Risky business: Sex differences in mortality and dispersal in a polygynous, monomorphic lemur

1 **Risky business: Sex differences in mortality and dispersal in a polygynous, monomorphic**

2 **lemur**

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26 **Running title:** Lemur mortality and dispersal

1 **Abstract**

2   Sexually selected traits and the use of strategies to enhance male reproductive success

3 (e.g., competition and dispersal) can yield sex differences in metabolic requirements, rates and

4 durations of growth and maturation, and the propensity for risky behavior, which are suggested

5 to result in age-specific sex differences in mortality and lifespan. We investigated age-specific

6 sex ratios, mortality, and dispersal in *Propithecus edwardsi* in Ranomafana National Park,

7 Madagascar. We predicted that, due to similarities in growth rates and body sizes, male and

8 female juvenile mortality rates would be comparable; because both sexes disperse and have

9 intense intersexual competition and aggression, adult mortality would be similar; and given

10 similarities in dispersal frequency and distance, the timing of dispersal would not differ. We used

11 80 group-years births, deaths, and dispersals ($N_{females}$=41, N_{males}=34) collected over 23y to

12 calculate sex ratios and survival curves. Females lived longer than males (maximum 32 and 19y,

13 respectively). Sex ratios were male-biased from sexual maturity through 17y, and female-biased

14 at birth and older ages. Infant survival probabilities were similar. Thus, differential development

15 and maturation are unlikely explanations for longer female lifespan in this species. Males were

16 more likely to survive from 2-18y. However, male annual survival probability declined quickly

17 around 13-18y; males continued to disperse until their deaths while females generally stopped

18 dispersing after 11y. We suggest that sex differences in the timing of dispersal and the unique

19 challenges of risky behavior at older ages may be sufficient to yield differences in male and

20 female lifespan.

21

22 **Keywords**: Sex ratio, *Propithecus edwardsi*, survival curve, dispersal, mortality, primate

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1   It is common to observe skewed adult sex ratios in mammals, despite the prediction by

2   Fisher (1930) of balanced sex ratios. Frequently, skewed adult sex ratios are the result of

3   differential mortality between males and females (Clutton-Brock et al.1977, 1982), with females

4   commonly living longer than males. Empirical studies of a broad array of mammalian and avian

5   species support the general theory that male survival is lower than female survival (Clutton-

6   Brock et al. 1982; Jorgenson et al. 1997; Modafferi and Becker 1997; Christe et al. 2006;

7   Bronikowski et al. 2011). This difference is often interpreted as a cost of sexually selected traits

8   and the propensity for risky behavior that enhances male reproductive success (Promislow 1992;

9   Moore and Wilson 2002; Setchell et al. 2005; Kraus et al. 2008). Variation in mortality and

10   reproduction between the sexes has important demographic, sexual selection, and life history

11   consequences (Gaillard et al. 1989; Magnhagen 1991; Andersson 1994). As a result,

12   understanding sex differences in life history patterns has been a central theme in ecological and

13   evolutionary disciplines (Bonduriansky et al. 2008).

14   Sexual conflict between males and females, particularly as it pertains to costs of

15   reproductive effort, has been proposed as an *ultimate* cause of sex-specific lifespan and mortality

16   patterns (Arnqvist and Rowe 2005; Bonduriansky et al. 2008). Increased male mortality due to

17   predation (Owen-Smith 1993), male-biased dispersal and movement patterns (Fedigan and Zohar

18   1997; Kraus et al. 2008), increased metabolic requirements (Clutton-Brock et al. 1982; 1985;

19   Bribiescas 2006), male-male competition (Clutton-Brock et al. 1982), and the possible

20   immunosuppressive effects of testosterone (Folstad and Karter, 1992; Roberts et al. 2004) have

21   all been suggested as *proximate* causes for the sex differences in survival and lifespan

22   (Bonduriansky et al. 2008; Bronikowski et al. 2011). However, without examining when

23   mortality occurs, understanding the factors determining sex-specific differences is limited. For

1   example, faster growth rates of males (compared to females) can lead to nutritional stress that

2   may make them more vulnerable during juvenility (Clutton-Brock et al. 1985; Fedigan and Zohar

3   1997), resulting in higher juvenile mortality. The 'fragile male' hypothesis addresses the

4   differential developmental trajectories of males and females and predicts higher rates of male

5   mortality during the juvenile period of development, particularly if there are periods of resource

6   scarcity (van Schaik and de Visser 1990; Janson and van Schaik 1993).

7   An alternative hypothesis, 'high risk, high gain', predicts higher male mortality rates

8   during adolescence and adulthood due to risky behavior (e.g., male-male competition or

9   dispersal; Trivers 1985; Rajpurohit and Sommer 1991). Empirical support for this hypothesis has

10 been documented across primate species (yellow baboons, *Papio cynocephalus*: Alberts and

11 Altmann 1995; vervet monkeys, *Chlorocebus aethiops:* Fairbanks et al. 2004; gray mouse

12 lemurs, *Microcebus murinus*: Kraus et al. 2008). Alternatively, higher average male mortality

13 may not be age-related, but rather due to increased risk of mortality during the breeding season

14 (Hoogland 2006; Kraus et al. 2008) or when environmental conditions are unfavorable (Coulson

15 et al. 2001; Bonenfant et al. 2002; Toïgo and Gaillard 2003). When the environment is

16 predictably unpredictable, sex differences in reproductive costs may cause females to forego

17 reproduction in suboptimal years and thus follow a 'bet hedging' strategy (Stearns, 1976, 1992;

18 Wright 1995; Gaillard and Yoccoz 2003). This strategy leads to the 'live slow, die old'

19 hypothesis (Bonduriansky et al. 2008), where disparities between male and female growth,

20 maturation, and life span may be due to females slowing down growth and development to

21 compensate for inter-annual climatic unpredictability. This results in 'early bloomer' males

22 (Richard et al. 2002) and longer female lifespans (Charnov and Berrigan 1993). This hypothesis

23 would suggest that mortality at all ages is expected to be higher in males than females.

