The influence of body mass, diet, and phylogeny on lemur gestation length, age-at-first-birth, and interbirth interval length

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Abstract

Life history theory is an important topic in primatology: studying a species' life history enables us to understand their social system and can have major implications for conservation. As Malagasy lemurs are the most threatened group of mammals on earth, and understanding their life history traits and the biological factors that impact them may inform conservation efforts, this is an area of research with great consequence. This study examined the impact of body mass, diet, and phylogeny on the life history traits of gestation length, age-at-first-birth, and interbirth interval in 25 lemur species. I collected data on species from the families *Indriidae*, *Cheirogaleidae*, *Lemuridae,* and *Lepilemuridae* from previously published papers. The next step was to run linear regressions to determine how their body mass, diet, and phylogeny (measured using family) impact the aforementioned life history traits. An increased body mass was associated with a slow life history strategy, with a relatively late age-at-first-birth as well as a long gestation length and interbirth intervals. Diet did not have a significant impact on any of these life history traits, while phylogeny had a significant impact on gestation length, but not age-at-first-birth or interbirth interval. These results highlight how lemur life histories are distinctive from those of other nonhuman primates: due to the highly stochastic environment of Madagascar and the numerous unique traits lemurs possess, we cannot assume that trends seen in the life history traits of other primates will also be seen in lemurs

Keywords

lemurs, life history, gestation, interbirth interval, age-at-first-birth

Introduction

Compared to similarly sized animals, primates generally have relatively slow life history traits (Borries et al. 2011; Jones 2012) including gestation length, age-at-first-birth, and interbirth intervals. There are numerous hypotheses used to explain this trend, one of which hypothesises that as brain development is an energetic and time-consuming process, the overall development of primates may be slowed at least partially as a result of their relatively large brain volumes (Charnov and Berrigan 1993; Leigh 2004; Borries et al. 2011). It is also thought that slow life histories may be a response to the long juvenile periods of primates that result from either an increased risk of predation and starvation or from the need to amass a certain amount of social skills before adulthood. Whatever the cause, it is hypothesised that long juvenile periods may consequentially result in slow life histories.

Body mass may also influence aspects of primate life history (Gingerich et al. 1982; Harvey and Clutton-Brock 1985; Ross 1989; Charnov 1991; Fleagle et al. 1999). The larger the primate species, the slower its life history, as it takes individuals more time to grow to their adult size, resulting in longer juvenile periods (Charnov 1991; Charnov and Berrigan 1993; Purvis and Harvey 1995). Body mass also influences an organism's specific production rate, which is defined by Sibly and Brown (2007:1) as the rate at which biomass can be produced per unit of body mass. The larger an organism's body mass, the higher their specific reproduction rate, thus, larger species tend to reproduce slower compared to those with a lower body mass (Sibly and Brown 2007).

Diet is another factor that is widely thought to influence life history traits, although its influence is less clear given the existence of two conflicting hypotheses (Borries et al. 2011). The first suggests that a primates' basal metabolic rate (BMR) is correlated with the timing of life history events (i.e. a slower BMR is associated with a slower life history) (Ross 1992; Borries et al. 2011). For example, as folivorous primates ingest a diet that is primarily 'low quality' leaves, they are also thought to have a slow BMR compared to frugivores, and therefore slower life histories (Young et al. 1990; Ross 1992; Snodgrass et al. 2007; Borries et al. 2011). However, contrary to this hypothesis, the ecological aversion hypothesis predicts that folivorous species may actually have faster life histories than frugivorous species (Godfrey et al. 2004; Borries et al. 2011) owing to their reduced feeding competition and less seasonal food supply, resulting in juvenile folivores being less vulnerable to starvation than frugivores (Borries et al. 2011; O'Mara 2015). This theory, however, is also being contested as recent research shows that folivorous primates may show similar feeding competition to frugivores (Borries et al. 2011; Dröscher and Kappeler 2014).

