RESEARCH ARTICLE

An empirical estimate of the generation time of mouse lemurs

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Abstract

The generation time of organisms drives the rate of change in populations and across evolutionary times. In long-lived species, generation time should also account for overlapping generations, and the average age of parents has been proposed as a best approximation under these conditions. This study uses this definition to estimate the generation time of a widely studied small primate, *Microcebus murinus*, based on parentage data generated for a free-living population over a 6-year period in northwestern Madagascar. The average age of parents was calculated separately for mothers and fathers of three different offspring cohorts that differed in the degree of demographic uncertainty. In addition, adult survival rates were calculated for males and females based on long-term capture data from the same population to estimate the possible upper limits of generation time. Adult survival was low with only 44% of adult females and 38% of adult males being recaptured at the beginning of their second breeding season. The average age of mothers was 1.56–1.91 years, pointing toward a 2-year female generation time due to the high proportion of 1-year old mothers in all three cohorts. Female generation time estimates were fairly stable across the three offspring cohorts. In contrast, the average age of fathers differed by more than 1 year from the first to the third offspring cohort (1.71–2.83 years) pointing toward a 3-year generation time, but also suggesting a higher degree of demographic uncertainty in the early years of the study. For future modeling purposes, we, therefore, propose to use the average, 2.5 years, of male and female values as new estimate for the generation time of mouse lemurs.

KEYWORDS
Madagascar, *Microcebus murinus*, molecular evolution, sex difference, survival

1 | INTRODUCTION

The generation time of organisms, intuitively thought of as the average time span between two consecutive generations, though having multiple definitions, is a central concept in biology. It is an essential parameter driving the rate of change within populations and across evolutionary timescales. Generation time has been shown to correlate negatively with population size (Chao & Carr, 1993) and metabolic rate (Martin & Palumbi, 1993), whereas it increases with body size (Martin & Palumbi, 1993; Zimmermann & Radespiel, 2015) and various life history traits (e.g., lifespan, Nabholz, Glemin, & Galtier, 2008). Moreover, species with shorter generation time can experience more rapid population dynamics and may be more prone to stochastic demographic processes (Allendorf, Luikart, & Aitken, 2013). Variation in generation time has furthermore been associated with variation in mutation rates and thus the rate of molecular evolution (Martin &

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Palumbi, 1993; Thomas, Welch, Lanfear, & Bromham, 2010; Tsantes & Stelper, 2009; Wu & Li, 1985). Differences in substitution rates of rodents and artiodactyls, for example, have been attributed to a shorter generation time in the former (Laird, McConaughy, & McCarthy, 1969). Such findings have inspired the generation time effect hypothesis stating that species with a shorter generation time have a faster molecular clock than those with a longer generation time, since they go through more generations per time unit (Li, Ellsworth, Krushkal, Chang, & Hewett-Emmett, 1996). Finally, generation time is strongly impacting various evolutionary parameters, such as the effective population size (Lawler, 2011) and the divergence times between taxonomic clades (e.g., Langergraber et al., 2012), or the inference of the demographic history of species or populations (e.g. Craul et al., 2009; Xue et al., 2015).

There are at least five ways to characterize and define the generation time in an organism (A–E). From a demographer's perspective, this could be (A) the time it takes for a population to grow by a factor of R_0, where R_0 is the net reproductive rate, (B) the average age of a cohort of parents who have produced offspring over their lifetime, or (C) the average age of parents of offspring in a population at a stable age distribution (Caswell, 2001). In a population that is at equilibrium (not growing or shrinking), the latter two estimates are equivalent. Such estimates of generation time are contingent on time scale, adult survival and sample size under consideration.

Two other estimates have been used as proxies for generation time: (D) Average length of the reproductive career which was estimated as the equivalent of the average adult lifespan (AAL) (Yoder et al., 2016) and calculated as AAL = $\alpha + [s/(1 − s)]$ with α being the age at maturity and s the expected adult survival rate (Lande, Engen, & Sæther, 2003). However, life expectancy or survival does not necessarily correspond to successful reproduction and such an estimate may, therefore, differ from the generation time that is relevant to understand the rate of evolutionary change in a population (Charlesworth, 1980). Finally, (E) the average age at first reproduction (e.g., Martin & Palumbi, 1993; Tsantes & Stelper, 2009; Weir & Schluter, 2008) is still widely used as a proxy for generation time, although this estimate seems inappropriate for species with over-lapping generations where older offspring start breeding in parallel to the continued reproduction of their parents, as is typical for many mammals and in particular primates. A considerable discrepancy between the "average female age at first reproduction" and the "average age of mothers" was already demonstrated in a comparative study across seven primate species (Bronikowski et al., 2016a) revealing that the "average age of mothers" exceeded the "age at first reproduction" by the factor 2.0–4.2 (Bronikowski et al., 2016b).