1   In this paper, we investigate the life history strategies of male and female Milne-

2   Edwards' sifaka (*Propithecus edwardsi*). Understanding *P. edwardsi* life history and specifically

3   evaluating sex differences in lifespan can greatly add to evolutionary theory of sex-biased traits,

4   as this species lacks many characteristics commonly proposed to influence differences in male

5   and female lifespans in other species. For example, differential growth rates (Clutton-Brock et al.

6   1985; Fedigan and Zohar 1997) and sexual dimorphism (Promislow 1992) are predicted to drive

7   mortality differences among male and female juveniles, and adult lifespan. However, these traits

8   are not observed in *P. edwardsi* (King et al. 2011). Therefore, *P. edwardsi* females do not likely

9   follow the 'live slow, die old' strategy, despite living in an area of annual climatic and resource

10   variability (King et al. 2011) and having high female infant and juvenile mortality (Pochron et al.

11   2004). Sex differences in predation rates in many species may also explain differences in male

12   and female survival at various life stages (Christe et al. 2006), but there is no evidence for sex-

13   biased predation on *P. edwardsi* (Irwin et al. 2009). Although male-biased dispersal is known to

14   result in higher male mortality (e.g., yellow baboons: Alberts and Altmann 1995), both male and

15   female *P. edwardsi* disperse, with no significant differences in the frequency or distance of

16   dispersal detected (Morelli et al. 2009). Finally, male-biased aggression and competition for

17   mating opportunities may explain differences in lifespan (Clutton-Brock and Isvaran 2007);

18   however *P. edwardsi* are polygynous, and both males and females are aggressive and often

19   violent towards both sexes (Wright 1995, 1999; P. Wright unpublished data). Furthermore, total

20   testosterone levels do not differ between the sexes (Tecot et al., in prep.).

21   We examine age-based sex ratios and mortality to determine if there are sex-biased

22   survival rates and lifespans with *P. edwardsi*. Using 15 years of demographic data collected from

23   the same population as in this study, Pochron et al. (2004) explored patterns of female mortality

1 and fertility, and their implications for group sex ratios. We build upon this work by analyzing an

2 additional nine years of data, investigating both males and females, and studying population-

3 wide sex ratios. The 'fragile male' and 'high risk, high gain' hypotheses both predict sex-based

4 differences in mortality at different life stages, resulting in differences in sex ratios and male and

5 female lifespans. Given the lack of traits typically associated with divergent male and female

6 mortality rates and sex-biased longevity in primates and other mammals, we expected that males

7 and females would have similar sex ratios and lifespans. Specifically, we predicted that 1) due to

8 similarities in growth rates and body sizes, male and female juvenile mortality rates would be

9 comparable, and 2) because both sexes disperse and there is intense intersexual competition and

10 aggression, adolescent and adult mortality would be similar, resulting in similar lifespans. Given

11 the similarities in dispersal frequency and distance reported for this species (Morelli et al. 2009),

12 we also predicted that there would be no difference in the timing of dispersal that would lead to

13 divergent mortality rates. Lastly, we compare our findings with sex differences in survival and

14 group transfer or dispersal in other species, and discuss causal factors likely driving observed

15 patterns.

16

17 **Methods**

18 **Study Site**

19 Data were derived from a long-term and ongoing study (1986-present) of *Propithecus edwardsi*

20 in Ranomafana National Park (RNP) in southeastern Madagascar (21º16S latitude and 47º20E

21 longitude; Wright 1992). RNP consists of approximately 43,500 hectares of sub-montane

22 rainforest, which ranges from 559-1396 m in elevation, has an average temperature of 21ºC, and

23 receives an average of 3090 mm of rain per year (Tecot 2008; Wright et al. 2008). The climate at

1   RNP varies seasonally with higher rainfall and temperature during the months of December-

2   March than during the remainder of the year (Overdorff 1993; Hemingway 1996; Wright 2006).

3   Within this seasonal pattern there is considerable inter-annual variation with the monthly

4   distributions of rain and fruit being unpredictable from year to year (King et al. 2011).

5   Individuals in our study were members of four social groups in the area of RNP known as

6   Talatakely. The Talatakely study site is at an altitude of 900-1100 m and is accessible to

7   researchers through a system of trails.

8

9   **Study Subjects**

10   *Propithecus edwardsi* are sexually monomorphic with both males and females having an

11   adult body mass averaging 5.7 kg (King et al. 2011). Social groups range in size from 2-9

12   individuals and typically include one or two breeding females (Pochron and Wright 2003a;

13   Morelli et al. 2009). Reproduction is highly seasonal and most births occurred from May to July

14   (with the exception of 1 in 54 births, which occurred in September; P. Wright unpublished data).

15   Dispersal by both sexes peaks during September and individuals may disperse several times in

16   their lifetime (Morelli et al. 2009). Pochron et al. (2004) describe the history of research and

17   habituation of the study groups, and aspects of demography have been published previously

18   (Wright 1995; Pochron and Wright 2003a; Pochron et al. 2004). Male and female growth rates

19   and durations do not differ (King et al. 2011), and age categories for both sexes were defined as

20   follows: infants <1 year; juveniles 1-3.5 years; adults >3.5 years (Morelli et al. 2009).

