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Sex and age-specific survival and life expectancy in a free ranging population of *Indri indri* (Gmelin, 1788)

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Abstract

The critically endangered indri (*Indri indri*) is the largest extant lemur species and its population size is projected to decline over the next three generations due to habitat loss, hunting and climate change. Accurate information on the demographic parameters driving the population dynamics of indri is urgently needed to help decision-making regarding the conservation of this iconic species. We monitored and followed the life histories of 68 individually recognizable indris in 10 family groups in the Maromizaha New Protected Area (Madagascar) for 12 years. We estimated age and sex-specific survival trajectories using a Bayesian hierarchical survival model and found that the survival curves for male and female indris show a similar pattern, consistent with what found typically in primates; i.e., a high infant mortality rate which declines with age in the juvenile phase and increases again for adults. Also, life expectancies at 2 years of age (e2), were found to be similar between the sexes (e2 females = 7.8 years; e2 males = 7.5 years). We suggest that the lack of strong differences in the survival patterns for male and female indris are related to the strictly monogamous mating system and the lack of sexual dimorphism in this species. Our study provides, for the first time, robust estimates for demographic parameters of indris and one of the very few datasets on survival trajectories available for primates.

Keywords: *Lemur, lifespan, ageing, monogamy, population ecology*

Introduction

The assessment of the conservation status of threatened species can be improved by the quantitative analysis of extinction risk over time, requiring reliable information on population dynamics based preferably on data from long-term monitoring of demographic parameters in free-ranging populations (Lande 1988; Kappeler et al. 2017). Obtaining the necessary long-term data on individual life histories may, however, prove challenging when dealing with animals with a long lifespan (Clutton-Brock & Sheldon 2010). Long-term studies on the demography of non-human primates are particularly rare, not only because of the distinctive long lifespan of many species but also due to the difficulties in maintaining long-term research projects in the wild (Pollock 1975a; Bronikowski et al. 2011). As remarked by Bronikowski et al. (2011), primates represent a valuable example of a class with an average long life expectancy but for which demographic data is scarce. The general mortality rate pattern in primates presents high infant mortality that decreases during the juvenile phase, followed by a period of age-specific increasing mortality in the mid and late life (Sibly et al. 1997; Gage 1998; Bronikowski et al. 2011; Larson et al. 2016). In addition, contrary to most other mammals, primates exhibit a longer average life expectancy relatively to their body size (Didier et al. 2016).

Mortality rate in primates varies across species, in accordance with their ecology and is often related to their social organization. Males and females of

monogamous species tend to age at comparable rates, whereas polygynous species present differences between the sexes (Clutton-Brock & Isvaran 2007). Rates of mortality and ageing are usually considerably higher for males, compared to conspecific females, in species where males compete for mating opportunities (Bronikowski et al. 2011) - other mortality causes concern extrinsic sources (e.g. predation, climatic conditions, rainfalls or severe winters) or intrinsic sources (e.g. infanticides, migration, short parental care). Studies carried out in zoos and primate centers offer more detailed information on juvenile mortality in primates, showing that infants' mortality ranges between 25 and 45% in Lemuriformes, with lower values for lemuroidea (Debyser 1995).

Indri (*Indri indri*, Gmelin 1788) is the largest extant lemur species and it inhabits the eastern rainforests of Madagascar, living exclusively on trees and feeding mainly on leaves and flowers (Britt et al. 2002; Borruso et al. 2021). The species occupies exclusive territories (Pollock 1975a) whose defense is achieved through advertisement songs that can be heard from 3–4 kilometers distance (Giacoma et al. 2010; Torti et al. 2013). Songs allow individuals to (i) identify the location of other groups (Giacoma et al. 2010; Gamba et al. 2016) and (ii) avoid physical conflicts and wounds, with consequent mortality (Bonadonna et al. 2017, 2020) and (iii) communicate the reproductive potential of the individuals of the group (Torti et al. 2013, 2017). Indris live in family groups composed of a monogamous and stable reproductive pair, eventually with their offspring and sub-adults up to six members (Torti et al. 2017; Bonadonna et al. 2019). Females give birth to a single offspring every 2–3 years (Quinn & Wilson 2002). Indris start singing around 1 year of age (De Gregorio et al. 2021) and, although both sexes disperse (Gamba et al. 2013), recent work showed that males could remain in their natal group until 8 years of age, while females until 4.5 years of age (De Gregorio et al. 2021)