Among all these definitions, the "average age of parents" is regarded by many authors as the best available approximation of generation time (Allendorf et al., 2013; Charlesworth, 1980; Felsenstein, 1971; Hill, 1979) and will also be used in this study. Such an empirical measure allows for overlapping generations and takes into account possible age-dependent changes and potential sex-specific differences in reproductive success (Fenner, 2005; Webster & Wilson Sayres, 2016).

The aim of this study is to empirically estimate the generation time of the Gray Mouse lemur (Microcebus murinus) in a free-living population. Previously used generation times in this taxon vary considerably ranging from 1 year (e.g. G. L. Olivieri, Sousa, Chikhi, & Radespiel, 2008; Schad, Ganzhorn, & Sommer, 2005) approx-imating the age at first reproduction (Perret, 1982; Radespiel & Zimmermann, 2003; Zimmermann & Radespiel, 2015) to 3.0–4.5 years which was a previous rough estimate of the average length of the reproductive career in the wild (Hawkins et al., 2018; Yoder et al., 2016). Mouse lemurs (Microcebus spp.) can live up to 8 or even 10 years in the wild (Hämäläinen et al., 2014; Zohdy et al., 2014), although adult survival rates are generally low and yearly turnover rates can be high (Kraus, Eberle, & Kappeler, 2008; Radespiel, Sarikaya, Zimmermann, & Bruford, 2001). Under these conditions, adult survival is constraining the maximum age of parents and therefore impacts the generation time of mouse lemurs indirectly.

A major constraint for mouse lemur demographic research is that age determination is notoriously difficult. In general, mouse lemurs are seasonal breeders with infants being born during the rainy season (Rina Evasoa et al., 2018; Schmelting, Ehresmann, Lutermann, Randrianambinina, & Zimmermann, 2000). Surviving offspring can already reproduce in the subsequent mating season that starts toward the end of the next dry season (Kraus et al., 2008, Schmelting et al., 2000; Zohdy et al., 2014). At that time point, young adults cannot be reliably distinguished any more by their outer appearance from older animals (Schmelting, Zimmermann, Berke, Bruford, & Radespiel, 2007). Under these conditions, the first year of the capture of an individual is typically classified as the first year of its life (Schmelting et al., 2007). This classification is justified if preceding capture years ended with very high recapture rates and thus a good coverage of the population. However, complete knowledge of populations of mouse lemurs is never achieved, as immigrations from and emigrations to the surrounding forest and deaths can occur over the course of the year.

The discrepancies between the published generation time values of mouse lemurs raise concerns, as mouse lemurs are widely used as models to understand evolutionary processes for which generation time is highly influential. This includes studies on the drivers of species diversification (e.g., Blair, Heckman, Russell, & Yoder, 2014; G. Olivieri et al., 2007; Schneider, Chikhi, Currat, & Radespiel, 2010; Weisrock et al., 2010; Yoder et al., 2016), the influence of forest fragmentation on genetic structure (e.g., Aleixo-Pais et al., 2019; Sgarlata et al., 2018), and studies to infer the demographic history of populations in view of historic and anthropogenic habitat changes (e.g., Blair et al., 2014; G. L. Olivieri et al., 2008).

This study will estimate the generation time of male and female M. murinus based on the average estimated age of parents that was inferred for a free-living population during a 6-year study in north-western Madagascar (Lutermann, Schmelting, Radespiel, Ehresmann, & Zimmermann, 2006; Schmelting et al., 2007). To complement this estimation, adult survival rates will also be presented for both sexes of the same population, because they impact the maximum possible age of parents and therefore limit generation time indirectly.