Phylogeny is another factor thought to have significant impact on life history traits, and comparative studies are often done under the assumption that this is the case (Stearns 1983; Gittleman et al. 1996; Kamilar and Cooper 2013). Many characteristics that are inherited from a common ancestor, including both life history and ecological traits, are more similar among closely related taxa (Kappeler 1996; Kamilar and Cooper 2013). There is some evidence, however, that at least for ecological traits, this may not always be the case across primates, as it does not always apply to lemurs. Fleagle et al. (1999) studied a large number of different primates and found little correlation between lemur phylogeny and ecology, which was not the case for the other primates in the study. This trend may be explained by the large degree of variation between lemur environments, where closely related lemur species are often found in different environments and occupying different ecological niches (Fleagle et al. 1999; Kamilar and Muldoon 2010; Kamilar and Cooper 2013).

Lemurs are endemic to Madagascar, which has a highly stochastic environment, with variable rain patterns, frequent droughts and a high frequency of cyclones (Wright 1999; Richard et al. 2002). This stochasticity has had a major impact on lemur evolution and lemurs have evolved unique adaptations that allow them to survive in this harsh environment (Wright 1999). Some of these adaptations include: high rates of folivory, female dominance, a low metabolic rate, and the ability to enter torpor (Wright 1999; Richard et al. 2002). Additionally, many species of lemurs have highly seasonal breeding to align the period of maximum parental investment with the period of maximum food availability (Wright 1999). These adaptations likely have a large impact on the life history traits of lemurs (Wright 1999). In fact, while lemurs are generally thought to have relatively fast life histories compared to other primates, lemur life history traits can range from the slow to fast end of the continuum (Richard et al. 2002; Catlett et al. 2010). For example, *Propithecus verreauxi verreauxi* tend to have a longer lifespan than species of other mammals and a longer reproductive lifespan than other similarly-sized primate species (Richard et al. 2002). Trying to tease apart the predictors of lemur life history is important because lemurs are the most threatened group of mammals on earth (Schwitzer et al. 2014) and as life history traits can provide a good indication of how vulnerable a species is to extinction (Matthews et al. 2011), understanding them is vital to conservation efforts.

This paper aims to determine the effect of 1) body mass, 2) diet, and 3) phylogeny on gestation length, interbirth interval, and age-at-first-birth of lemurs. These traits were specifically chosen as they provided enough data points for further analysis. I predicted that, despite the unique nature of lemurs and their environment, body mass and phylogeny would have a significant impact on all life history traits studied. Specifically, I expect a greater body mass to be associated with a slower life history strategy (as indicated by a longer gestation period, a later age-at-first-birth and longer interbirth intervals). I also predicted that diet would have a significant impact on the lemur life history traits. Specifically, I expected folivorous species to have a relatively slow life history strategy due to a slow BMR. I suspected that a hypothesis such as the ecological aversion hypothesis, which relates to food competition, would be unlikely to apply to species in an environment as stochastic as Madagascar. Additionally, I expected that the four lemur families included in this study (*Indriidae*, *Cheirogaleidae*, *Lemuridae,* and *Lepilemuridae*) would differ significantly in life history traits.

Materials and Methods

Data Collection

The methods used in this paper are based largely on those of Borries et al. (2011). I collected data on relevant variables from previously published papers (Table 1.1). Diet classifications were made based on what item makes up the largest component of the species' diet. It should be noted that this method of gathering data from multiple sources can be problematic, as there will always be variation in the quality of data (Harvey and Clutton-Brock 1985; Patterson et al. 2014). Different sources may record different values for the same life history trait due to variation in the way the trait is measured (Borries et al. 2013). This is an intrinsic limitation to this method which could not be avoided, although steps were taken to minimise its impact. For example, although captive data were used for body mass, data for all other variables were preferentially taken from wild populations, with captive data only being used where wild data were unavailable. Furthermore, no data were taken from databases, as they are often not frequently updated and may therefore contain outdated information (Borries et al. 2011). In addition, reported values for gestation length and interbirth interval often varied between populations of the same species. When this occurred, I used the overall mean of these values for the final statistical analysis. For gestation length, the largest difference between two values was 0.10 year for *Lepilemur ruficaudatus*, while for interbirth intervals, the largest difference was 0.5 years for *Propithecus verreauxi*. Another intrinsic limitation that should be considered is that it is not easy to measure gestation length in primates (Patterson et al. 2014). Researchers are not always present for parturition and female mating behaviour cannot be used to determine conception (Patterson et al. 2014). Again, it is impossible to avoid this problem but it should be kept in mind while considering the results. Overall, I collected data on 25 species belonging to the families *Indriidae*, *Cheirogaleidae*, *Lemuridae,* and *Lepilemuridae* (Table 1.2).