Indri plays an important role in the Malagasy culture, being protected by a traditional taboo ("fady"). Through these unwritten rules the local population is culturally linked to the forest, hence, hunting or eating indri is generally avoided, as they are believed to be the ancestors of Malagasy people (Jones et al. 2008). Despite this, indri population size is decreasing and the rate of decline is expected to continue over the next three generations due to habitat loss, hunting and climate change (King et al. 2020). For these reasons, indri has been classified as Critically Endangered in the IUCN Red List of Threatened Species (King et al. 2020).

A better understanding of the demographic parameters regulating the population dynamics of indri is therefore needed to support conservation activities and help decision-making for the effective management of existing populations, and consequently contribute to guarantee the future survival of this species (Schwitzer et al. 2013). Due to the scarcity of long-term studies on the life histories of individually recognisable indris, their general life expectancy is not well known. Here we model for the first time the age-sex specific survival trajectories of indris, using a Bayesian hierarchical approach proposed by Colchero and Clark (2012), to analyse a long-term dataset on the life histories of individually recognisable indri collected over 12 years in the Maromizaha Forest, Eastern Madagascar. We specifically aim to verify if there are differences in the survival patterns of males and females in this pair-living genetically monogamous and monomorphic (Bonadonna et al. 2014, 2019) species and estimate sex-specific life expectancies.

Materials and methods

Study area

The study area is located in the Maromizaha New Protected Area (NAP), a primary rainforest located in the Alaotra-Mangoro Region, in the District of Moramanga, eastern-central Madagascar (18°56′49″ S, 48°27′33″ E). The forest covers an area of 2,150 hectares (GERP 2019) and it is part of the Ankeniheny-Zahamena Corridor (CAZ), which expands for 371,000 hectares across the eastern regions of the country. The forest extension guarantees a crucial link between the northern and southern rainforests that still persist in the country (Gamba et al. 2013). The altitude ranges between 794 and 1,224 m asl, providing the typical environment for a tropical mid-altitude evergreen rainforest with an annual average rainfall of 1779 mm (Randrianarison et al. 2015).

Maromizaha is home to a wide range of animal and plant species, most of which are endemic to Madagascar (Randrianarison et al. 2015). Concerning the fauna, 13 lemurs, 85 birds (96% of which are endemic to the island), 25 amphibians, 34 reptiles, and more than 800 moths species have been identified (GERP 2018; Gamba et al. 2013). Three lemur species are of particular conservation concern and classified as Critically Endangered by the IUCN red list (IUCN 2020): *Indri indri*, *Propithecus diadema*, and *Varecia variegata editorum*. It has been estimated that between 55 and 100 indri groups in total inhabit the forest (Bonadonna et al. 2017).

Indris' predators can be both aerial and terrestrial (Fichtel & Kappeler 2002). In fact, these lemurs

possess a distinct type of alarm call according to the source of potential risk (Pollock 1975a; Petter & Charles-Dominique 1979; Thalmann et al. 1993; Macedonia & Stanger 1994; Maretti et al. 2010): *honks* are given when terrestrial predators are presents (e.g., fossa - *Cyptoprocta ferox* and Malagasy civet, also known as striped civet or fanaloka - *fossa fossana*), while *roars* are emitted in the presence of aerial predators (e.g., Madagascar harrier-hawk - *Polyboroides radiatus*). All these predators are active in Maromizaha.

Field data collection

Following a standardised protocol (Torti et al. 2013; Bonadonna et al. 2017, 2019), data were collected for 12 years, from 2009 to 2020. Monitoring is active all year round, and the focal group is changed every week to ensure that all the surveyed individuals are regularly under observation (Bonadonna et al. 2017). All 10 groups monitored in the study have been habituated to human presence since 2009.

To limit any possible disturbance, we always made behavioural observations at a distance of at least 10 meters. The animals could be identified thanks to their individual external features, which are rather variable and detectable from the viewing distance: the colour of the fur, the size, and the presence of any peculiar traits (Gamba et al. 2014; Bonadonna et al. 2020). For each individual there is an identification card, which facilitates correct identification over time (see Supplementary materials SM1). The card includes name, group, sex, age, reproductive status, along with pictures of the animal and a description of its main characteristics.