2 | METHODS

2.1 | Study site and fieldwork

Details of the study site and the field methods are provided in Radespiel et al. (2001) and in Radespiel, Lutermann, Schmelting, Bruford, and Zimmermann (2003). Briefly, all individual *M. murinus* were sampled in the study site Jardin Botanique A (JBA, 46°48′ E, 16°19′S), a 30.6-ha patch of dry deciduous forest that is part of the Ankarafantsika National Park. Field data for this study were collected between 1995 and 2000 by means of capture-mark-recapture sessions spaced approximately 1 month apart during all dry seasons and during two intermittent rainy seasons (in detail: August to October 1995, September to November 1996, May to November 1997, May 1998 to April 1999, and August 1999 to November 2000). All animals were released on the evening of their day of capture at their individual capture position. All field methods and procedures were approved every 6 months by the relevant Malagasy authorities at that time (Commission Tripartite of the Malagasy government, Department des Eaux et Forêts (DEF), Association pour la Gestion des Aires Protégées (ANGAP)). The study adhered to the ASP Principles for Ethical Treatment of Non-Human Primates.

To calculate and evaluate male and female generation times defined as average age of parents in an open population of small cryptic animals with high population turnover, the following steps have been taken: (a) Age estimation of parents and offspring, (b) parentage analysis, and (c) evaluation of adult survival, as adult survival is constraining the maximum age of parents and therefore limits the generation time estimate.

2.2 | Age estimation of parents and offspring

The yearly study seasons always ended with very high recapture rates in the study area, ranging from 81.8% to 100% (mean = 90.5%) on the last two capture days in October across the study years 1995–1999 (unpublished results). This means that the vast majority of the yearly capture populations was known at the end of each study season, and thus new members appearing in the subsequent study season were most likely offspring or young immigrants born in the intermittent rainy season. For all individuals, the year of the first capture in the study area is known and this was operationally defined as their first year of life (Schmelting et al., 2007). For example, if an animal was first captured in the dry season of 1998, it was counted as 1-year old in that year. Whereas this can be regarded as a rather reliable age approximation in the case of offspring who were first captured from 1996 onwards, the age of parents captured during the first year of the study (1995) may be underestimated with this approach as they may have already lived in the study area before the current study.

Three approaches were taken to minimize the impact of this potential source of error: First, the age of parents was only calculated for infants born in 1997 or later. Second, the average parent age was calculated for three different offspring clusters that differed in their sensitivity to this demographic uncertainty (see below). Third, adult

survival rates were calculated for the 1996–1998 birth cohorts of the study population to evaluate the relevance of parental age uncertainty in 1995 in more detail (see below).

The age of parents was defined as the year of the first capture of offspring minus the year of the first capture of the parent. For example, if the offspring was first caught in 1999 and the mother was first caught in 1998, the mother's age was calculated as one (1999–1998 = 1), as the female gave birth presumably in her first year of life.

To evaluate the effect of the mentioned demographic uncertainty, the average age of parents was calculated separately for three infant cohorts which include (a) all offspring first captured between 1997 and 2000 (Cohort 1), (b) all offspring first captured between 1998 and 2000 (Cohort 2), and (c) all offspring first captured between 1999 and 2000 (Cohort 3). Due to the high yearly population turnover (see below), we assumed that the ages of parents from infants of 1997 carry a larger uncertainty than the ages of parents from infants of 1999. Therefore, the overall demographic uncertainty should decrease from Cohorts 1 to 3 and the direction and amount of change in the generation time estimate for these three cohorts indicate the relevance of demographic uncertainty for the results. We did not restrict the analyses to Cohort 3 with the highest demographic certainty, since sample sizes were smallest for that cohort.

The average age of parents (generation time) was calculated separately for mothers and fathers to explore the potential effects of different reproductive strategies between the sexes (Eberle & Kappeler, 2004a, 2004b; Lutermann, 2001; Schmelting et al., 2007). Mothers and fathers could contribute more than one datapoint to the analyses, as the sample size was defined by the number of infants for which parents could be determined. The age of fathers and mothers was compared for each cohort by means of a non-parametric the Mann–Whitney U test due to the lack of normality in the data set.

2.3 | Parentage analyses

Parentage data were directly taken from previous molecular analyses that were previously published in Lutermann et al. (2006), Radespiel et al. (2003), and Schmelting et al. (2007). Briefly, parentage was inferred based on a set of multilocus genotypes (compiled from eight polymorphic microsatellites) that were obtained for a total of 255 individuals (154 males and 101 females) captured between 1995 and 2000. For the purpose of this study, offspring were only included if they were captured for the first time in 1997 or later (*n* = 151, see above for reasoning).