21   Data used in this study represent 80 group-years of observations (24 years each for Group

22   I and Group II; 19 years for Group III; 13 years for Group IV). Study animals (n=41 females, 34

23   males) were habituated to the presence of humans; each group was followed for a minimum of

1   five days per month, during which time focal follows continued from dawn to dusk. All births,

2   deaths, immigrations, and emigrations were recorded *ad libitum* and are accurate to within an

3   average of one week (see Pochron et al. 2004 for details). Individuals were identifiable by collar-

4   tag combinations (see Wright 1995 for capture and marking procedures used with this

5   population).

6   The date of birth for most individuals born since the start of this study is known within

7   two weeks (n=30 females, 22 males), and the ages of some individuals that entered the study

8   groups from unmonitored groups as well as some of those who were born before 1986 were

9   estimated on the basis of tooth wear documented during captures (n= 8 females, 8 males; King et

10   al. 2005; Wright et al. 2008). The ages of the remaining individuals (dates of birth not observed

11   and dental molds not taken) were estimated (n=3 females,46 males) by PCW, facilitated by

12   seasonal breeding and obvious differences in body mass in 1-, 2-, 3-, and 4-year olds. The ages

13   of two older individuals (female,7 years; male 6 years) were estimated during captures on the

14   basis of body mass, tooth tartar and tooth sharpness.

15   All work was approved by the Stony Brook University Institutional Animal Care and Use

16   Committee. All procedures conformed to the American Society of Primatologists' Principles for

17   the Ethical Treatment of Non Human Primates and to the laws of the Republic of Madagascar.

18

19   **Data and Analyses**

20   We analyzed sex ratios by calculating the proportion of females to the population as a

21   whole over the entire course of the study (1986-2009) for each age, and annually. Using survival

22   analyses, we examined the pattern of age-specific exits from social groups and evaluated the

23   effect of sex on the cumulative probability of exiting. Survival analyses are a flexible framework

1 useful for determining the time it takes for an event to occur; our events were exits from a social

2 group, which were defined as: 1) confirmed death or 2) confirmed dispersal (within or out of the

3 study population). Dispersals are defined generally as any transition from a group and not

4 restricted to dispersal from an animal's natal group. Despite best efforts, 10 events could not be

5 reliably classified as either dispersal out of the study area or a death, but were definitely an exit

6 from the study area. Instead of removing the observations or censoring the individuals, which

7 would introduce bias, as their exclusion would not be random but conditioned on the events in

8 which we are interested (White and Garrott 1990), we provide two analyses of dispersals and

9 survival: 1) assuming unknowns are all deaths, and 2) assuming unknowns are all dispersals.

10 Either assumption is extreme, such that we expect the true cumulative distribution to lie in

11 between the two. We restrict our interpretation of results as it pertains to the effect of sex only if

12 both analyses agree.

13   Survival data included 26 observations of males and 38 observations of females in the

14 study area. Individuals that dispersed outside of the study area were not followed until death.

15 Thus, we assumed that dispersing within, out of, and into the study area are stochastic processes

16 rather than Markovian, such that observed dispersals are a random variable, sampled from a

17 greater population. We observed males disperse 19 times and females disperse 15 times, in total

18 for each.

19   We used the Cox proportional hazards regression model (Cox 1972) implemented in the

20 R package eha (Göran 2012) to estimate cumulative distributions of exits. We were interested in

21 comparing two nested models, null (no covariates) and sex (included sex effect on survival

22 cumulative distribution), for estimating 1) the time until a group dispersal, and 2) time until

23 death. We considered t, the time until an event, as a random variable where our model of event i

1   was defined (specifically for the model including the sex covariate) as $h_i(t|\text{Sex}) = h_0(t) * e^{(\beta_1 * \text{Sex})}$.

2   The cox model allows the baseline hazard function (h_0) to be unspecified while a linear model is

3   used to incorporate covariate effects on the survival distribution; as such, the model is semi-

4   parametric. Depending on the individual, observations may span an individual's entire life, are

5   left truncated when individuals transfer into the study population, or right censored when animals

6   transfer out of the study population. Parameter estimation was done using maximum-likelihood

7   as it is more robust to tied-data (Broström 2002), and model parsimony was evaluated using

8   Akaike's Information criterion with a second-order bias correction for small sample size (AIC_c;

9   Burnham and Anderson 2002). We compared models to evaluate the effect of sex on both

10   dispersals and survival by calculating model probabilities, Pr(model j| data), known as 'Akaike

11   weight' (Burnham et al. 2011). The proportional hazards assumption of our model was tested for

12   each analysis using weighted residuals (Grambsch and Therneau 1994) and implemented in the

13   R package survival (Therneau 2012); we used α = 0.05 to determine statistical significance.

14

15   **RESULTS**

16   **Sex Ratios**

17   Age-specific population sex ratios were female-biased at birth until 2-2.9 years, at which

18   point they became equal (Appendix S1, Figure 1a). After 2.9 years of age, sex ratios became

19   male-biased and remained so until age 17. At age 17-17.9, the number of females was again

20   equal to or greater than the number of males. Therefore, for the majority of age categories, the

21   sex ratio of this population was male-biased, but with more young and old females than males.

22   The mean sex ratio of this population was in flux from year to year and not consistently male- or

23   female-biased (Appendix S2, Figure 1b).