In indri males and females look the same but sing differently (De Gregorio et al. 2019a, 2019b). Consequently, we could not determine the sex of 13 infants that died before they start singing, which occurs at around 1 year of age (De Gregorio et al. 2021).

As described by Pollock (1975a), indris have a short diurnal activity period, starting at dawn and ending before sunset. For this reason, the observations started early in the morning (6.00 a.m.) and the animals were followed and monitored in all their activities until they were no longer active (Torti et al. 2013).

Dataset

This study is based on 10 individually identifiable groups of indris. The total number of individuals included in the study is 68. For each individual, the following variables were collected during the fieldwork: i) Sex (male or female); ii) Reproductive status (reproductive or non-reproductive); iii) Year of birth (if known); iv) Year of death (if known); v) Presence or Absence of the individual in each year (from 2009 to 2020).

We identified four age classes, in which we grouped the individuals according to their life stage (Pereira & Altmann 1985):

1. *Infants*: individuals under 1 year of age. Infants cannot survive outside the group, can be recognized for their smaller size but it is not possible to recognize their sex.
2. *Yearlings*: individuals ranging from 1 to 2 years of age. Yearlings interact with other group members independently from their parents. Most of them start singing allowing sex identification.
3. *Juveniles*: non-reproductive individuals above 2 years of age. Juveniles typically have acquired the ability to provide for their own sustenance.
4. *Adults*: individuals of the reproductive pair in a family group.

Individuals were considered dead with certainty only if their body was found or, in the case of infants if they disappeared overnight, as they are still dependent on their mother for their survival. The disappearance of older individuals could not be assumed to be caused by death as juveniles up to the age of nine can disperse from their natal group, and we cannot trace them if they move out of the study area.

Survival analysis

Data was modelled in the open-source statistical environment R (R Development Core Team 2019) using the package BaSTA (Bayesian survival trajectory analysis; Colchero et al. 2012). BaSTA implements the Bayesian hierarchical survival model for capture-mark-recapture/resight data proposed by Colchero and Clark (2012) and it copes with datasets like ours, characterised by missing data and a large proportion of unknown ages and unknown birth and death times. The complete dataset, structured as required by the BaSTA package, along with details can be found in Supplementary materials SM2. We compared the fit of four different possible mortality probability functions to describe the age-specific survival trajectories of indris using the *multibasta* function in BaSTA: a) the Gompertz function, assuming an exponential change in age-specific mortality (Gompertz 1825; Pletcher 1999); b) the Weibull function (Pinder III et al. 1978); c) the

Logistic function (Perks 1932; Vaupel et al. 1979; Pletcher 1999) and d) the simple Exponential function (Cox & Oakes 1984).

We also tested if the models would be improved by the addition of additional terms to more accurately describe the shape of the mortality curves, i.e., a Makeham structure (Pletcher 1999), which adds a constant to the mortality rate, or a bathtub structure (Siler 1979) which adds a declining Gompertz function and a constant to the basic mortality rate. Mathematical details about the four functions and their shape terms can be found in the Supporting information of Colchero et al. (2012). For each model, we run 4 MCMC simulations for 100,000 steps, a burn-in period of 10,001 steps, and a thinning interval of 100 steps each. The optimal combination of jump standard deviations was found by an additional initial simulation of 10,000 steps setting the *updateJumps* argument in the *multibasta* function as TRUE. We conditioned all survival models to start after 2 years of age to account for the lack of data concerning sex identification in the first years of life, while early mortality was assumed to be exponential.

As recommended by Colchero et al. (2012), we selected the best fitting model as the one with the lowest DIC (Deviance Information Criterion, Spiegelhalter et al. 2002) value. We compared models assuming sex differences in the model parameters (Sex-Age specific survival models) against models assuming no differences between the sexes (Age-specific survival models) and we evaluated if adding sex as a covariate improved our model fit based on their DIC values. We report the Kulbach-Leibler discrepancies (KLD; Kullback & Leibler 1951) for each pair of parameters for males and females in the best fitting Sex-Age specific survival model to measure how much sex affects each parameter in the survival

model. The KLD value ranges from 0.5 to 1 where a value of 0.5 indicates complete overlap while 1 indicates no overlap in the distribution of the parameter (McCulloch 1989). Life expectancy at age 2 (*e2*) was extracted from the life table obtained with the output of the best fitting model, calculated as in Larson et al. (2016).

