus*, with females of each species reaching adult body mass after either 418 (*N. pygmaeus*) or 437 days (*N. coucang*), and males after either 294 (*N. pygmaeus*) or 366 days (*N. coucang*). Bootstrapped 95% confidence intervals for difference in growth parameters between the two species indicate that the difference in growth rate between species is significant for both sexes. The difference in duration of growth between species is not significant for either sex, likely due to the large variability in sex-specific adult body mass in *N. coucang* (Fig. 1) and thus a poorer fit and larger confidence intervals in the *N. coucang* growth model (Table 2).

Comparisons between Lorisoidea and Lemuridae. The lemurids analyzed here have higher absolute growth rates and longer durations of growth than the smaller-

TABLE 4. Growth parameters as identified by the iterative two-piece model used in this study for comparison of lorisoid and lemurid growth patterns

Clade	Species	Sex	Mean birth mass (gm)	Asymptotic adult mass (gm)	Duration of growth (days)	Mean growth rate (gm/day)	*n* growing	*n* adult	R^2
Lemuridae	*Eulemur coronatus*	F	67[a]	1721.9	1027	1.61	49	81	0.727
		M	67	1719.1	920	1.80	62	81	0.743
	Eulemur flavifrons	F	92	2497.2	876	2.75	43	19	0.921
		M	79.5	2279.5	578	3.81	26	77	0.929
	Eulemur sanfordi	F	71	2267.2	988	2.22	12	27	0.764
		M	94	2105.7	579	3.42	9	18	0.861
	Eulemur macaco	F	79.5	2633.3	834	3.06	100	165	0.853
		M	79.5[a]	2433.5	791	2.98	106	218	0.721
	Eulemur mongoz	F	63.17	1748.2	1066	1.58	139	155	0.829
		M	68.83	1774.5	1063	1.60	95	219	0.594
	Eulemur rubriventer	F	89	2037.1	528	3.69	14	42	0.939
		M	72.5	1993.4	696	2.76	38	44	0.955
	Varecia variegata	F	102.1[b]	3740.8	1175	3.11	58	98	0.662
		M	102.1[b]	3564.8	976	3.56	55	123	0.806
	Hapalemur griseus	F	45.2[c]	917.8	706	1.13	44	114	0.974
		M	45.2[c]	1036.0	777	1.15	53	101	0.971
Lorisoidea	*Galago moholi*	F	12.8	158.6	262	0.56	153	367	0.851
		M	16.46	184.3	319	0.53	270	541	0.834
	Loris tardigradus	F	11.21	179.5	280	0.60	70	342	0.769
		M	10	183.0	302	0.57	44	286	0.764
	Nycticebus coucang	F	54.39	1199.3	437	2.62	105	615	0.597
		M	50.42	1138.7	366	2.97	76	359	0.683
	Nycticebus pygmaeus	F	23.48	525.1	418	1.20	131	161	0.939
		M	23.67	496.3	294.1	1.61	191	220	0.928
	Otolemur garnettii	F	49.93	983.1	445	2.10	176	370	0.880
		M	53	1166.2	529	2.10	198	314	0.877

Sample sizes are given for number of data points in the growth portion of the model (*n* growing) and adult portion (*n* adult).
[a] Birth mass based on value for opposite sex.
[b] Birth mass taken from Kappeler and Pereira (2003).
[c] Birth mass taken from Wright (1990).

TABLE 5. Regression parameters for the log rate and log duration of growth regressed againstadult body mass presented in Figure 3

		Lorisoidea	Lemuridae
Growth Rate	Intercept	−2.01	−2.704
	Slope (95% C.I.)	0.787 (0.666–0.908)	0.929 (0.565–1.292)
	R^2	0.966	0.682
	F-statistic$_{df}$	$255.8_{1,8}$	$30.01_{1,14}$
	p-value	<0.001	<0.001
Duration of Growth	Intercept	1.946	2.392
	Slope (95% C.I.)	0.227 (0.109–0.346)	0.159 (−0.206–0.524)
	R^2	0.710	0.059
	F-statistic$_{df}$	$19.62_{1,8}$	$0.8748_{1,14}$
	p-value	0.002	NS

bodied lorisoids (Table 4). However, adult body mass is widely divergent among these groups with an order of magnitude difference between the smallest and largest species in the sample. When relationships with adult body mass are taken into account, 95% confidence intervals of the log of rate regressed on log body mass indicate that scaling relationships for the rate of growth are the same for the lorisoids and lemurids (Table 5, Fig. 3A). As a group, lorisoid growth rates are shifted higher than the lemurids and reflect rapid growth to a lower overall body size (Fig. 3A). The scaling of growth duration to body mass is more challenging to interpret due to the non-significant relationship present in lemurids (Table 5). In general it appears that lorisoids grow for a shorter duration than do lemurids (Table 5, Fig. 3B).

