

## Original Article

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

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Sexually selected traits and the use of strategies to enhance male reproductive success (e.g., competition and dispersal) can yield sex differences in metabolic requirements, rates and durations of growth and maturation, and the propensity for risky behavior, which are suggested to result in age-specific sex differences in mortality and life span. We investigated age-specific sex ratios, mortality, and dispersal in *Propithecus edwardsi* in Ranomafana National Park, Madagascar. We predicted that, due to similarities in growth rates and body sizes, male and female juvenile mortality rates would be comparable; because both sexes disperse and have intense intersexual competition and aggression, adult mortality would be similar; given similarities in dispersal frequency and distance, the timing of dispersal would not differ. We used 80 group-years births, deaths, and dispersals ( $N_{\text{females}} = 41$ ,  $N_{\text{males}} = 34$ ) collected over 23 years to calculate sex ratios and survival curves. Females lived longer than males (maximum 32 and 19 years, respectively). Sex ratios were male biased from sexual maturity through 17 years and female biased at birth and older ages. Infant survival probabilities were similar. Thus, differential development and maturation are unlikely explanations for longer female life span in this species. Males were more likely to survive from 2 to 18 years. However, male annual survival probability declined quickly around 13–18 years; males continued to disperse until their deaths, whereas females generally stopped dispersing after 11 years. We suggest that sex differences in the timing of dispersal and the unique challenges of risky behavior at older ages may be sufficient to yield differences in male and female life span.

**Key words:** dispersal, mortality, primate, *Propithecus edwardsi*, sex ratio, survival curve. [*Behav Ecol*]

## INTRODUCTION

It is common to observe skewed adult sex ratios in mammals despite the prediction by Fisher (1930) of balanced sex ratios. Frequently, skewed adult sex ratios are the result of differential mortality between males and females (Clutton-Brock et al. 1977, 1982), with females commonly living longer than males. Empirical studies of a broad array of mammalian and avian species support the general theory that male survival is lower than female survival (Clutton-Brock et al. 1982; Jorgenson et al. 1997; Modaferrri and Becker 1997; Christe et al. 2006; Bronikowski et al. 2011). This difference is often interpreted as a cost of sexually selected traits and

the propensity for risky behavior that enhances male reproductive success (Promislow 1992; Moore and Wilson 2002; Setchell et al. 2005; Kraus et al. 2008). Variation in mortality and reproduction between the sexes has important demographic, sexual selection, and life-history consequences (Gaillard et al. 1989; Magnhagen 1991; Andersson 1994). As a result, understanding sex differences in life-history patterns has been a central theme in ecological and evolutionary disciplines (Bonduriansky et al. 2008).

Sexual conflict between males and females, particularly as it pertains to costs of reproductive effort, has been proposed as an ultimate cause of sex-specific life span and mortality patterns (Arnqvist and Rowe 2005; Bonduriansky et al. 2008). Increased male mortality due to predation (Owen-Smith 1993), male-biased dispersal, and movement patterns (Fedigan and Zohar 1997; Kraus et al. 2008), increased metabolic requirements (Clutton-Brock et al. 1982, 1985; Bribiescas 2006), male–male competition

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(Clutton-Brock et al. 1982), and the possible immunosuppressive effects of testosterone (Folstad and Karter 1992; Roberts et al. 2004) have all been suggested as proximate causes for the sex differences in survival and life span (Bonduriansky et al. 2008; Bronikowski et al. 2011). However, without examining when mortality occurs, understanding the factors determining sex-specific differences is limited. For example, faster growth rates of males (compared with females) can lead to nutritional stress that may make them more vulnerable during juvenility (Clutton-Brock et al. 1985; Fedigan and Zohar 1997), resulting in higher juvenile mortality. The “fragile male” hypothesis addresses the differential developmental trajectories of males and females and predicts higher rates of male mortality during the juvenile period of development, particularly if there are periods of resource scarcity (van Schaik and de Visser 1990; Janson and van Schaik 1993).

An alternative hypothesis, “high risk, high gain,” predicts higher male mortality rates during adolescence and adulthood due to risky behavior (e.g., male–male competition or dispersal; Trivers 1985; Rajpurohit and Sommer 1991). Empirical support for this hypothesis has been documented across primate species (yellow baboons, *Papio cynocephalus*: Alberts and Altmann 1995; vervet monkeys, *Chlorocebus aethiops*: Fairbanks et al. 2004; gray mouse lemurs, *Microcebus murinus*: Kraus et al. 2008). Alternatively, higher average male mortality may not be age related, but rather due to increased risk of mortality during the breeding season (Hoogland et al. 2006; Kraus et al. 2008) or when environmental conditions are unfavorable (Coulson et al. 2001; Bonenfant et al. 2002; Toïgo and Gaillard 2003). When the environment is predictably unpredictable, sex differences in reproductive costs may cause females to forego reproduction in suboptimal years and thus follow a “bet hedging” strategy (Stearns 1976, 1992; Wright 1995; Gaillard and Yoccoz 2003). This strategy leads to the “live slow, die old” hypothesis (Bonduriansky et al. 2008), where disparities between male and female growth, maturation, and life span may be due to females slowing down growth and development to compensate for interannual climatic unpredictability. This results in “early bloomer” males (Richard et al. 2002) and longer female life spans (Charnov and Berrigan 1993). This hypothesis would suggest that mortality at all ages is expected to be higher in males than in females.