Table 1.1: Variables in this study

	Variable	**Units or categories**	**Description**
independent variables	body mass	kg	Only studies that used adult female body mass without including adult males were used.
	diet	folivorous (including bamboo) and frugivorous	Lemur species were divided into different categories depending on their dietary patterns: folivory and frugivory. Dietary patterns were determined based on the food item that is the largest component of their diet. Bamboo specialists were treated as folivores. The diet of *Mirza coquereli* was not included, as it is the only omnivorous species used in this study (Viguier 2004).
	phylogeny	family	Species were divided into families using the lemur taxonomy described by Mittermeier et al. (2008).
dependent variables	age-at-first-birth	years	This was collected for females only. As there are relatively few studies that provide this information, when this information was unavailable, age of female first mating was used instead.
	interbirth interval	years	This was defined as the period of time between a female successfully giving birth two times in succession (Harvey and Clutton-Brock 1985).
	gestation length	years	Data were collected from both behavioural and hormonal studies.

Table 1.2: Gestation length, age-at-first-birth, and body mass of lemur species

		Gestation length		**Age-at-first-birth**		**Interbirth interval**		**Body mass**		**Diet**	
Family	**Species**	**mean (yr)**	**ref**	**mean (yr)**	**ref**	**mean (yr)**	**ref**	**mean (kg)**	**ref**	**type**	**ref**
Cheirogaleidae	*Cheirogaleus major*	0.19	3	1.75	32	1	3	0.362	26	frugivore	32
	Cheirogaleus medius	0.17	3			1	3	0.282	26	frugivore	4
	Microcebus rufus	0.156	2					0.067	26	frugivore	1
	Microcebus murinus	0.1686	2; 3	0.83	7	1	3	0.063	26	frugivore	18
	Mirza coquereli	0.247	3; 27	0.89	27	1	3	0.326	26		
Indriidae	*Avahi laniger*	0.43	3	3	32	1	3	1.32	26	folivore	30
	Indri indri	0.42	3	8	24	2	3	6.84	26	folivore	30
	Propithecus coquereli	0.433	21							frugivore	31
	Propithecus diadema	0.5	3	4	10	1.78	3; 23	6.12	26	folivore	30
	Propithecus tattersalli	0.51	3			1	3	3.463	26	frugivore	31
	Propithecus verreauxi	0.43	3			1.25	3; 25	3.615	26	folivore	30
Lemuridae	*Eulemur coronatus*	0.34	15					1.35	26	frugivore	30
	Eulemur collaris									frugivore	5
	Eulemur fulvus	0.43	3	4	23	1.1	13; 22	2.077	26	frugivore	30
	Eulemur macaco	0.34	3			1	3	2.135	26	frugivore	30
	Eulemur mongoz			0.36	3			1.585	26	frugivore	30
	Eulemur rubriventer	0.34	3	5.5	16	1	3	1.94	26	frugivore	30
	Hapalemur aureus			2	20			1.39	26	folivore (bamboo)	29
	Hapalemur griseus	0.38	3			1	3	0.787	26	folivore (bamboo)	29; 30
	Lemur catta	0.38	17	2.5	11; 17	1	17; 28	2.205	26	frugivore	30
	Hapalemur simus			3	9	1	9	1.3	26	folivore (bamboo)	29
	Varecia variegata	0.28	3	2	8	1	3	3.515	26	frugivore	30
Lepilemuridae	*Lepilemur leucopus*	0.48	12			1	12	0.594	26	folivore	6
	Lepilemur mustilinus	0.38	3			1	3			folivore	19
	Lepilemur ruficaudatus	0.43	3; 13			1	3; 13	0.779	26	folivore	14