Given that the animals living in JBA are part of an open population, parentage relationships cannot be solved with 100% certainty but can only be inferred with a certain likelihood (Marshall, Slate, Kruuk, & Pemberton, 1998). Our analytical approaches to reconstruct parentage relationships are described in detail in Radespiel et al. (2003) and in Schmelting et al. (2007). Briefly, maternity relationships were determined by (a) allowing for a maximum of one allelic exclusion, (b) a significant likelihood for a mother-offspring relationship (Goodnight & Queller, 1999), and (c) a significant LOD score (log likelihood of parentage) that was determined on the basis of 10,000 permutations with a significance

level of 0.05 (Lutermann, 2001; Radespiel et al., 2003). Paternities were determined with the software CERVUS 2.0 (Marshall et al., 1998) which was run with 10,000 simulation cycles, 1% error rate, 99.8% completeness of genotypes, and an estimated 53% (mothers) and 63% (fathers) of all possible parents sampled to determine the critical delta value (ΔLOD = 1.11) for an 80% confidence of paternity within the data set (for more details, see Schmelting et al., 2007).

Among the 151 investigated offspring, a total of 35 (15 males and 20 females) could be assigned to their most likely father (Schmelting et al., 2007), whereas 64 offspring (26 males and 38 females) could be assigned to their most likely mother (Lutermann, 2001). These numbers correspond to an overall success rate of 42.4% to identify the mother and of 23.2% to identify the father.

2.4 | Analyses of adult survival

Mouse lemurs have a large number of natural predators, such as snakes, owls, viverrids or raptors (reviewed in Blanco, Rasoazanabary, & Godfrey, 2015). As a consequence, the yearly population turnover in the study population was very high, with only between 24.7% and 44.9% of any yearly population being recaptured in the following year (Schmelting et al., 2007). The survival analysis applied the Kaplan–Meier method (Kramer, 1988) to three birth cohorts adding up to 168 individuals (106 males and 62 females) first captured between 1996 and 1998 in the same study population (Lutermann et al., 2006; Schmelting et al., 2007). The analysis was based on the assumption that the starting point (=birth) for an individual in the survival analysis was December of the year before its first capture, chosen as intermediate date within the birth period (November–January) that is typical for this population (Schmelting et al., 2000). This assumption was made as offspring from the two possible successive litters cannot be reliably distinguished from each other during the following mating season. It was assumed that only the percentage of the population that was recaptured (i.e. "survived") was present in the study site and those not recaptured (i.e., "deaths") were assumed to have disappeared. This previous analysis revealed that only 7% of the females and 14% of the males in this population survived until their third breeding season (Lutermann et al., 2006).

Since that analysis also incorporated infant and juvenile mortality, a separate step was added to derive the adult survival rates for the current study. Recapture rates (i.e., "survival") were calculated just for the subpopulation of those males and females that were included in the previous survival analysis and survived until their first breeding season (age: approximately 10 months, 85 males and 50 females).

3 | RESULTS

3.1 | Generation time

The average age of mothers for the three offspring cohorts was calculated as 1.56 ± 0.85 years (Cohort 1, n = 64 offspring), 1.71 ± 0.96 years (Cohort 2, n = 42 offspring), and 1.91 ± 1.12 years (Cohort 3, n = 22 offspring), respectively (Figure 1). Irrespective of

the cohort considered, more than half (54.5–62.5%) of all offspring had mothers of about 1 year of age. The assignable offspring of the three cohorts stemmed from 41 (Cohort 1), 33 (Cohort 2), and 18 different mothers (Cohort 3), respectively. Females first captured in 1995 were identified as mothers for 17.2% (n = 11) of the offspring from Cohort 1, but only for 11.9% (n = 5) of the offspring from Cohort 2 and for 13.6% (n = 3) of the offspring from Cohort 3.

The average age of fathers inferred for the three offspring cohorts was 1.71 ± 0.81 years (Cohort 1, n = 35 offspring), 2.13 ± 0.96 years (Cohort 2, n = 16 offspring), and 2.83 ± 0.68 years (Cohort 3, n = 6 offspring), respectively (Figure 2). In contrast to the females, the proportion of 1-year old fathers in the cohorts declined from 48.6% (Cohort 1) to 0% (Cohort 3). The offspring of these three cohorts were sired by 26 (Cohort 1), 14 (Cohort 2), and 5 different fathers (Cohort 3), respectively. Males first captured in 1995 were identified as fathers for 28.6% (n = 10) of the offspring from Cohort 1, but only for 18.8% (n = 3) of the offspring from Cohort 2 and for 16.7% (n = 1) of the offspring from Cohort 3.