In this article, we investigate the life-history strategies of male and female Milne-Edwards’ sifaka (*Propithecus edwardsi*). Understanding *P. edwardsi* life history and specifically evaluating sex differences in life span can greatly add to evolutionary theory of sex-biased traits, as this species lacks many characteristics commonly proposed to influence differences in male and female life spans in other species. For example, differential growth rates (Clutton-Brock et al. 1985; Fedigan and Zohar 1997) and sexual dimorphism (Promislow 1992) are predicted to drive mortality differences among male and female juveniles, and adult life span. However, these traits are not observed in *P. edwardsi* (King et al. 2011). Therefore, *P. edwardsi* females do not likely follow the “live slow, die old” strategy, despite living in an area of annual climatic and resource variability (King et al. 2011) and having high female infant and juvenile mortality (Pochron et al. 2004). Sex differences in predation rates in many species may also explain differences in male and female survival at various life stages (Christe et al. 2006), but there is no evidence for sex-biased predation on *P. edwardsi* (Irwin et al. 2009). Although male-biased dispersal is known to result in higher male mortality (e.g., yellow baboons: Alberts and Altmann 1995), both male and female *P. edwardsi*

disperse, with no significant differences in the frequency or distance of dispersal detected (Morelli et al. 2009). Finally, male-biased aggression and competition for mating opportunities may explain differences in life span (Clutton-Brock and Isvaran 2007); however, *P. edwardsi* are polygynous, and both males and females are aggressive and often violent toward both sexes (Wright 1995, 1999; Wright P, unpublished data). Furthermore, total testosterone levels do not differ between the sexes (Tecot SR, Zohdy S, Jernvall J, Wright PC, in preparation).

We examine age-based sex ratios and mortality to determine if there are sex-biased survival rates and life spans with *P. edwardsi*. Using 15 years of demographic data collected from the same population as in this study, Pochron et al. (2004) explored patterns of female mortality and fertility and their implications for group sex ratios. We build on this work by analyzing an additional 9 years of data, investigating both males and females, and studying population-wide sex ratios. The “fragile male” and “high risk, high gain” hypotheses both predict sex-based differences in mortality at different life stages, resulting in differences in sex ratios and male and female life spans. Given the lack of traits typically associated with divergent male and female mortality rates and sex-biased longevity in primates and other mammals, we expected that males and females would have similar sex ratios and life spans. Specifically, we predicted that 1) due to similarities in growth rates and body sizes, male and female juvenile mortality rates would be comparable and 2) because both sexes disperse and there is intense intersexual competition and aggression, adolescent and adult mortality would be similar, resulting in similar life spans. Given the similarities in dispersal frequency and distance reported for this species (Morelli et al. 2009), we also predicted that there would be no difference in the timing of dispersal that would lead to divergent mortality rates. Lastly, we compare our findings with sex differences in survival and group transfer or dispersal in other species and discuss causal factors likely driving observed patterns.

## METHODS

### Study site

Data were derived from a long-term and ongoing study (1986–present) of *P. edwardsi* in Ranomafana National Park (RNP) in south-eastern Madagascar (lat 21°16'S and long 47°20'E; Wright 1992). RNP consists of approximately 43 500 ha of submontane rainforest, which ranges from 559 to 1396 m in elevation, has an average temperature of 21 °C, and receives an average of 3090 mm of rain per year (Tecot 2008; Wright et al. 2008). The climate at RNP varies seasonally with higher rainfall and temperature during the months of December–March than during the remainder of the year (Overdorff 1993; Hemingway 1996; Wright 2006). Within this seasonal pattern, there is considerable interannual variation with the monthly distributions of rain and fruit being unpredictable from year to year (King et al. 2011). Individuals in our study were members of 4 social groups in the area of RNP known as Talatakely. The Talatakely study site is at an altitude of 900–1100 m and is accessible to researchers through a system of trails.

### Study subjects

*P. edwardsi* are sexually monomorphic with both males and females having an adult body mass averaging 5.7 kg (King et al. 2011). Social groups range in size from 2 to 9 individuals and typically include 1 or 2 breeding females (Pochron and Wright 2003a; Morelli et al. 2009). Reproduction is highly seasonal and most births occurred

from May to July (with the exception of 1 in 54 births, which occurred in September; Wright P, unpublished data). Dispersal by both sexes peaks during September, and individuals may disperse several times in their lifetime (Morelli et al. 2009). Pochron et al. (2004) describe the history of research and habituation of the study groups, and aspects of demography have been published previously (Wright 1995; Pochron and Wright 2003a; Pochron et al. 2004). Male and female growth rates and durations do not differ (King et al. 2011), and age categories for both sexes were defined as follows: infants <1 year, juveniles 1–3.5 years, and adults >3.5 years (Morelli et al. 2009).