Data were collected from previously published papers, when more than one reference was used the average value is recorded. [1] Atsalis 1999 [2] Blanco 2010 [3] Catlett et al. 2010 [4] Curtis and Zaramody 1998 [5] Donati et al. 2007 [6] Dröscher 2014 [7] Eberle and Kappeler 2004 [8] Foerg 1982 [9] Frasier et al. 2015 [10] Glander et al. 1992 [11] Harvey and Clutton-Brock 1985 [12] Hilgartner 2006 [13] Hilgartner et al. 2008 [14] Hilgartner et al. 2012 [15] Kappeler 1987 [16] Karpanty 2006 [17] Koyama et al. 2001 [18] Lahann 2006 [19] Lehman 2007 [20] Lindenfors 2002 [21] Richard 1978 [22] Overdorf et al. 1999 [23] Pochron et al. 2004 [24] Pollock 1979 [25] Richard et al. 1991 [26] Smith and Jungers 1997 [27] Stranger et al. 1995 [28] Sussman 1991 [29] Tan 1999 [30] Viguier 2004 [31] Wallace et al. 2016 [32] Wright 1992

Data Analysis

Three multivariate linear regressions models were constructed, each of which contained the three independent variables (body mass, diet, and phylogeny) along with one of the three dependent variables (age-at-first-birth, interbirth interval, and gestation; Table 1.3). The inclusion of all three independent variables in each regression allowed for the relationship between each variable to be tested while also accounting for any effect the other two variables may have. Regressions were done using the 'lme4' package (Bates et al. 2016) and graphs were made using 'ggplot2' (Wickam 2009) on R v. 3.4.3.

Table 1.3: Statistical analyses

Analyses	Independent variables	Dependent variable
multivariate linear regression 1	body mass	age-at-first-birth
	diet	
	phylogeny	
multivariatelinear regression 2	body mass	interbirth interval
	diet	
	phylogeny	
multivariate linear regression 3	body mass	gestation
	diet	
	phylogeny	

Source: Data were collected from previously published papers, as seen in footnote for Table 1.2; when more than one reference was used the average value was recorded.

Results

Body mass was a significant predictor of gestation length, interbirth interval, and age-at-first-birth (Table 1.4). A greater body mass was associated with a longer gestation ($t = 4.19$: $p < 0.001$), longer interbirth intervals ($t = 7.57$; $p < 0.001$) and later age-at-first-birth ($t = 4.16$; $p = 0.001$) (Table 1.4). Diet did not have a significant impact on any of the life history traits examined while phylogeny only impacted gestation length ($p = 0.004$) (Table 1.4). The most notable difference in the gestation length of the families is that *Cheirogaleidae* species tend to have a considerably short gestation length compared to other families (Figure 1.1).

Table 1.4: The impact of body mass, diet, and phylogeny on lemur gestation, age-at-first-birth, and interbirth interval.

		Regression coefficient (*B*)	Standard error	*t-value*	*p*-value
gestation	body mass	0.033	0.007	4.19	**<0.001**
	diet	0.023	0.015	1.52	0.147
	phylogeny	0.052	0.015	3.36	**0.004**
age-at-first-birth	body mass	0.807	0.194	4.16	**0.001**
	diet	0.048	0.358	0.134	0.895
	phylogeny	-0.207	0.424	-0.488	0.633
interbirth interval	body mass	0.135	0.018	7.57	**<0.001**
	diet	0.056	0.034	1.64	0.125
	phylogeny	-0.084	0.039	-2.15	0.051

Source: Data were collected from previously published papers, as seen in the footnote for Table 1.2; when more than one reference was used the average value was recorded. Regressions were done using the 'lme4' package of R v. 3.4.3.