DISCUSSION

SSD and adult body masses of *G. moholi, O. garnettii*, and *L. tardigradus* are consistent with previous studies on these species (Table 1), with the two *Nycticebus* species as notable exceptions (Kappeler, 1990, 1991, 1996; Wiens and Zitzmann, 2003; Nekaris and Bearder, 2010). The 5–6% reversed SSD of *N. coucang* and *N. pygmaeus* in this captive sample fits with general observations of the slow lorises that show either sexual monomorphism or larger females (Streicher, 2004). Differences in *N. pygmaeus* body mass and SSD between this study and Kappeler (1990, 1991) likely reflect the sample sizes of the analyses. It is interesting, however, that there are such pronounced differences in the *Nycticebus* species

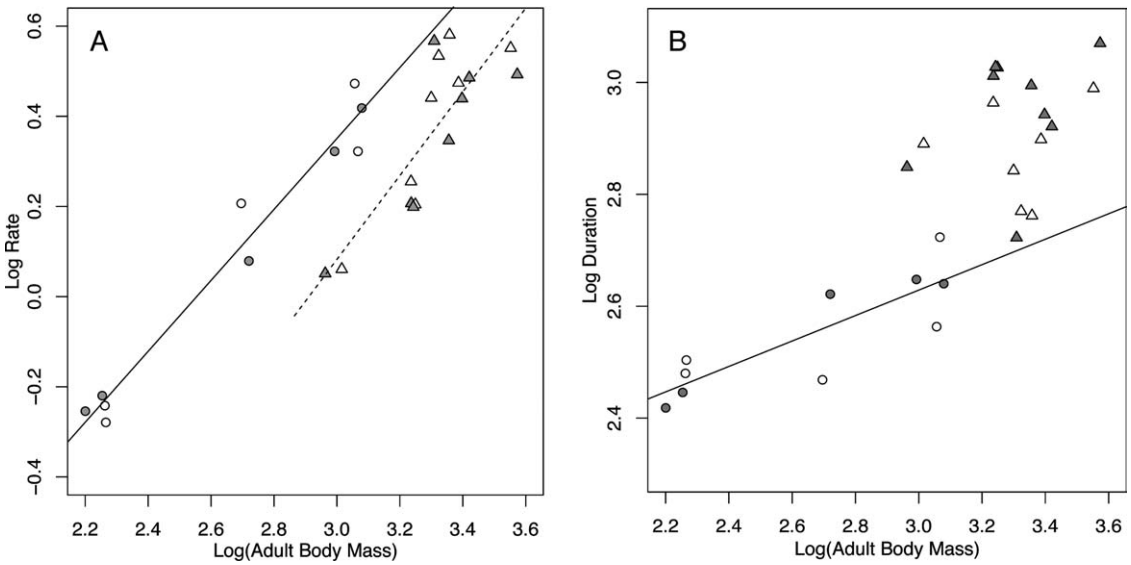

Fig. 3. Logged values of mean growth rate (**A**) and duration of growth (**B**) for lorisoids and lemurids plotted against the log of average adult body mass (Table 4). Circles and a solid regression line indicate lorisoids, and triangles and a dashed regression line indicate lemurids; females are shown as open symbols and males are filled in gray. Regression parameters are presented in Table 5.

between these results and those of Kappeler (1990, 1991), considering both studies include animals from the Duke colony. Average adult body masses were calculated differently between the two studies. However, masses are similar for the other species between the studies, indicating that the differences in method do not account for the discrepancy. Differences in *N. coucang* may be a result of more variability in adult body weight in this species, indicated by lower model R^2 values. The cause of the variation in body mass of this species is unknown.

Galagos show higher degrees of dimorphism than do *Nycticebus* species. Galago males are up to 20% larger than females, and *Nycticebus* females are between 5 and 6% larger than males. The degree of SSD for galagos is similar to that for polygynous anthropoids (Plavcan and van Schaik, 1997). Differences in galago and loris SSD likely are related to differences in the dispersed social systems of these two groups. The relatively few data on social organization of the groups, primarily radio tracking studies and range overlap analysis, suggest that galagos tend to show dispersed multi-male/multi-female group whereas many loris species are organized in a dispersed unimale/unifemale system (Nash and Harcourt, 1986; Bearder, 1999; Wiens and Zitzmann, 2003; Nekaris and Bearder, 2010).

Bimaturism and galago dimorphism

Bimaturism characterizes both galago species in our study, with *G. moholi* and *O. garnettii* males growing at the same rate, but for longer periods of time than females. SSD levels in the galagos is consistent with predictions by Jarman (1983) and suggests that larger male size does confer a mating advantage, although the overall small size of the species may also permit alternative reproductive tactics based on locomotor agility and crypsis (Lindenfors, 2002; Lawler et al., 2005). During the mating season, wild *G. moholi* males increase both body mass and testicle size, and the largest males have the highest observed mating success (Pullen et al., 2000). However, Pullen et al., (2000) also found strong evidence of sperm competition, with two-thirds of females mating with multiple males during estrus. Thus it is difficult to identify the relative strength of contest and scramble competition for mating opportunities among *G. moholi* males, and it remains to be seen whether selection may favor both larger males (through contest competition) and smaller, more cryptic males (through scramble competition).