Data used in this study represent 80 group-years of observations (24 years each for Group I and Group II, 19 years for Group III, and 13 years for Group IV). Study animals ( $n = 41$  females, 34 males) were habituated to the presence of humans; each group was followed for a minimum of 5 days per month, during which time focal follows continued from dawn to dusk. All births, deaths, immigrations, and emigrations were recorded ad libitum and are accurate to within an average of 1 week (see Pochron et al. 2004 for details). Individuals were identifiable by collar-tag combinations (see Wright 1995 for capture and marking procedures used with this population).

The date of birth for most individuals born since the start of this study is known within 2 weeks ( $n = 30$  females, 22 males), and the ages of some individuals that entered the study groups from unmonitored groups as well as some of those who were born before 1986 were estimated on the basis of tooth wear documented during captures ( $n = 8$  females, 8 males; King et al. 2005; Wright et al. 2008). The ages of the remaining individuals (dates of birth not observed and dental molds not taken) were estimated ( $n = 3$  females, 46 males) by author Patricia Wright, facilitated by seasonal breeding and obvious differences in body mass in 1-, 2-, 3-, and 4-year-old individuals. The ages of 2 older individuals (female, 7 years and male, 6 years) were estimated during captures on the basis of body mass, tooth tartar, and tooth sharpness.

All work was approved by the Stony Brook University Institutional Animal Care and Use Committee. All procedures conformed to the American Society of Primatologists' Principles for the Ethical Treatment of Non-Human Primates and to the laws of the Republic of Madagascar.

## Data and analyses

We analyzed sex ratios by calculating the proportion of females to the population as a whole over the entire course of the study (1986–2009) for each age, and annually. Using survival analyses, we examined the pattern of age-specific exits from social groups and evaluated the effect of sex on the cumulative probability of exiting. Survival analyses are a flexible framework useful for determining the time it takes for an event to occur; our events were exits from a social group, which were defined as 1) confirmed death or 2) confirmed dispersal (within or out of the study population). Dispersals are defined generally as any transition from a group and not restricted to dispersal from an animal's natal group. Despite best efforts, 10 events could not be reliably classified as either dispersal out of the study area or a death, but were definitely an exit from the study area. Instead of removing the observations or censoring the individuals, which would introduce bias, as their exclusion would not be random but conditioned on the events in which we are interested (White and Garrott 1990), we provide 2 analyses of dispersals and survival: 1) assuming unknowns are all deaths

and 2) assuming unknowns are all dispersals. Either assumption is extreme, such that we expect the true cumulative distribution to lie in between the 2. We restrict our interpretation of results as it pertains to the effect of sex only if both analyses agree.

Survival data included 26 observations of males and 38 observations of females in the study area. Individuals that dispersed outside of the study area were not followed until death. Thus, we assumed that dispersing within, out of, and into the study area are stochastic processes rather than Markovian, such that observed dispersals are a random variable, sampled from a greater population. We observed males disperse 19 times and females disperse 15 times, in total for each.

We used the Cox proportional hazards regression model (Cox 1972) implemented in the R package *eha* (Göran 2012) to estimate cumulative distributions of exits. We were interested in comparing 2 nested models, null (no covariates) and sex (included sex effect on survival cumulative distribution), for estimating 1) the time until a group dispersal and 2) time until death. We considered  $t_i$  the time until an event, as a random variable where our model of event  $i$  was defined (specifically for the model including the sex covariate) as  $h_i(t|\text{sex}) = h_0(t)e^{(\beta_i \text{sex})}$ . The Cox model allows the baseline hazard function ( $h_0$ ) to be unspecified, whereas a linear model is used to incorporate covariate effects on the survival distribution; as such, the model is semiparametric. Depending on the individual, observations may span an individual's entire life, are left truncated when individuals transfer into the study population, or right censored when animals transfer out of the study population. Parameter estimation was done using maximum likelihood as it is more robust to tied data (Broström 2002), and model parsimony was evaluated using Akaike's information criterion ( $AIC_c$ ) with a second-order bias correction for small sample size (Burnham and Anderson 2002). We compared models to evaluate the effect of sex on both dispersals and survival by calculating model probabilities,  $\Pr(\text{model } j|\text{data})$ , known as "Akaike weight" (Burnham et al. 2011). The proportional hazards assumption of our model was tested for each analysis using weighted residuals (Grambsch and Therneau 1994) and implemented in the R package *survival* (Therneau 2012); we used  $\alpha = 0.05$  to determine statistical significance.