1 **Survival**

2   Neither survival analysis rejected the proportional hazards assumption (P > 0.05; Table

3 1). When unknowns were assumed to be dead, AIC_c values for our two models were 319.10

4 (null) and 317.66 (sex). Akaike weight was 0.67 (sex) and 0.32 (null), such that the model with

5 the effect of sex was 2.06 times the more parsimonious model, given our data. Under the sex

6 model, the median predicted lifespan of males and females were 1.1 (0.50 – 3.25, 95% CI) and

7 2.8 (0.50 – 12.2, 95% CI), respectively. When assuming the unknowns were all dispersals, AICc

8 values were 297.39 (null) and 294.53 (sex). Akaike weight was 0.81 (sex) and 0.19 (null); thus

9 the model with the effect of sex was 4.16 times the more parsimonious model, given our data.

10 Under the sex model, the median predicted lifespans of males and females were 2.17 (1.10 –

11 4.21, 95% CI) and 3.1 (1.85 – 4.67, 95% CI), respectively.

12   Overall, regardless of the assumption with the unknowns, there is moderate support for a

13 difference in cumulative probabilities of age-specific survival for males and females; the effect

14 of sex was in the same direction (Table 1). Both sexes experience high mortality during the first

15 two years of life (Figure 2). After about two years, male and female cumulative survival

16 probabilities diverge, irrespective of the assumption regarding the unknowns; generally more

17 males are likely to survive during the ages of 2 to 18. However, between the ages of 9 and 18,

18 male survival probability declines quickly whereas the decline for females is more gradual.

19 After age 18, the probability of female but not male mortality approaches zero. The oldest male

20 observed in this study was 19 years old; there is no evidence within our study area of males

21 living beyond this age. In contrast, females that reach 19 years of age are likely to live into their

22 early 30s.

23

1 **Dispersals**

2   We found the proportional hazards assumption was not rejected for either dispersal

3 analyses (P > 0.05). When assuming the unknowns had all died, the AIC_c values of the dispersal

4 analyses were 371.52 (null) and 368.68 (sex). Akaike weight was 0.81 (sex) and 0.19 (null), such

5 that the model with the effect of sex was 4.15 times the more parsimonious model, given the

6 data. Given the sex model, the median predicted ages of dispersal of males and females were

7 7.12 (5.01 – 8.00, 95% CI) and 4.58 (4.25 – 6.00, 95% CI), respectively. When assuming the

8 unknowns had all dispersed, AICc values were 531.47 (null) and 528.82 (sex). Akaike weight

9 was 0.79 (sex) and 0.21 (null); thus the model with the effect of sex was 3.77 times the more

10 parsimonious model, given the data. Given the sex model, the median predicted ages at dispersal

11 of males and females were 7.81 (6.62 – 8.91, 95% CI) and 4.81 (4.62 – 7.11, 95% CI),

12 respectively.

13   There was moderate support for a difference in cumulative probabilities of age-specific

14 dispersal in both males and females, regardless of the assumptions made for unknowns, and the

15 effect of sex was in the same direction (Table 1). Neither males nor females disperse before they

16 are 3-4 years of age (Figure 3). Males have a consistently higher probability of dispersing,

17 especially between the ages of 6-10. The highest probability of female dispersal occurs between

18 the ages of 4-6 and then declines quickly; by age 10 females have less than a 0.1 probability of

19 dispersing. Due to a single unknown female exit from the population at 27 years of age, it is

20 unclear whether females stop dispersing at the age of 21 (last confirmed dispersal) or continue to

21 have a small probability of dispersing until they die.

22

23 **Discussion**

1   Sexual selection theory predicts that intense competition in males for reproductive

2 opportunities results in higher mortality rates in males over the course of their lifetime (Trivers

3 1972). Across polygynous species of mammals, including primates, there is consistent support

4 for accelerated mortality in males (Clutton-Brock and Isvaran 2007; Bronikowski et al. 2011).

5 As we predicted, and contrary to the 'fragile male' and 'live slow, die old' hypotheses, males and

6 females experienced similar probabilities of infant survival. After age two (during juvenility),

7 males, not females, were more likely to survive until approximately 18. Because growth rates

8 and durations also do not differ in this species (Morelli et al. 2009; King et al. 2011), we can

9 reject differential development and maturation as significant factors influencing longevity in this

10 species. Males appear to live 'faster' lives simply by virtue of dying younger. This pattern differs

11 from the 'early blooming' observed in male *P. verreauxi* (Richard et al. 2002).

12   Although we expected that male and female survivorship would be approximately equal

13 during adulthood, males had higher survival than females during adulthood. Though both sexes

14 are aggressive, and testosterone levels do not differ among males and females (or are seasonally

15 higher in males) (Tecot et al., in prep.), higher female mortality may be related to female

16 dominance in this species (Pochron and Wright 2003b). However, as predicted by the 'risky

17 male' hypothesis, at around 13-18 years of age male annual survival probability declined

18 quickly. After the age of 18, male mortality exceeded that of females, potentially as a

19 consequence of continuous dispersal by males at older ages. Our data reveal that variability in

20 the timing and causes of sex-specific mortality lead to complex patterns of sexual asymmetries in

21 survivorship at different life stages.

22 ***Sex-Ratios***

1   Our data show that birth sex ratios were skewed towards females, in contrast with several

2   other primate species where birth sex ratios are typically nearly equal (see Fedigan and Zohar

3   1997), or male-biased, as in the closely related Verreaux's sifaka *(Propithecus verreauxi)*

4   (Richard et al. 1991, 2002). Although infant mortality was high in both sexes, as is typical for

5   lemurs (Wright 1999; Richard et al. 2002), sex ratios became male-biased prior to natal

6   dispersal, indicating that juvenile mortality was greater for females than males. Given the greater

7   probability of female mortality during the juvenile period of development, our data are

8   inconsistent with the 'fragile male hypothesis' supported for other species (Clutton-Brock et al.