We estimated infant and yearling mortalities with a simple Bayesian binomial model using the *stan_glm* function in the R package *rstanarm* (Goodrich et al. 2020) as an interface to the probabilistic programming language Stan (Stan Development Team 2019). The Stan model was run using the default weakly informative normal prior for the intercept (location = 0, scale = 2.5) running 4 chains of 2000 iterations each (warmup = 1000). We used the same procedure to estimate age independent overall mortality of reproductive adults. The complete dataset and R script used for this analysis can be found on Figshare (Link in Supplementary Materials SM2).

Results

A data summary of the indri population structure in Maromizaha Forest is reported in Table I. Yearly group composition varied from pairs of adults without offspring to a maximum of 5 individuals (the reproductive pair, 1 or 2 offspring and/or 1–2 young joining from a different family group). Among the 68 individuals, 30 were males, 25 were females. For the remaining 13 individuals, sex is unknown because they disappeared before we could analyse their song for sex determination.

There were 22 reproductive adults in total (11 males and 11 females). In group 3MZ the adult male died in 2015 (likely due to the injuries reported

Table I. Summary of the data collected on 10 indri groups monitored from 2009 to 2020 in Maromizaha, Madagascar.

Group code	Years monitored	Total no of individuals	Total no of infants	Tot no. of dispersed juveniles	Tot no of recorded deaths (with sex and status)
1MZ	2009–2020	9	6	3	2 I
2MZ	2009–2020	8	6	2	2 I
3MZ	2009–2020	11	6	6	1 A; M
4MZ	2009–2020	7	4	0	1 I
5MZ	2009–2020	7	3	3	1 A; F
6MZ	2009–2020	6	3	3	0
8MZ	2010–2020	7	4	1	1 J; F
9MZ	2011–2020	7	4	2	0
10MZ	2014–2020	5*	2	1	0
13MZ	2017–2020	2	0	0	0
TOTAL	**2009–2020**	**68**	**38**	**20**	**8**

I: Infant, J: Juvenile, A: Adult; F: Female; M: Male; Sex of dead Infants could not be determined. *including a juvenile female immigrated from Group 1MZ.

after a physical fight with the adult male of the neighbouring group) and was substituted by another immigrant male. In group 5MZ the adult female died in 2018 after a cyclone and was substituted by a female joining from a different family group. Since 2009, we documented a total of 39 infants, resulting in mean natality of 0.37 infants per group/year. Infants surviving until sex could be determined had a female-biased sex ratio of 1:1.5 (8/12 males/females).

In the population, 20 juveniles (13 males, 7 females) disappeared and we recorded the death of only Mika, a 4 years old female, seen wounded for unknown causes. Generally, we did not succeed in tracking juveniles after their dispersal. However, two cases have been reported of individuals moving from their native group and entering a new one in the study area:

- Case 1: Maintso born in 2010, left the natal group 1MZ in 2013, when she reached 3 years of age, she joined group 10MZ. She stayed within 10MZ without reproducing until 2014, then she moved away from the study area or died.

- Case 2: In 2014, Joeline (juvenile female, group 6MZ) dispersed when she was at least 6 years old and became the reproductive female in group 10MZ.

Variability of age at dispersal is very large, as we see that some individuals disappeared at 2 years, but others were staying in the native group at least until 8 years of age. This is true for two males in two different groups: Gibet from group 4MZ and Zafy from group 8MZ who were both born in 2012 and disappeared in 2020 at 8 years of age.

Age and sex specific survival models

We found that age specific survival is best described by a Gompertz function with a bathtub shaped curve (Table II). Coefficient estimates for the parameters of this general model are provided in Table III.