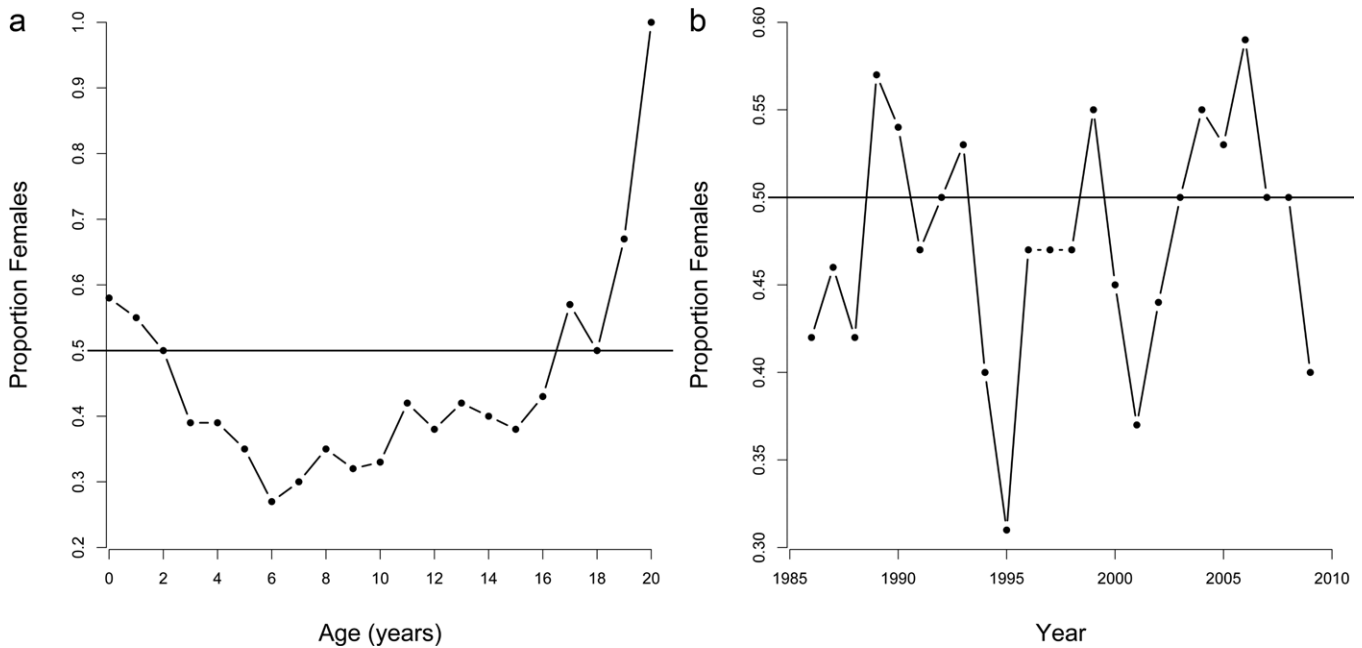
## RESULTS

### Sex ratios

Age-specific population sex ratios were female biased at birth until 2–2.9 years, at which point they became equal (Appendix S1 and Figure 1a). After 2.9 years of age, sex ratios became male biased and remained so until age 17. At age 17–17.9, the number of females was again equal to or greater than the number of males. Therefore, for the majority of age categories, the sex ratio of this population was male biased, but with more young and old females than males. The mean sex ratio of this population was in flux from year to year and not consistently male or female biased (Appendix S2 and Figure 1b).

### Survival

Neither survival analysis rejected the proportional hazards assumption ( $P > 0.05$ ; Table 1). When unknowns were assumed to be dead,  $AIC_c$  values for our 2 models were 319.10 (null) and 317.66 (sex). Akaike weight was 0.67 (sex) and 0.32 (null), such that the model with the effect of sex was 2.06 times the more parsimonious model, given our data. Under the sex model, the



**Figure 1**

Proportion of female *Propithecus edwardsi* in RNP, Madagascar, from 1986 to 2009 by (a) age and (b) year. The horizontal line represents an equal sex ratio.

median predicted life span of males and females were 1.1 (95% CI, 0.50–3.25) and 2.8 (95% CI, 0.50–12.2), respectively. When assuming the unknowns were all dispersals, AICc values were 297.39 (null) and 294.53 (sex). Akaike weight was 0.81 (sex) and 0.19 (null); thus the model with the effect of sex was 4.16 times the more parsimonious model, given our data. Under the sex model, the median predicted life spans of males and females were 2.17 (95% CI, 1.10–4.21) and 3.1 (95% CI, 1.85–4.67), respectively.

Overall, regardless of the assumption with the unknowns, there is moderate support for a difference in cumulative probabilities of age-specific survival for males and females; the effect of sex was in the same direction (Table 1). Both sexes experience high mortality during the first 2 years of life (Figure 2). After about 2 years, male and female cumulative survival probabilities diverge, irrespective of

the assumption regarding the unknowns; generally more males are likely to survive during the ages of 2–18. However, between the ages of 9 and 18, male survival probability declines quickly, whereas the decline for females is more gradual. After age 18, the probability of female but not male mortality approaches zero. The oldest male observed in this study was 19 years old; there is no evidence within our study area of males living beyond this age. In contrast, females that reach 19 years of age are likely to live into their early 30s.