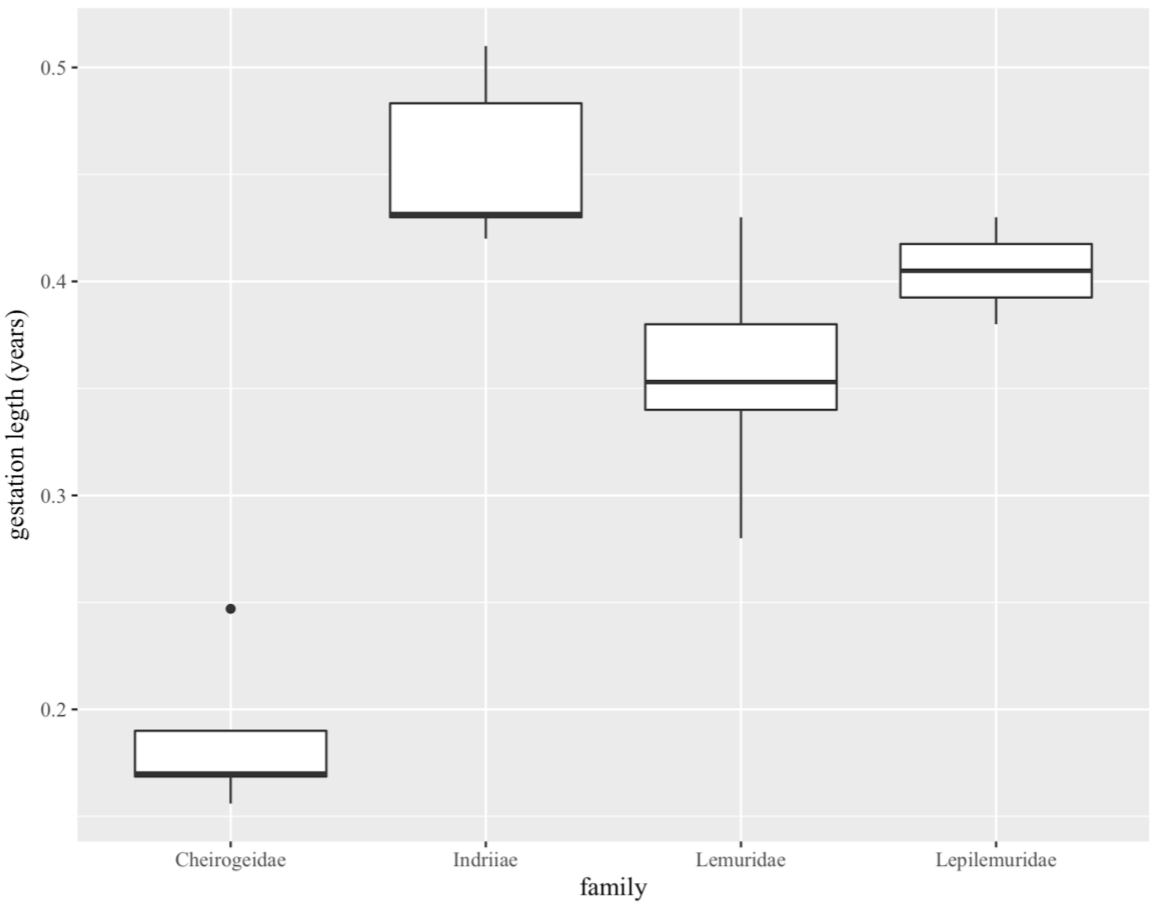

Figure 1.1: Phylogeny as a predictor of lemur gestation. Gestation length significantly varies between families (p = 0.012).

Source: This was created using ‘ggplot2’ in R v. 3.4.3.

Discussion

The results supported my first hypothesis that body mass would have a significant impact on all the life history traits examined, with higher body mass being associated with a slower life history strategy. However, it did not support my prediction that diet would also have a significant impact on these same traits. Additionally, my third hypothesis was only partially supported in that only gestation length was significantly impacted by phylogeny.

My results show that adult body mass is a predictor of lemur life history variables in the lemur species used in this study. This supports the many previous studies done across primate taxa that show the same result: body mass is a significant predictor of life history strategy (Stearns 1983; Harvey and Clutton-Brock 1985; Ross 1992; Richard et al. 2002; Borries et al. 2011). This is likely because larger primates take longer to grow into their full adult body size prior to their first reproduction. This is then expected to delay age-at-first-birth and generally slow all reproductive traits (Charnov 1991; Charnov and Berrigan 1993; Purvis and Harvey 1995).