Also, for the models including sex as a categorical variable, a Gompertz function with a bathtub shaped curve was the best fitting model, with mortality first decreasing up to 5 years of age and then increasing exponentially with age in both sexes (Table IV; Figure 1). Parameter estimates for the best fitting age-specific survival model including sex as a covariate are provided in Table V. This model, with a DIC = 1062.54, outperforms the previous best fitting model non assuming sex differences in survival (DIC = 1085.58; DDIC = 23.04) suggesting differences in the survival trajectories between males and females. Differences, if present, were relatively small though, with KLDc values below 0.55 for all parameters with the only exception of the c parameter (KLDc = 0.59), indicating a marginally

Table II. Ranked performances for different combinations of mortality functions and shape terms for models of age specific survival in the indri population in Maromizaha, Madagascar.

Model	Shape	k	DIC	ΔDIC
Gompertz	Bathtub	6	1085.58	0.00
Weibull	Makeham	4	1106.00	20.42
Weibull	Bathtub	6	1107.03	21.45
Exponential	Simple	2	1123.86	38.28
Logistic	Bathtub	7	1128.54	42.96
Logistic	Makeham	5	1146.00	60.42
Weibull	Simple	3	1149.51	63.93
Gompertz	Simple	3	1153.71	68.13
Logistic	Simple	4	1161.76	76.18
Gompertz	Makeham	4	1162.09	76.51

Ranked performance of the Gompertz, Weibull, Logistic and Exponential functions has been measured by the values of their Deviation Information Criterion (DIC). The lowest DIC value corresponds to the best-fitting model. ΔDIC shows the difference of DIC values between each model and the best fitting model. k is the number of estimated parameters.

Table III. Coefficient estimates and 95% credibility intervals (CI) for the parameters of the Gompertz bathtube model (the best fitting model) for age specific survival in the indri population in Maromizaha, Madagascar. The recapture probability for 2009 is included as pi.

Parameter	Estimate	Lower 95% CI	Upper 95% CI
a0	−2.12	−3.75	−1.11
a1	0.47	0.07	1.80
c	0.04	0.00	0.10
b0	−4.20	−5.82	−2.85
b1	0.03	0.00	0.09
pi	0.92	0.89	0.95

Table IV. Ranked performances for different combinations of mortality functions and shape terms for models of sex and age specific survival in the indri population in Maromizaha, Madagascar.

Model	Shape	DIC	ΔDIC	k
Gompertz	Bathtub	1062.54	0.00	11
Weibull	Makeham	1080.70	18.16	7
Weibull	Bathtub	1098.84	36.29	11
Logistic	Bathtub	1100.77	38.23	13
Logistic	Makeham	1102.91	40.37	9
Exponential	Simple	1113.58	51.04	3
Logistic	Simple	1126.89	64.35	7
Gompertz	Makeham	1127.40	64.85	7
Weibull	Simple	1131.31	68.77	5
Gompertz	Simple	1145.22	82.68	5