## Dispersals

We found the proportional hazards assumption was not rejected for either dispersal analyses ( $P > 0.05$ ). When assuming the unknowns had all died, the AICc values of the dispersal analyses were 371.52 (null) and 368.68 (sex). Akaike weight was 0.81 (sex) and 0.19 (null), such that the model with the effect of sex was 4.15 times the more parsimonious model, given the data. Given the sex model, the median predicted ages of dispersal of males and females were 7.12 (95% CI, 5.01–8.00) and 4.58 (95% CI, 4.25–6.00), respectively. When assuming the unknowns had all dispersed, AICc values were 531.47 (null) and 528.82 (sex). Akaike weight was 0.79 (sex) and 0.21 (null); thus the model with the effect of sex was 3.77 times the more parsimonious model, given the data. Given the sex model, the median predicted ages at dispersal of males and females were 7.81 (95% CI, 6.62–8.91) and 4.81 (95% CI, 4.62–7.11), respectively.

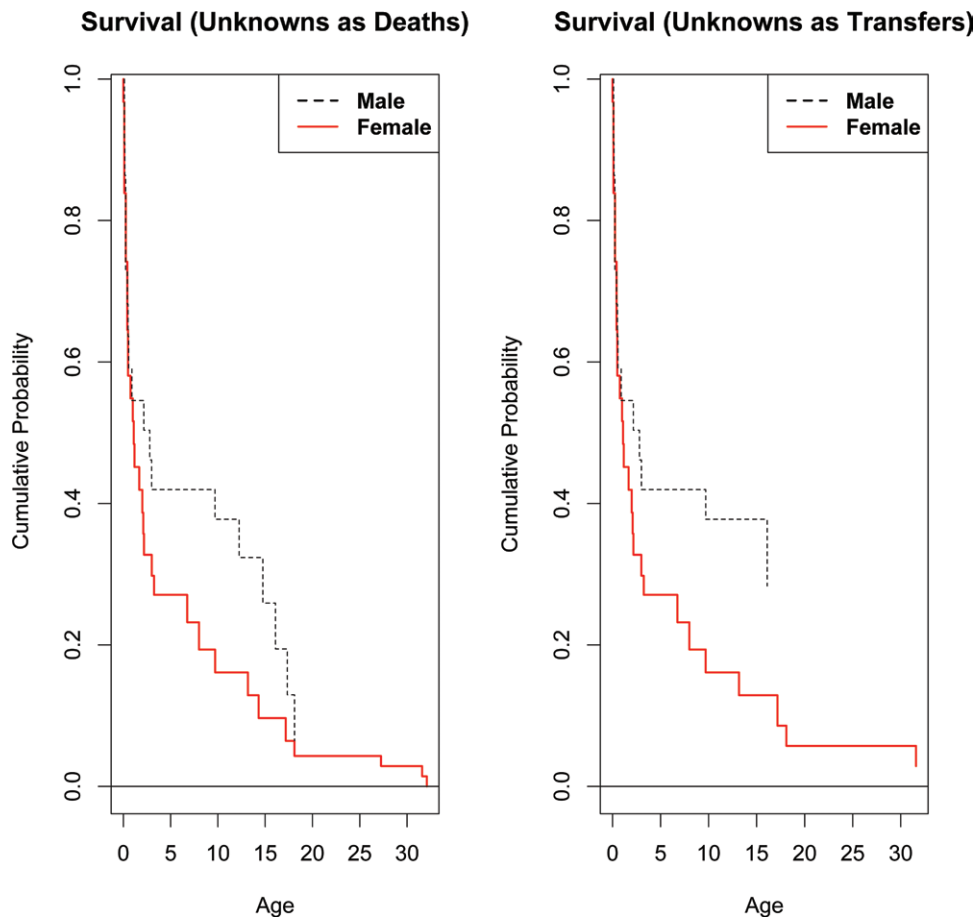
There was moderate support for a difference in cumulative probabilities of age-specific dispersal in both males and females, regardless of the assumptions made for unknowns, and the effect of sex was in the same direction (Table 1). Neither males nor females disperse before they are 3–4 years of age (Figure 3). Males have a consistently higher probability of dispersing, especially between the ages of 6 and 10. The highest probability of female dispersal occurs between the ages of 4 and 6 and then declines quickly; by age 10, females have less than a 0.1 probability of dispersing. Due to a single unknown female exit from the population at 27 years of

**Table 1**

**Proportional hazards regression estimates, statistical tests of significance, and test of model assumptions of *Propithecus edwardsi* survival and dispersal**

Analysis type	Analysis	$\hat{\beta}_{\text{sex}}$	$SE(\hat{\beta}_{\text{sex}})$	$\chi^2$	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

NA indicates the cell is “not applicable” to the row–column combination. Analyses 1 and 3 assume unknown exits died, and analyses 2 and 4 assume unknown exits transferred.



**Figure 2**

Cumulative probability of survival for male and female Milne-Edwards' sifaka (*Propithecus edwardsi*) in RNP, Madagascar, between 1986 and 2009.

age, it is unclear whether females stop dispersing at the age of 21 (last confirmed dispersal) or continue to have a small probability of dispersing until they die.