9   1982; van Schaik and de Visser 1990; Owen-Smith 1993; Fedigan and Zohar 1997; Loison et al.

10   1999; Alberts and Altmann 2003; Setchell et al. 2005; see van Schaik and de Visser 1990 for

11   review). Though birth sex ratios differ in *P. edwardsi* and *P. verreauxi*, patterns of sex-based

12   infant and early juvenile mortality suggest that males in neither species are fragile. On the

13   contrary, females appear to be the fragile sex during infancy. If females have a greater mortality

14   rate from infancy through development and maturation, why is it that we ultimately see greater

15   female longevity?

16   ***Patterns of Dispersal***

17   Because previous research on this species reported that male and female average

18   dispersal frequency or distance did not differ (Morelli et al. 2009), we predicted similar patterns

19   in the rate and timing of dispersal. Instead, our data reveal that there were differences in the

20   timing and rates of dispersal between males and females. Specifically, males continued to

21   disperse until their deaths, while females generally stopped dispersing after approximately 11

22   years of age. Only one female dispersed after 11, at age 21 (with one additional unknown

23   disappearance at age 27). The cause of this dispersal remains unknown. The continued dispersal

1   by males throughout their lifetime and subsequent mortality is consistent with the 'high risk,

2   high gain' hypothesis, predicting higher mortality rates in males during adolescence and

3   adulthood due to risky behavior (Trivers 1985; Rajpurohit and Sommer 1991; Fedigan and Zohar

4   1997). Because mortality risk can be greater in dispersers relative to their philopatric

5   conspecifics (e.g., Isbell et al. 1993; Alberts and Altmann 1995), males continue to incur this risk

6   later in life compared with females. We suggest that dispersal between groups affects male

7   longevity by removing individuals from the population not just as emigrants, but by reducing the

8   survival of individuals due to the risks incurred during dispersal.

9   Research on blackbirds (Greenwood and Harvey 1976) indicates that large differences in

10   lifespan can exist between dispersing and non-dispersing individuals. The sources of risk for

11   emigrants may include increased predation risk (Isbell et al. 1990; Hass and Valenzuela 2002),

12   decreased knowledge of resources (Waser and Jones 1983), and social costs associated with the

13   loss of familiar group-mates (Isbell and van Vuren 1996). Our study suggests that dispersal

14   carries great risk for individuals. *Propithecus edwardsi* groups tend to remain in discrete home

15   ranges, and emigration consists of movement out of a familiar area, typically by a single

16   individual (Wright 1995; P. Wright unpublished data). Male survival curves incorporating both

17   types of exits (mortality and dispersal; data not shown), were age independent, with cumulative

18   exits occurring at a near constant rate throughout life, reflecting the dispersal patterns observed.

19   In contrast, female survival curves were age-dependent, showing a declining rate of exiting the

20   population (via mortality and dispersal) with age, a result that is also consistent with observed

21   dispersal behavior. While correlative, these results suggest that dispersal is met with higher

22   mortality, and the longer female lifespan in this species may be due to a lack of females

23   transferring groups at older ages.

1   Why, in this species, do males continue to disperse later in life? Although lacking the

2   sexually dimorphic characteristics of many polygynous species, *Propithecus edwardsi* are

3   polygynous, and intrasexual competition may explain differences in male and female dispersal

4   behavior. Often, in a polygynous mating system there is rank-related reproductive success,

5   resulting in significant reproductive skew (e.g., Setchell et al. 2005). Furthermore, the

6   cumulative detrimental effects of intense intrasexual competition also limit male breeding

7   success. Thus, males are under weaker selection to live long lives relative to females (Clutton-

8   Brock and Isvaran 2007; Bronikowski et al. 2011). In *P. edwardsi,* competition among males is

9   particularly violent during the dispersal and mating seasons (P. Wright, unpublished data).

10 Similar to male ringtailed lemurs (*Lemur catta*), who also disperse outside of the mating season

11 (Parga and Lessnau 2008), secondary dispersal by both male and female *P. edwardsi* has a

12 reproductive function (Morelli et al. 2009). During the four months of the dispersal season, the

13 frequency of scent-marking increases (Pochron et al. 2005ab), androgens are at their peak (Tecot

14 et al. 2010; S. Tecot in prep.), and testes begin to increase in size, reaching their maximum

15 during the mating season (Pochron and Wright 2002; Pochron et al. 2002; Morelli 2008).

16   Male-directed aggression by both males and females during the mating and dispersal

17 seasons can be severe, leading to deep lacerations, castration, and even death (Wright 1995,

18 1999; P. Wright unpublished data), similar to that observed during the mating season of other

19 species (e.g., *Propithecus verreauxi*: Jolly 1966; Lawler et al. 2005). These intense fights

20 typically occur between residents and immigrants (Morelli 2008), as groups seldom contain more

21 than one adult male for extended periods of time (Morelli et al. 2009). It is important to note that

22 both males and females disperse, reproductive competition occurs among females as well as

23 males (Morelli et al. 2009), and both sexes benefit reproductively by dispersal behavior. For

1   instance, infanticidal events during hostile group takeovers by a dispersing individual result in

2   increased reproductive opportunities for the invader, whether male or female (Morelli et al.

3   2009).