Ranked performance of the Gompertz, Weibull, Logistic and Exponential functions has been measured by the values of their Deviation Information Criterion (DIC). The lowest DIC value corresponds to the best-fitting model. ΔDIC shows the difference of DIC values between each model and the best fitting model. k is the number of estimated parameters.
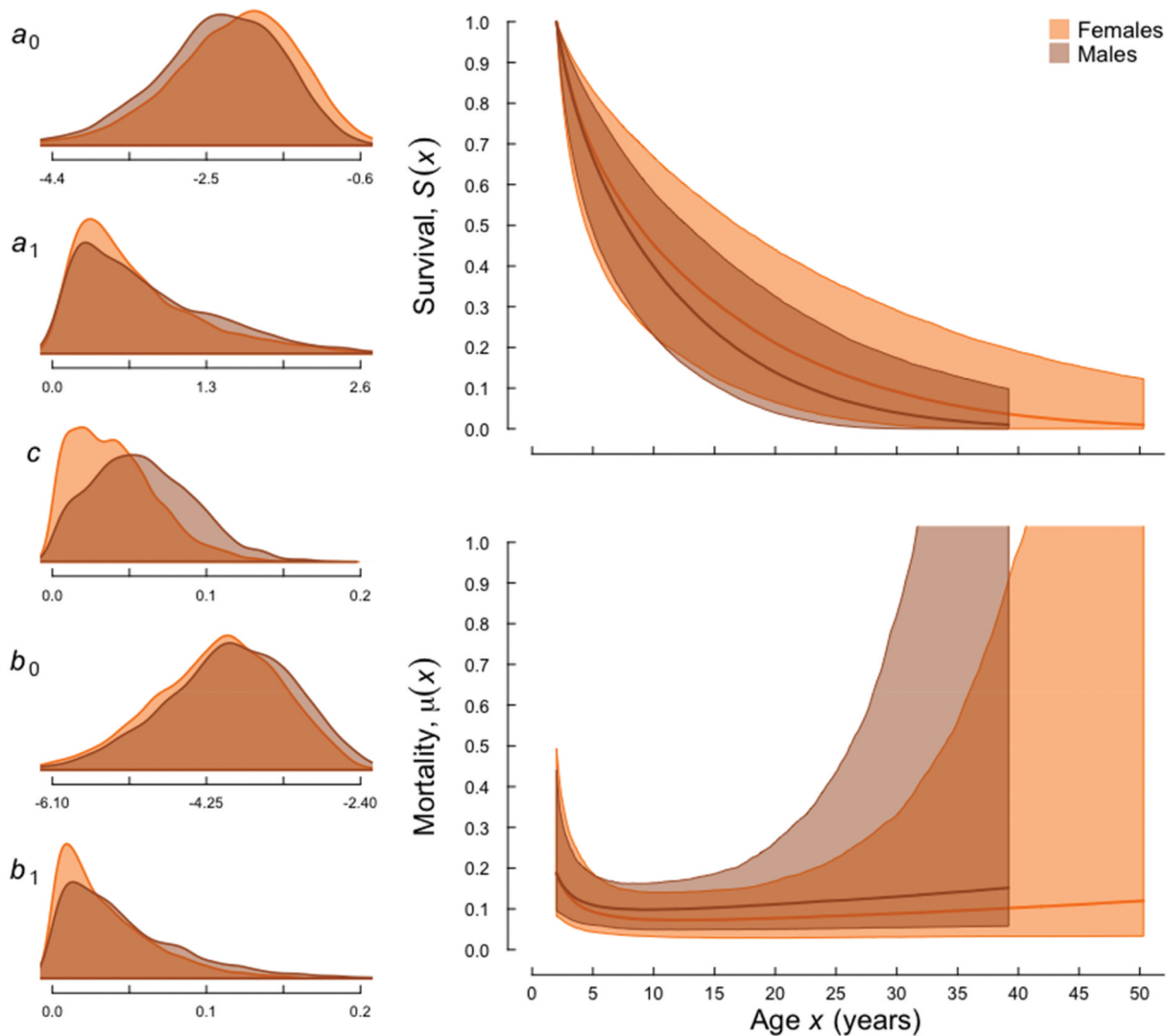
Figure 1. Age-Sex specific survival and mortality trajectories for *Indri indri* in the Maromizaha protected area, Madagascar. The survival and mortality curves for males and females have been estimated following a Gompertz function with a "bathtub" shape term. The coloured areas represent the 95% credibility intervals. Credibility intervals have been cut at a maximum mortality rate value of 1.0 to make the figure more readable at the lower bound. Probability density plots for the estimated parameters of the model are presented on the left.

higher age-independent mortality in males compared to females (Table IV; Figure 1). Estimates of lifespan, the maximum age individuals are known to be able to reach in the wild, was 30 years for males and 35 for females.

Life expectancies at 2 years of age were similar between the sexes ($e2$ females = 7.8 years; $e2$ males = 7.5 years). Infant mortality (6 out of 39 infants) was estimated to be within a 95% posterior CI going from 0.07–0.25 (median posterior estimate = 0.14). Yearling mortality (4 out of 32 individuals), ranged from 0.02–0.17 (median posterior estimate = 0.07) while overall mortality of reproductive adults (independently from age) had a median posterior estimate of 0.1 (95%CI: 0.03–0.23).