## DISCUSSION

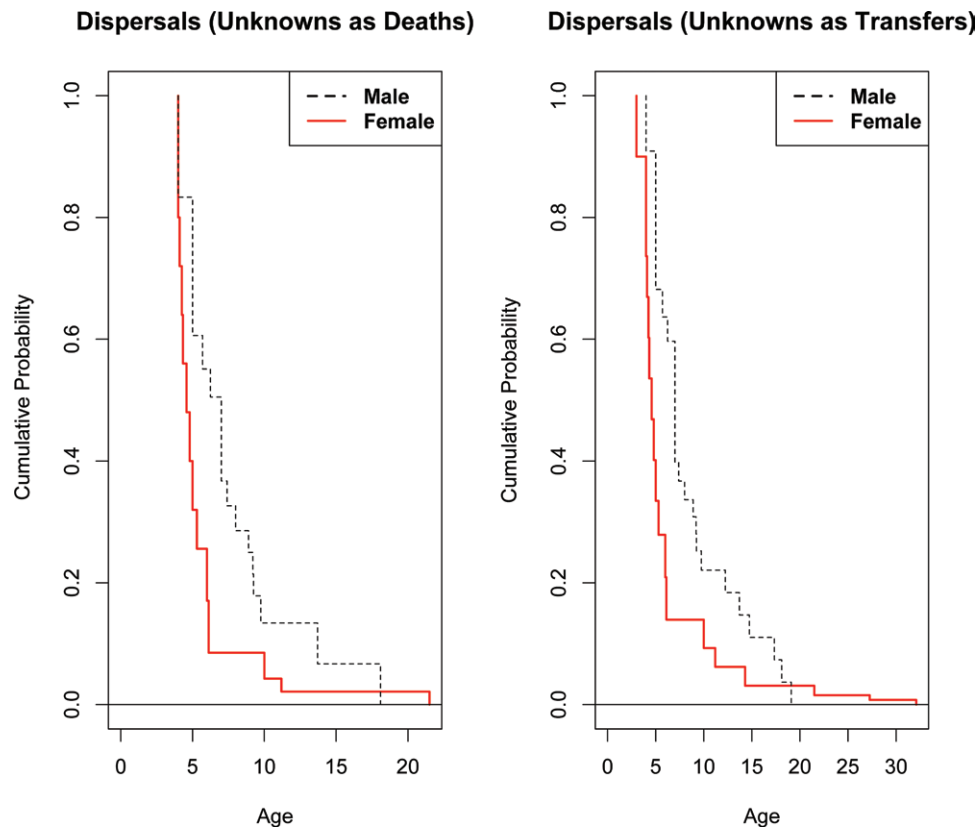
Sexual selection theory predicts that intense competition in males for reproductive opportunities results in higher mortality rates in males over the course of their lifetime (Trivers 1972). Across polygynous species of mammals, including primates, there is consistent support for accelerated mortality in males (Clutton-Brock and Isvaran 2007; Bronikowski et al. 2011). As we predicted, and contrary to the “fragile male” and “live slow, die old” hypotheses, males and females experienced similar probabilities of infant survival. After age 2 (during juvenility), males, not females, were more likely to survive until approximately 18. Because growth rates and durations also do not differ in this species (Morelli et al. 2009; King et al. 2011), we can reject differential development and maturation as significant factors influencing longevity in this species. Males appear to live “faster” lives simply by virtue of dying younger. This pattern differs from the “early blooming” observed in male *Propithecus verreauxi* (Richard et al. 2002).

Although we expected that male and female survivorship would be approximately equal during adulthood, males had higher survival than females during adulthood. Though both sexes are aggressive, and testosterone levels do not differ among males and females (or

are seasonally higher in males) (Tecot et al., in preparation), higher female mortality may be related to female dominance in this species (Pochron and Wright 2003b). However, as predicted by the “risky male” hypothesis, at around 13–18 years of age, male annual survival probability declined quickly. After the age of 18, male mortality exceeded that of females, potentially as a consequence of continuous dispersal by males at older ages. Our data reveal that variability in the timing and causes of sex-specific mortality lead to complex patterns of sexual asymmetries in survivorship at different life stages.

## Sex ratios

Our data show that birth sex ratios were skewed toward females, in contrast with several other primate species where birth sex ratios are typically nearly equal (see Fedigan and Zohar 1997), or male biased, as in the closely related Verreaux's sifaka (*P. verreauxi*) (Richard et al. 1991, 2002). Although infant mortality was high in both sexes, as is typical for lemurs (Wright 1999; Richard et al. 2002), sex ratios became male biased prior to natal dispersal, indicating that juvenile mortality was greater for females than males. Given the greater probability of female mortality during the juvenile period of development, our data are inconsistent with the “fragile male hypothesis” supported for other species (Clutton-Brock et al. 1982; van Schaik and de Visser 1990; Owen-Smith 1993; Fedigan and Zohar 1997; Loison et al. 1999; Alberts and Altmann 2003; Setchell et al. 2005; see van Schaik and de Visser 1990 for review). Though birth



**Figure 3**

Cumulative probability of dispersal for male and female Milne-Edwards' sifaka (*Propithecus edwardsi*) in RNP, Madagascar, between 1986 and 2009.

sex ratios differ in *P. edwardsi* and *P. verreauxi*, patterns of sex-based infant and early juvenile mortality suggest that males in neither species are fragile. On the contrary, females appear to be the fragile sex during infancy. If females have a greater mortality rate from infancy through development and maturation, why is it that we ultimately see greater female longevity?