4   Despite the information we have on aggressive behavior in this species, several things

5   remain unclear. For instance, we do not know whether males or females incur more wounds or

6   differentially participate in such heightened aggressive bouts. In addition, we do not know

7   whether old individuals are more likely than young individuals to be seriously injured in such

8   bouts. Such detailed data would help determine whether death as a result of dispersal-related

9   aggression might explain the sex-biased mortality patterns observed. Fedigan and Zohar (1997)

10   determined that mortality in male Japanese macaques (*Macaca fuscata*) was higher in the

11   birth/emigration season than the mating season. Because emigration in *P. edwardsi* is also

12   largely seasonal, a seasonal analysis can help test the hypothesis that dispersal is directly related

13   to higher rates of male mortality. It is also likely that dispersal may impose unique challenges for

14   aged sifaka. The chances of engaging in intense intrasexual competition and incurring costs

15   associated with such competition may cause 'cumulative phenotypic damage' in males (Clutton-

16   Brock and Isvaran 2007), suggesting that immigration is physiologically riskier the more it

17   occurs. Experimental research on the soil mite (*Sancassania berlesei*) model system found

18   greater per capita mortality in old adults versus younger adults during dispersal (Bowler and

19   Benton 2009), suggesting that dispersing at older ages carries greater costs. As individuals age,

20   the ability to perform certain activities may deteriorate (e.g., reduced sensory acuity or

21   locomotion), increasing the difficulty of detecting or escaping predators, locating resources, or

22   assimilating into new groups. There is preliminary evidence to suggest that locomotion in

23   *Propithecus edwardsi* may be compromised as individuals age: old females spend more time

1   feeding and less time traveling than young females, particularly when traveling on steep terrain

2   (E. Achilles et al. in prep), and trabecular bone volume in the femoral head may decrease in aged

3   females (A. Chan et al. unpublished data). If males undergo similar age-related declines as

4   females, the costs of dispersal may be exacerbated in older males as they continue to disperse. If

5   males, like females, incur these additional costs, why continue dispersing? The answer may lie in

6   sex ratios. Sex ratios and the availability of mates within a group are known to influence whether

7   an individual disperses (Morelli et al. 2009). Aggression is typically directed toward the most

8   numerous sex in the group, thus skewing the sex of individuals driven out of the group (Wright

9   1995; P. Wright unpublished data). Because males outnumber females from ages 2.9 to 17, males

10   may be driven out of the group more frequently than females throughout their lives.

11

12   ***Kin, Dispersal, and Mortality***

13   This study has broader implications for understanding social dynamics. In general it is

14   predicted that relatives show kin bias, participating in more affiliative and cooperative behavior

15   with one another (Hamilton 1963), resulting in direct fitness benefits (*Alouatta seniculus*: Pope,

16   1990, 2000; *Macaca fuscata*: Pavelka et al. 2002; *Cercopithecus aethiops sabaeus*: Fairbanks

17   1988). When there is a lack of sex-biased dispersal, there tends to be a bias in dispersal distance

18   such that one sex is more likely to encounter relatives in their non-natal groups than the other

19   (Waser et al. 1994; reviewed in Kappeler 2008). For instance, in the solitary Coquerel's dwarf

20   lemur *(Mirza coquereli)* females have shorter dispersal distances than males, resulting in a

21   dispersed matrilineal population structure (Kappeler et al. 2002), creating the opportunity for

22   sex-specific kin bias. Despite an overall lack of dispersal bias in this species (Morelli et al.

23   2009), same-sex pairs living together were biased, with female pairs living together longer than

1 male pairs (Morelli et al. 2009; P. Wright unpublished data). While the sample sizes are small,

2 sex differences in group tenure are notable: female adult relatives lived together 5-10 years,

3 while male adults (relatives and non-relatives) lived together 1-2 years on average (and one of

4 these males was typically born into the group; P. Wright unpublished data). The slower rate of

5 female dispersal after 5-8 years of age that we report in this study can explain why females are

6 more likely to live with other females for longer periods of time, and suggests that opportunities

7 for long-term relationships are greater for females than males (though it should be noted that low

8 fertility and high infant and juvenile mortality reduce opportunities for large kin groups in the

9 species as a whole [Pochron et al. 2004]). As a consequence, males may experience social stress

10 more often than females. In both nonhuman primates and humans, individuals well integrated into

11 strong social relationships have a greater likelihood of surviving than those in weak social

12 relationships (Holt-Lunstad et al. 2010; Silk et al. 2010), demonstrating the potential influence of

13 such relationships on mortality and lifespan.

14

15 **Conclusions**

16 In our population, early female-biased sex ratios and high mortality resulted in male-

17 biased sex ratios from sexual maturity through 18 years of age, a pattern also observed in other

18 lemur species (Kappeler 2000; Ostner and Kappeler 2004), including the closely related

19 *Propithecus verreauxi*. Although male and female mortality rates were more similar to each

20 other by age 5 years, our data reveal that females dispersed earlier than males. Coupled with

21 higher female infant mortality, this resulted in an initially higher rate of females leaving the

22 population, either through dispersal or death. Exit rates between males and females then

23 converged at age 10, with males and females being equally likely to exit the population, either

24 through death or dispersal until age 14. After 14 years of age, males continued to disperse from

1   the population steadily, whereas females remained until their deaths. This continued dispersal by

2   males is the primary explanation for female-biased sex ratios at older ages and, ultimately, longer

3   female lifespans.