Parent age did not differ significantly between mothers and fathers in the three offspring cohorts, although there was a statistical trend (with α set to .05) for a difference in Cohort 3 (the Mann–Whitney U test: $U_{cohort1} = 977.5$, $n_{m1} = 64$, $n_{f1} = 35$, $p = .299$; $U_{cohort2} = 249$, $n_{m2} = 42$, $n_{f2} = 16$, $p = .133$; $U_{cohort3} = 33.5$, $n_{m3} = 22$, $n_{f3} = 6$, $p = .068$).

3.2 | Adult survival

Of those individuals who survived until their first breeding season (=month 10; 85 males and 50 females), less than half (44% of females and 38% of males) were still recaptured at the beginning of their second breeding season (=month 22), less than a quarter (12% of females and 24% of males) were recaptured at the beginning of their third breeding season (=month 34), and less than 10% (2% of females
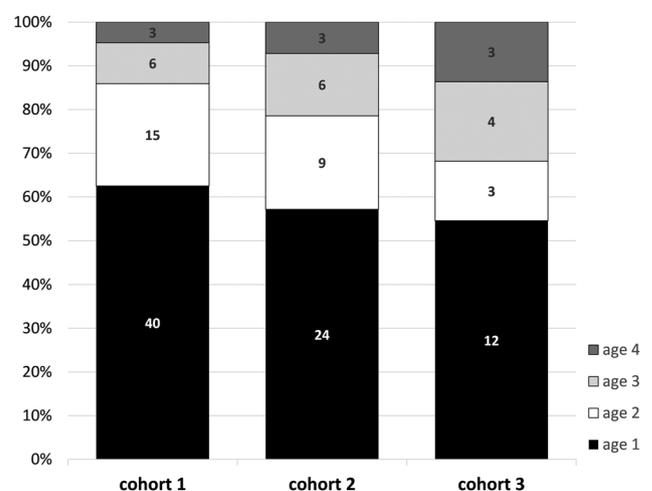

FIGURE 1 Relative age composition of mothers for the three different offspring cohorts used for analyses (see Section 2.2 for details). Absolute numbers of females falling into each age category are provided in each column partition. Black: 1-year old mothers, white: 2-year old mothers, light gray: 3-year old mothers, dark gray: 4-year old mothers
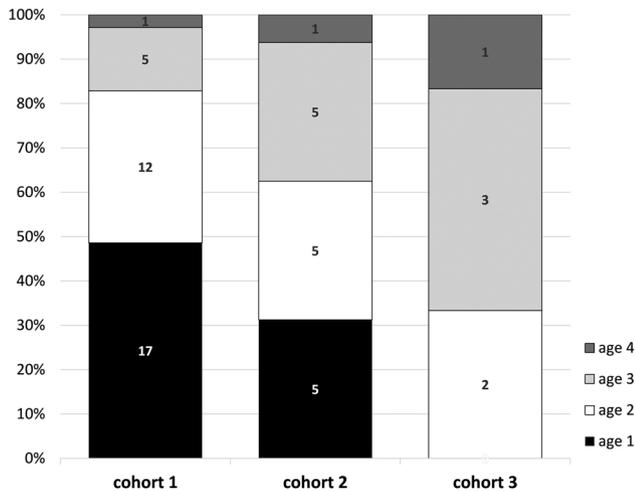
FIGURE 2 Relative age composition of fathers for the three different offspring cohorts used for analyses (see Section 2.2 for details). Absolute numbers of males falling into each age category are provided in each column partition. Black: 1-year old fathers, white: 2-year old fathers, light gray: 3-year old fathers, dark gray: 4-year old fathers

and 9% of males) were recaptured at the beginning of their fourth breeding season (=month 46). During the study period, only one individual (male) was recaptured until a presumed age of 6 years (Schmelting, 2001; Schmelting et al., 2007).

4 | DISCUSSION

This study was conceptualized to generate new and empirical values for the generation time of both sexes of the Gray Mouse lemur (M. murinus) as estimates of the average age of parents. Our analyses revealed that the empiric generation time estimates (females: 1.56–1.91 years, males: 1.71–2.83 years) fall in the range of values that have been used previously for the study species.