### Patterns of dispersal

Because previous research on this species reported that male and female average dispersal frequency or distance did not differ (Morelli et al. 2009), we predicted similar patterns in the rate and timing of dispersal. Instead, our data reveal that there were differences in the timing and rates of dispersal between males and females. Specifically, males continued to disperse until their deaths, whereas females generally stopped dispersing after approximately 11 years of age. Only 1 female dispersed after 11, at age 21 (with 1 additional unknown disappearance at age 27). The cause of this dispersal remains unknown. The continued dispersal by males throughout their lifetime and subsequent mortality is consistent with the “high risk, high gain” hypothesis, predicting higher mortality rates in males during adolescence and adulthood due to risky behavior (Trivers 1985; Rajpurohit and Sommer 1991; Fedigan and Zohar 1997). Because mortality risk can be greater in dispersers relative to their philopatric conspecifics (e.g., Isbell et al. 1993; Alberts and Altmann 1995), males continue to incur this risk later in life compared with females. We suggest that dispersal between groups affects male longevity by removing individuals from the population not just as emigrants, but by reducing the survival of individuals due to the risks incurred during dispersal.

Research on blackbirds (Greenwood and Harvey 1976) indicates that large differences in life span can exist between dispersing and nondispersing individuals. The sources of risk for emigrants may include increased predation risk (Isbell et al. 1990; Hass and Valenzuela 2002), decreased knowledge of resources (Waser and Jones 1983), and social costs associated with the loss of familiar group-mates (Isbell and van Vuren 1996). Our study suggests that dispersal carries great risk for individuals. *P. edwardsi* groups tend to remain in discrete home ranges, and emigration consists of movement out of a familiar area, typically by a single individual (Wright 1995; Wright P, unpublished data). Male survival curves incorporating both types of exits (mortality and dispersal; data not shown) were age independent, with cumulative exits occurring at a near constant rate throughout life, reflecting the dispersal patterns observed. In contrast, female survival curves were age dependent, showing a declining rate of exiting the population (via mortality and dispersal) with age, a result that is also consistent with observed dispersal behavior. Although correlative, these results suggest that dispersal is met with higher mortality, and the longer female life span in this species may be due to a lack of females transferring groups at older ages.

Why, in this species, do males continue to disperse later in life? Although lacking the sexually dimorphic characteristics of many polygynous species, *P. edwardsi* are polygynous, and intrasexual competition may explain differences in male and female dispersal behavior. Often, in a polygynous mating system, there is rank-related reproductive success, resulting in significant reproductive skew (e.g., Setchell et al. 2005). Furthermore, the cumulative detrimental effects of intense intrasexual competition also limit

male breeding success. Thus, males are under weaker selection to live long lives relative to females (Clutton-Brock and Isvaran 2007; Bronikowski et al. 2011). In *P. edwardsi*, competition among males is particularly violent during the dispersal and mating seasons (Wright P, unpublished data). Similar to male ring-tailed lemurs (*Lemur catta*), who also disperse outside of the mating season (Parga and Lessnau 2008), secondary dispersal by both male and female *P. edwardsi* has a reproductive function (Morelli et al. 2009). During the 4 months of the dispersal season, the frequency of scent marking increases (Pochron, Morelli, Scirbona, et al. 2005; Pochron, Morelli, Terranova, et al. 2005), androgens are at their peak (Tecot et al. 2010; Tecot S, in preparation), and testes begin to increase in size, reaching their maximum during the mating season (Pochron and Wright 2002; Pochron et al. 2002; Morelli 2008).

Male-directed aggression by both males and females during the mating and dispersal seasons can be severe, leading to deep lacerations, castration, and even death (Wright 1995, 1999; Wright P, unpublished data), similar to that observed during the mating season of other species (e.g., *P. verreauxi*; Jolly 1966; Lawler et al. 2005). These intense fights typically occur between residents and immigrants (Morelli 2008), as groups seldom contain more than 1 adult male for extended periods of time (Morelli et al. 2009). It is important to note that both males and females disperse, reproductive competition occurs among females as well as males (Morelli et al. 2009), and both sexes benefit reproductively by dispersal behavior. For instance, infanticidal events during hostile group takeovers by a dispersing individual result in increased reproductive opportunities for the invader, whether male or female (Morelli et al. 2009).