4   The results of this study begin to address the importance of how different life history

5   strategies can influence longevity. We found support for the 'Risky Male' hypothesis, wherein

6   risky behavior occurs at older ages in males than in females, resulting in shorter male lifespans.

7   Our results also highlight critical shifts in mortality and dispersal rates that produced the specific

8   sex-ratio patterns observed at any given point in time and may further elucidate the causes for

9   female-biased lifespan in other monomorphic lemuroidea (*Propithecus verreauxi:* Richard et al.

10 2002; *Lemur catta:* Gould et al. 2003; *Microcebus murinus:* Kraus et al. 2008). Further studies

11 are needed to investigate cause of death and help determine why females have higher early

12 mortality, why males continue to disperse later in life, and what factor(s) are interacting to

13 contribute to the patterns observed in this population.

14

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20

Acknowledgments

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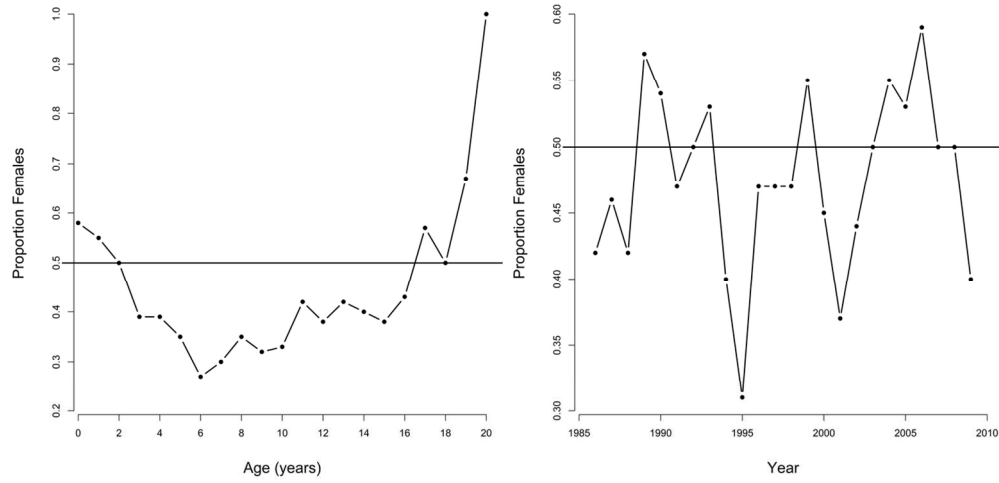
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3   1   Figure 1. Proportion of female *Propithecus edwardsi* in Ranomafana National Park, Madagascar
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5   2   from 1986-2009 by (a) age, and (b) year. The horizontal line represents an equal sex ratio.
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11   4   Figure 2. Cumulative probability of survival for male and female Milne-Edwards' sifaka
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13   5   (*Propithecus edwardsi*) in Ranomafana National Park, Madagascar between 1986-2009.
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15   6
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18   7   Figure 3. Cumulative probability of dispersal for male and female Milne-Edwards' sifaka
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20   8   (*Propithecus edwardsi*) in Ranomafana National Park, Madagascar between 1986-2009.
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1   **Table 1.** Proportional hazards regression estimates, statistical tests of significance, and test of

2   model assumptions of *Propithecus edwardsi* survival and dispersal

Analysis Type	Analysis	$\hat{\beta}_{\text{sex}}$	$SE(\hat{\beta}_{\text{sex}})$	χ^2	df	P
Assumption Test						
	1	NA	NA	0.06	1	0.812
	2	NA	NA	1.55	1	0.213
	3	NA	NA	2.65	1	0.103
	4	NA	NA	1.77	1	0.183
Survival						
	1	-0.374	0.21	3.8	1	0.05
	2	-0.547	0.26	4.4	1	0.035
Dispersal						
	3	-0.483	0.225	4.6	1	0.032
	4	-0.418	0.211	3.9	1	0.048