Discussion

We observed 10 habituated groups of indris from 2009 to 2020 in the Maromizaha forest, Madagascar. Group size, including always a pair of reproductive adults, varied from 2 to 5 individuals. The mean birth rate was 0.37 per group/year with an estimated sex ratio at one year of age of 1:1.5. Our age-specific survival model suggests minimal differences in the survival trajectories between males and females and similar life expectancies at 2 years of age (7.5 for males and 7.8 for females). The pattern of the survival probability curves follows what is commonly found in other primate species (Sibly et al. 1997; Gage 1998; Bronikowski

Table V. Coefficient estimates and 95% credibility intervals (CI) for the parameters of the Gompertz bathtub model (the best fitting model) for sex and age specific survival for male (M) and female (F) indri in Maromizaha, Madagascar. KLDC (Kullback-Leibler discrepancy calibration) mean values measure the difference between sexes and ranges from 0.5 to 1.

Parameter	Estimate		Lower 95% CI		Upper 95% CI		KLDC
	F	M	F	M	F	M	
a0	−2.15	−2.35	−3.88	−4.02	−0.81	−1.03	0.52
a1	0.71	0.80	0.08	0.08	2.14	2.22	0.51
c	0.04	0.06	0.00	0.00	0.10	0.13	0.59
b0	−4.12	−3.97	−5.74	−5.62	−2.77	−2.60	0.51
b1	0.04	0.05	0.00	0.00	0.12	0.16	0.55
pi	0.92		0.89		0.95		

When the value is closer to 0.5 it means higher similarity. The recapture probability for 2009 is included as pi.

et al. 2011; Larson et al. 2016). According to these studies, the survival probability is low during the first years of life. Juveniles and adults present lower mortality rates, with a constant survival probability, while mortality increases with age in the last stages of life.

Long life expectancy, along with few offspring with high mortality in a species that receive extensive parental care are common characteristics of Primates (Jones 2011). In indris, infant mortality is 0.14 and 0.07 for yearlings (both values include males and females together, because sex is unidentifiable before the animals start singing). This result is interesting when compared to infants' mortality of Strepsirrhine primates in nature and in captivity, which has been reported to range between 0.25 and 0.45, with lower values for lemuroidea (Debyser 1995). In particular, age-specific survival data from the wild are available for Verraux's sifaka *Propithecus verrauxi*, a species belonging to the same family (Indriidae). Verraux's sifaka mortality in the first years of life is much higher 0.48 (Richard et al. 2006) as a possible consequence of living in larger groups and of sexual competition acting in their polygamous system. Similar values have been reported for the Greater Bamboo Lemur *Prolemur simus*, where infant mortality is close to 0.50 (Frasier et al. 2015). The reason has been related to infants increasing their independence from the mothers, hence resulting more vulnerable to predation (Frasier et al. 2015). Jolly et al. (2002) reported interesting values concerning birth rate in *Lemur catta*, with values ranging from 0.50 to 1 according to the troop size (larger troops had lower values). However, infant mortality showed no correlation

with troop size and values are lower than the above cited species, with the highest value being 0.23 and the lowest 0.50 (Jolly et al. 2002).

These comparisons may indicate that indri infants' survival is among the highest in Strepsirrhini, although survival estimates from captive condition may differ from the ones in wild populations. This comparative low infant mortality might be the result of Indri mothers keeping strict contact with the infant for many months. They carry the newborns until five months (Pollock 1975a) and share their activities for the first eight months of life (Thalmann et al. 1993).

Furthermore, an important behavioural factor that contributes to the low mortality caused by predators, is the constant group vigilance and specialized alert behaviour, which includes vocalisations, specific for aerial and terrestrial predators (Pollock 1975a; Maretti et al. 2010). Predation is not the only cause of infant mortality. In polygamous species, social and sex competition can expose infants to other environmental threats (Bronikowski et al. 2011).

We propose that indri territoriality, monogamy and family unit social organization reduce the impact of social causes of mortality present in polygamous species, such as infanticide or aggression between females (Mitani 1990).

Age-specific mortality shows a similar pattern between indri and sifaka, even if lifespan appears to be shorter in *P. verrauxi* (25–30 years) in comparison to the modelling estimates we obtained in indri of 30–35 years. This long lifespan is confirmed by field records from the nearby forest of Mitsinjo, where at least 1 individual is 35 years old (Rainer Dolch, personal communication). A shorter lifespan compared to indris is found also in baboons (*Papio cynocephalus*), which is around 27–28 years (Bronikowski et al. 2011). This species is terrestrial, has a polygamous mating system, and shows a similar mortality pattern, with high average mortality during the first and the second year of life of 0.30 (Altmann 1980).