Despite the information we have on aggressive behavior in this species, several things remain unclear. For instance, we do not know whether males or females incur more wounds or differentially participate in such heightened aggressive bouts. In addition, we do not know whether old individuals are more likely than young individuals to be seriously injured in such bouts. Such detailed data would help determine whether death as a result of dispersal-related aggression might explain the sex-biased mortality patterns observed. Fedigan and Zohar (1997) determined that mortality in male Japanese macaques (*Macaca fuscata*) was higher in the birth/emigration season than the mating season. Because emigration in *P. edwardsi* is also largely seasonal, a seasonal analysis can help test the hypothesis that dispersal is directly related to higher rates of male mortality. It is also likely that dispersal may impose unique challenges for aged sifaka. The chances of engaging in intense intrasexual competition and incurring costs associated with such competition may cause “cumulative phenotypic damage” in males (Clutton-Brock and Isvaran 2007), suggesting that immigration is physiologically riskier the more it occurs. Experimental research on the soil mite (*Sancassania berlesesi*) model system found greater per capita mortality in old adults versus younger adults during dispersal (Bowler and Benton 2009), suggesting that dispersing at older ages carries greater costs. As individuals age, the ability to perform certain activities may deteriorate (e.g., reduced sensory acuity or locomotion), increasing the difficulty of detecting or escaping predators, locating resources, or assimilating into new groups. There is preliminary evidence to suggest that locomotion in *P. edwardsi* may be compromised as individuals age: old females spend more time feeding and less time traveling than young females, particularly when traveling on steep terrain (Achilles E, Godfrey L, King SJ, Tecot SR, Wright PC, in preparation), and trabecular bone volume in the femoral head may decrease in aged females (Chan A, Chan NM, Wright PC, Boyer D, Gosselin-Ildari

A, Tecot SR, unpublished data). If males undergo similar age-related declines as females, the costs of dispersal may be exacerbated in older males as they continue to disperse. If males, like females, incur these additional costs, why continue dispersing? The answer may lie in sex ratios. Sex ratios and the availability of mates within a group are known to influence whether an individual disperses (Morelli et al. 2009). Aggression is typically directed toward the most numerous sex in the group, thus skewing the sex of individuals driven out of the group (Wright 1995; Wright P, unpublished data). Because males outnumber females from ages 2.9 to 17, males may be driven out of the group more frequently than females throughout their lives.

## Kin, dispersal, and mortality

This study has broader implications for understanding social dynamics. In general, it is predicted that relatives show kin bias, participating in more affiliative and cooperative behavior with one another (Hamilton 1963), resulting in direct fitness benefits (*Alouatta seniculus*: Pope 1990, 2000; *M. fuscata*: Pavelka et al. 2002; *Cercopithecus aethiops sabaues*: Fairbanks 1988). When there is a lack of sex-biased dispersal, there tends to be a bias in dispersal distance such that one sex is more likely to encounter relatives in their non-natal groups than the other (Waser et al. 1994; reviewed in Kappeler 2008). For instance, in the solitary Coquerel’s dwarf lemur (*Mirza coquereli*), females have shorter dispersal distances than males, resulting in a dispersed matrilineal population structure (Kappeler et al. 2002), creating the opportunity for sex-specific kin bias. Despite an overall lack of dispersal bias in this species (Morelli et al. 2009), same-sex pairs living together were biased, with female pairs living together longer than male pairs (Morelli et al. 2009; Wright P, unpublished data). Although the sample sizes are small, sex differences in group tenure are notable: female adult relatives lived together 5–10 years, whereas male adults (relatives and nonrelatives) lived together 1–2 years on average (and one of these males was typically born into the group; Wright P, unpublished data). The slower rate of female dispersal after 5–8 years of age that we report in this study can explain why females are more likely to live with other females for longer periods of time and suggests that opportunities for long-term relationships are greater for females than males (though it should be noted that low fertility and high infant and juvenile mortality reduce opportunities for large kin groups in the species as a whole; Pochron et al. 2004). As a consequence, males may experience social stress more often than females. In both nonhuman primates and humans, individuals well integrated into strong social relationships have a greater likelihood of surviving than those in weak social relationships (Holt-Lunstad et al. 2010; Silk et al. 2010), demonstrating the potential influence of such relationships on mortality and life span.

## CONCLUSIONS

In our population, early female-biased sex ratios and high mortality resulted in male-biased sex ratios from sexual maturity through 18 years of age, a pattern also observed in other lemur species (Kappeler 2000; Ooster and Kappeler 2004), including the closely related *P. verreauxi*. Although male and female mortality rates were more similar to each other by age 5 years, our data reveal that females dispersed earlier than males. Coupled with higher female infant mortality, this resulted in an initially higher rate of females leaving the population, either through dispersal or death. Exit

rates between males and females then converged at age 10, with males and females being equally likely to exit the population, either through death or dispersal until age 14. After 14 years of age, males continued to disperse from the population steadily, whereas females remained until their deaths. This continued dispersal by males is the primary explanation for female-biased sex ratios at older ages and, ultimately, longer female life spans.

The results of this study begin to address the importance of how different life-history strategies can influence longevity. We found support for the “risky male” hypothesis, wherein risky behavior occurs at older ages in males than in females, resulting in shorter male life spans. Our results also highlight critical shifts in mortality and dispersal rates that produced the specific sex-ratio patterns observed at any given point in time and may further elucidate the causes for female-biased life span in other monomorphic lemur-oida (*P. verreauxi*: Richard et al. 2002; *L. catta*: Gould et al. 2003; *M. murinus*: Kraus et al. 2008). Further studies are needed to investigate the cause of death and help determine why females have higher early mortality, why males continue to disperse later in life, and what factor(s) are interacting to contribute to the patterns observed in this population.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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