3   NA indicates the cell is "not applicable" to the row-column combination. Analyses 1 and 3

4   assume unknown exits died, and 2 and 4 assume unknown exits transferred

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Figure 1. Proportion of female *Propithecus edwardsi* in Ranomafana National Park, Madagascar from 1986-2009 by (a) age, and (b) year. The horizontal line represents an equal sex ratio.
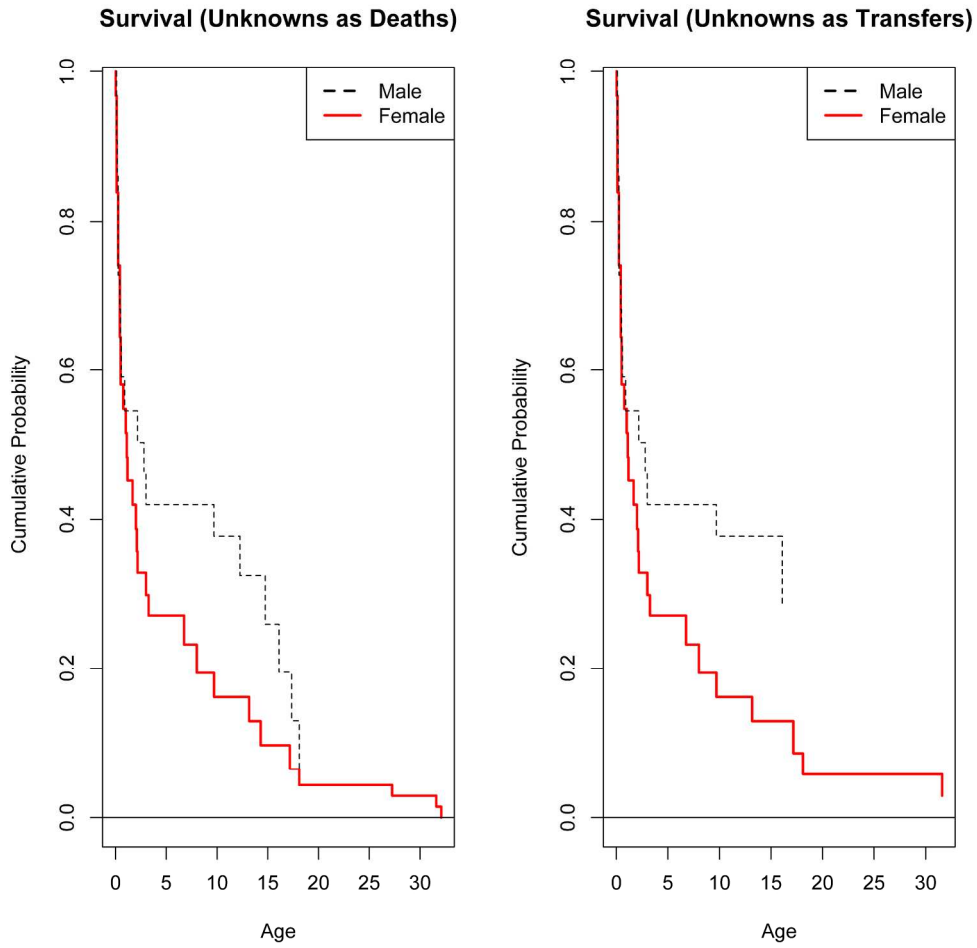63x31mm (600 x 600 DPI)

Figure 2. Cumulative probability of survival for male and female Milne-Edwards' sifaka (*Propithecus edwardsi*) in Ranomafana National Park, Madagascar between 1986-2009.
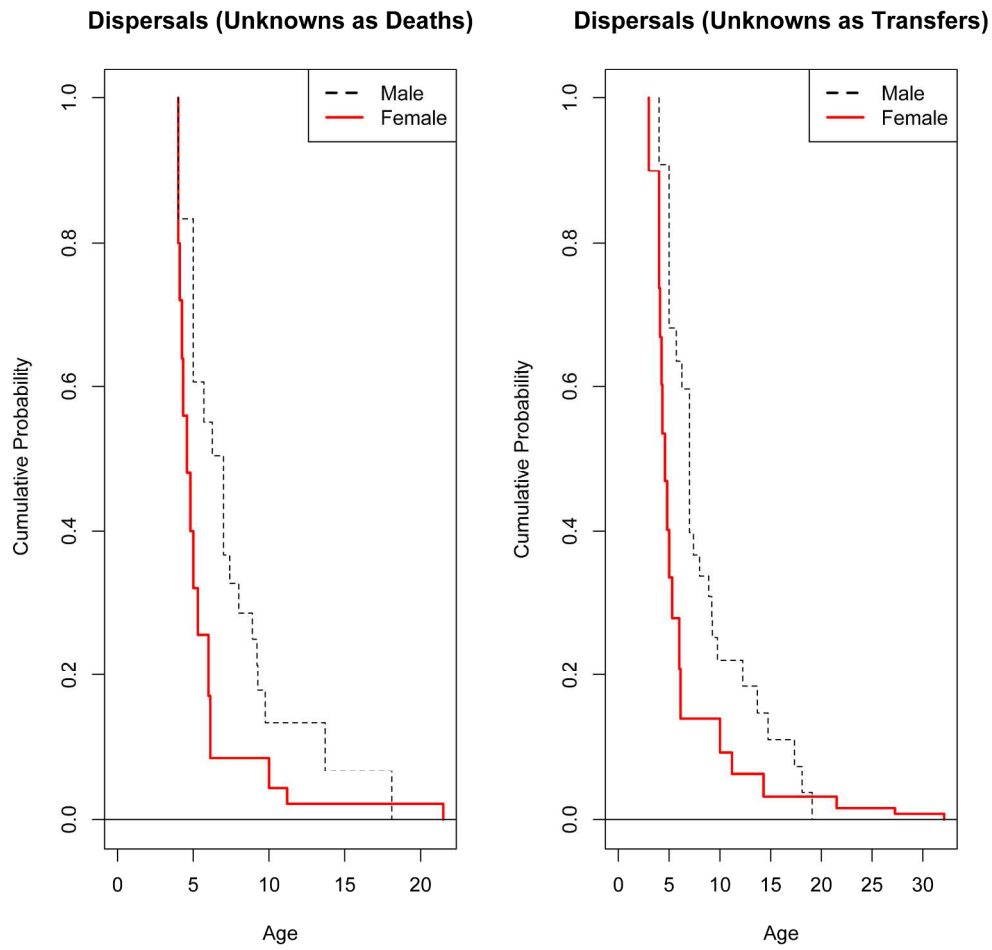105x105mm (600 x 600 DPI)

Figure 3. Cumulative probability of dispersal for male and female Milne-Edwards' sifaka (*Propithecus edwardsi*) in Ranomafana National Park, Madagascar between 1986-2009.
105x105mm (600 x 600 DPI)

Females of many mammal species live longer than males. We show that Milne-Edwards' sifaka, a lemur species lacking traits traditionally associated with longer female lifespan, also live longer than males. Longer female lifespan is not associated with sex differences in growth, body mass, competition, or rate and distance of dispersal. We suggest that the cumulative effects of risky behavior (dispersal) at older ages by males, and not females, cause males to live significantly shorter lives.