Ontogenetic diversity in the lorises

This study demonstrates that common growth patterns in the development of monomorphism among primate species may not reflect common causes. Monomorphism as exhibited by *Loris* results from males and females growing at identical rates for similar durations. In this way, male and female *Loris* exhibit ontogenetic trajectories similar to those of lemurids (Leigh and Terranova, 1998). The dispersed social organization of *L. tardigradus* is unknown, but other *Loris* species show variability in the demographics of their dispersed social groups. The ontogenetic trajectory shared by *Loris* and the lemurs may reflect the most common way for monomorphic, and potentially pair-bonded strepsirrhines to grow.

In contrast, the growth pattern displayed in *Nycticebus*, with females growing for a longer duration at slower rates than males to achieve only slightly greater adult mass is similar to ontogenetic patterns found in *Aotus, Leontopithecus, Callimico, Hylobates*, and *Symphalangus* (Leigh, 1992). The social data available suggest that slow lorises live in semi-dispersed unimale/unifemale groups (Nekaris and Bearder, 2010), likely with low intra-sexual contest competition. If dispersed unimale/unifemale social groups are on the same competitive landscape as diurnal pair-bonded primates, low levels of dimorphism are predicted. Additionally, decoupling rate and duration of growth may allow females to adjust growth rates to reach adult body mass at a more conservative pace over a longer period of time and mini-

mizes the competition with males for the same limited resources (Ralls, 1976; Leigh and Shea, 1996).

The results presented here mirror those of Rasmussen and Izard (1988) in that both found differences in growth profiles between some comparably sized loris and galago species; however, the two studies failed to find the same patterns. Our results show that lorises do not exhibit slower growth rates when compared to galagos, but instead rates of growth are similar, and in some instances growth rates of lorises are faster than galagos of similar adult size and higher BMR (Fig. 2; Table 1). The disparity between these two studies may be linked to their averaging of male and female growth curves that potentially masks sex differences in growth and decreases overall growth constants for lorises. While the ontogeny of adult body mass cannot be accounted for in a simple way by variation in either diet or BMR, the relatively slow life history of lorises may still be related to these variables.

Strepsirrhine growth

Except for growth spurts, strepsirrhine primates encompass nearly all of the ontogenetic pathways yielding SSD that have been described for primates. Lorisoid growth includes the typical anthropoid pattern of bimaturism (*Galago and Otolemur*) and reversed SSD through a combination of bimaturism and mixed rate and duration differences (*Nycticebus spp.*). Monomorphic adult body masses are the result of typical lemurid development in *Loris* with identical durations and rates of growth for males and females. When average growth rates are compared between the lorisoids and lemurids, there is considerable overlap in the absolute rate at which they grow to adult body mass. Overall, lorises and galagos grow faster and for shorter durations than lemurids. Lorisoids have higher growth rates for their body mass than do lemurids, and a positive relationship with body mass is apparent (Fig. 3A). A greater distinction is seen in duration of growth with the larger bodied lemurs growing for longer. However, the lemurid relationship between adult body mass and the duration of growth complicates the interpretation of these results. It is interesting to note that the positive scaling relationship present in the lorisoids between duration of growth and body mass is absent in the lemurids (see Table 5, Fig. 3B). This is consistent with previous work on the lemurids that points to tight links between growth to adult body mass and environmental constraints on the lack of SSD (Leigh and Terranova, 1998; Wright, 1999). The results presented here for these two groups, especially the absence of a significant relationship between growth duration and overall size for lemurids suggests that a broader taxonomic survey could reveal more about patterns of strepsirrhine growth.

The few data that exist on the dispersed nature of the galago and loris social systems, and the potential for intrasexual competition, appear to reflect the distribution of SSD in these species. However, there are still many unanswered questions of how loris and galago social organization shapes their biology, and addressing these requires more data on social interactions and mating system. Future analyses of the ontogeny of adult body mass and SSD in the indriid and cheirogaleid primates, as well as the African lorises, will help clarify how the diversity of strepsirrhine development reflects social and ecological constraints.

ACKNOWLEDGMENTS

The authors thank Leanne Nash, Steve Leigh, and Randy Eubank for helpful discussions and advice, as well to Kate Ihle and three anonymous reviewers for comments that greatly improved this manuscript. Sarah Zehr (Duke Lemur Center) kindly supplied additional data. Special thanks are due to the care staff of the Duke Lemur Center who have provided invaluable information on primate behavior and evolution through their dedication to breeding, research, and maintenance of the world's strepsirrhine species. This is Duke Lemur Center publication number 1204.

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