In terms of diet, I had expected that folivorous species would have slower life history traits as they have a slower BMR (Young et al. 1990; Ross 1992; Snodgrass et al. 2007; Borries et al. 2011) and I did not expect the ecological aversion hypothesis to hold true in this case given that Madagascar is a highly stochastic environment with variable levels of food availability (Wright 1999; Richard et al. 2002), making the application of a theory relating to resource competition complex. However, it is recognised there are also problems with the assumption that folivorous primates tend have a low BMR and therefore slow life histories. For example, folivorous species have evolved mechanisms to help them digest leaves (i.e. a specialised digestive tract) and as such they may not require slower BMRs and thus should not have slower life histories (Ross 1992; Snodgrass et al. 2007; Borries et al. 2011). It should also not be ignored that there may be factors other than diet that impact the life history traits of folivorous primates. For example, many folivorous primates are also arboreal and therefore tend to live fairly sedentary life styles, which is associated with a low BMR (Borries et al. 2011). Arboreal primates also have relatively low mortality rates which is correlated with low fecundity and therefore an overall slow life history (Borries et al. 2011). In particular there are a considerable number of factors that may impact BMR in lemurs, therefore there are also considerable number of factors that may indirectly influence their life history (Wright 1999). For example, there are two genera of lemurs, *Microcebus* and *Cheirogaleus*, that enter into either daily or seasonal torpor, which is a period of hibernation-like behaviour in which they lower their BMR (Wright 1999; Schmid et al. 2000; Schmid and Ganzhorn 2009). Lemurs enter torpor to cope with the low temperatures and scarce food associated with the dry season of Madagascar (Wright 1999; Schmid et al. 2000). Both folivorous and frugivorous primates exhibit torpor, so the impact it has on BMR is not limited to species of any particular dietary pattern (Wright 1999; Schmid et al. 2000). Having a larger number of factors that influence BMR in lemurs compared to other primates may lead to a diminished impact of diet on BMR in this study, and therefore warrants further investigation.

The results did not support my hypothesis that phylogeny would have a significant impact on lemur age-at-first-birth and interbirth interval. This suggests that in lemurs these traits may instead be influenced by ecological or social factors as is seen in some other primates. For example, in *Macaca mulatta* higher ranked females reproduce earlier than their peers due to their better access to resources (Wilson et al. 1983) and it is possible this same trend may be seen in lemurs with dominance having more of an impact on this variable. Similarly, interbirth interval may be less constrained by phylogeny and more impacted by resource availability (Wright et al. 2015), maternal age (Roof et al. 2005) and offspring survival (Fürtbauer et al. 2010).

Unlike age-at-first-birth and interbirth interval, gestation length was significantly influenced by phylogeny. *Cheirogaleidae* species had noticeably shorter gestation lengths than the other three families examined. This family also has a relatively small body mass compared to the others, with an average of just 0.22 kg, compared to the 2 kg average body mass of the other families. Based on the influence of body mass alone we would expect *Cheirogaleidae* to have a relatively fast life history strategy with short gestation lengths (Charnov 1991; Charnov and Berrigan 1993; Purvis and Harvey 1995). However, my model found an impact of phylogeny independent of body mass indicating its standalone influence on gestation length. It could be that variation between the gestation length in each family is caused by species in each family being found in different environmental conditions. However, considering the lack of correlation between lemur phylogeny and ecology this seems unlikely (Fleagle et al. 1999).

Conclusion

My results showed that lemurs with a greater body mass tend to also have a slower life history strategy, with longer gestation lengths, interbirth intervals and age-at-first-birth. While there was no surprise with regards to body size—it is well recognised that larger animals have an overall slower reproduction rates (Charnov 1991; Charnov and Berrigan 1993; Purvis and Harvey 1995; Sibly and Brown 2007)—this does pose a problem for these species, as large-bodied primates are also the most vulnerable to hunting pressure and habitat loss (Peres 1990). As these animals are often the first to disappear following a disturbance—and will take the longest to return due to slow rates of reproduction—these species warrant special conservation attention.

Future research would benefit from considering the potential for other factors, such as social rank and resource availability, to influence lemur life history traits. Furthermore, future research on lemur life histories should also consider the unique characteristics of lemurs, such as torpor, and the impact these traits may have on their life history traits. Due to the unique traits possessed by lemurs, the results of this study indicate that trends seen in the life history traits of other primates do not necessarily apply to lemurs. Future research that considers this could greatly expand our understanding of lemur life history traits and the factors that impact them.

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