The new estimates are higher than the previously used "average age at first reproduction" (=1 year, e.g., G. L. Olivieri et al., 2008). This was expected, because there is a difference between the "average age at first reproduction" and the "average age of reproduction." The former, by definition, only accounts for the age of primiparous individuals, whereas the latter takes into account the entire reproductive career of individuals.

The new estimates were, on the other hand, smaller than a previously used estimate of "average length of the reproductive career" or "average adult survival" that was calculated for a population of M. rufus in eastern Madagascar (=3.0–4.5 years, Yoder et al., 2016). This was most likely due to the rather low survival rates in our study: Most adults (56% of females and 62% of males) did not even reach their second breeding season, and only very few could still be recaptured beyond their third breeding season (2% of females and 9% of males). The median adult survival (=the time to the loss of 50% of the individuals from the study site) in the study population was approximately 18 months (males) or 19 months (female), that is

below 2 years. These relatively low recapture rates will reduce generation time relative to that in other populations with higher adult survival. For example, a survival analysis conducted for M. rufus from Ranomafana National Park suggested that 16% of the mouse lemurs survived past the age of 4 years (Zohdy et al., 2014). A study on M. murinus in western Madagascar revealed a higher life expectancy of 2.3 years for females and comparable values (1.5 years) for males at the age of first reproduction (Kraus et al., 2008). Further research is clearly needed to fully evaluate the variability in generation time across different sites and species.

This study revealed no significant evidence for different generation times in males and females. However, as average parental age increased substantially (by more than 1 year) for fathers from Cohorts 1 to 3 compared with the slight increase (less than 6 months) for the respective mothers, adding more study years may reveal differences in generation time for both sexes. This would correspond to reported sex differences in reproductive strategies in M. murinus with all females reproducing during their first year (Eberle & Kappeler, 2004b; Lutermann, 2001; Schmelting et al., 2000), while age-dependent reproductive success has been reported for males (Eberle & Kappeler, 2004a; Schmelting, 2001; Schmelting et al., 2007). As young (1-year old) females account for a very high proportion of the female population, they also account for a high proportion of mothers and keep the generation time rather stable and short. Even a longer term estimate of the average age of mothers may not exceed much a value of 2 years, since very few females (2%) were recaptured (=survived) beyond their third breeding season. In contrast, 1-year old mouse lemur males are not equally successful as older, experienced males (Eberle & Kappeler, 2004a; Schmelting, 2001; Schmelting et al., 2007). Consequently, older males contribute a higher proportion of offspring than younger ones, and the average age of fathers will be biased toward older males as soon as reliable age information becomes available, which becomes visible when comparing the results for Cohort 1 to those of Cohort 3.

However, male generation time is also constrained by low survival probability, as only 9% of males were recaptured (=survived) beyond their third breeding season. It can, therefore, be expected that male generation time reaches a plateau probably at a value of around 3 years, at least in the study population. We acknowledge that generation times for males and females did not differ significantly in any of the cohorts, and therefore caution is warranted with regard to further interpretations of these findings.

Sex differences in generation intervals have previously been identified in humans (Fenner, 2005) and mountain gorillas (Langer-graber et al., 2012). In both studies, generation intervals were also longer in males than in females. More data on sex differences in the generation times across the Primate order are necessary to fully understand the variation in this parameter, its underlying evolutionary drivers, and its consequences for evolutionary change rates.

In conclusion, this study suggests new values for the generation time of gray mouse lemurs which could be roughly estimated as about 2 years for females and as about 3 years for males. However, given the high impact of adult mortality on the upper limit of the age of parents,

generation time estimates may vary between populations or species that have different adult survival rates. Mouse lemur reproductive strategies may also impact generation time and generate sex-specific differences. If future studies reveal that generation times of both sexes differ indeed in mouse lemurs and other species, it will become important to explore the evolutionary effects of such differences by simulations and to implement such an option in the available modeling tools (Webster & Wilson Sayres, 2016). In the meantime, we suggest to use the only available composite value, the average of male and female generation times (Charlesworth, 1980). We consequently propose to use 2.5 years as a new empirical estimate for the generation time of mouse lemurs.

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DATA AVAILABILITY STATEMENT

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

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