The general shape and pattern of the survival curves appear not to be strongly sex-related. The same sex-specific survival pattern has been documented in another monogamous primate, Azara's night monkey (*Aotus azarae*), which exhibits both biparental care and a mortality pattern comparable between males and females (Larson et al. 2016). Our own findings on mostly overlapping survival trajectories between sexes in indris can be explained by its strictly monogamous mating system and lack of sexual dimorphism. In fact, survival rate is highly influenced by sex differences in species in which males and females are very dimorphic,

whereas it is not when the opposite condition occurs (Bronikowski et al. 2011). Indris, with no sexual dimorphism and comparable rates of survival between the sexes, falls entirely in this frame.

An important additional factor is indri territoriality and family unit social organization that limits social conflicts. In fact, an important difference between primates concerns the level of intra-specific competition for females that can increase males' mortality, typical in chimpanzees (*Pan troglodytes*), spider monkeys (*Ateles paniscus*), and orangutans (*Pongo pygmaeus)* in particular (Allman et al. 1998). However, male competition mostly occurs in polygynous species (among Strepsirrhines *Microcebus murinus* provides a valuable example; Fietz 1999) and indris are monogamous: the reproductive male and female form a stable pair, with recent evidence of genetic monogamy (Bonadonna et al. 2019), despite a case of extra-pair copulation having been reported in the literature (Bonadonna et al. 2014). Monogamy can indeed provide a valuable explanation for males and females overlapping survival rates. As Bronikowski et al. (2011) argue in their comparative study, the two sexes of a monogamous species tend to age at the same rate. Conversely, in polygynous species, the ageing rates differ between the sexes.

The comparable survival pattern in males and females may also be in part related to offspring care. Species in which the mother is the one mostly responsible for offspring care are characterized by a longer lifespan for females, while when both parents are equally responsible for offspring care, there tends to be no significant difference in the two sexes' survival (Allman et al. 1998). To summarize with Allman's words (Allman et al. 1998): "the sex that bears the greater burden in the care of offspring will tend to survive longer". As an example, Verraux's sifaka (*Propithecus verreauxi*) females give birth for the first time later, continue reproducing longer, and live longer than other primates (Bronikowski et al. 2011). Concerning indris, the reproductive pair defends a territory with comparable investment in territory advertisement: they participate equally to the song (equal phonation length between male and female; see Giacoma et al. 2010; De Gregorio et al. 2019a) either of advertisement or defense. Males are more active when inter-group encounters occur, and although they may therefore face a higher risk than females, territorial encounters and physical fights between neighbouring groups are extremely rare (Bonadonna et al. 2020). This is certainly a strategy to reciprocally monopolize reproduction of the male and the female of the pair, but it is also a way to supply indirect parental care.

Primate slow life histories can be an adaptive strategy when infant mortality varies greatly as a consequence of climate or social conditions (Richard et al. 2006). A work by Wright et al. (2008) conducted in the rainforest of Ranomafana reported that, for *Propithecus edwardsi*, in years when rain has been decreased during lactation months, infants of senescent mothers died before weaning. Indris are mainly folivorous (although they can integrate their diet with fruits; Pollock 1975a; Powzyk & Mowry 2003), and food is available all year long in the rainforest.

Conclusion

In conclusion, here we showed that, in accordance with what is generally found in primates (Bronikowski et al. 2011) males and female indri appear to have overlapping survival and mortality trajectories. We suggest that this can be explained by the lack of sexual dimorphism and the strictly monogamous mating system that characterizes this species.

Our results on indris, besides contributing to the growing availability of data on survival patterns in primates and lemurs in particular (Bronikowski et al. 2011, 2016), provide for the first time rigorous estimates of age-specific survival rates in indris. These demographic parameters represent an essential element in the development of population viability analyses, which will be a valuable tool to help decision-making regarding the conservation of this critically endangered lemur species (Traill et al. 2010).

Geolocation information

Madagascar, Maromizaha New Protected Area, coordinates: 18°56′49" S; 48°27′ 33"E.

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No potential conflict of interest was reported by the author(s).

Supplementary material

Supplemental data for this article can be accessed here.

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