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SUMMARY

Male excess mortality is widespread among mammals and frequently interpreted as a cost of sexually selected traits that enhance male reproductive success. Sex differences in the propensity to engage in risky behaviours are often invoked to explain the sex gap in survival. Here we aim to isolate and quantify the survival consequences of two potentially risky male behavioural strategies in a small sexually monomorphic primate, the grey mouse lemur *Microcebus murinus*: (1) Most females hibernate during a large part of the austral winter, whereas most males remain active, and (2) during the brief annual mating season males roam widely in search for receptive females. Using a 10-year capture-mark-recapture data set from a population of *M. murinus* in Kirindy Forest, western Madagascar, we statistically modelled sex-specific seasonal survival probabilities. Surprisingly, we did not find any evidence for direct survival benefits of hibernation – winter survival did not differ between males and females. In contrast, during the breeding season males survived less well than females (sex gap: 16%). Consistent with the "risky male behaviour"-hypothesis, the period for lowered male survival was restricted to the short mating season. Thus, sex differences in survival can be substantial even in the absence of sexual dimorphism.

Key-Words: sex differences in survival, seasonal survival, risky male behaviour, female hibernation, male roaming, *Microcebus murinus*

1. INTRODUCTION

In most mammalian species, including humans, female average lifespan exceeds that of males (e.g. Austad 2006; Clutton-Brock & Isvaran 2007; Moore & Wilson 2002; Owens 2002; Promislow 1992; Toigo & Gaillard 2003). Apart from effects of deleterious recessive alleles in the heterogametic sex (XY), most hypotheses trying to explain male-biased mortality invoke arguments from sexual selection theory. Since male mammals usually have higher potential reproductive rates than females, male fitness is primarily limited by the number of available females, resulting in strong intrasexual competition among males over access to receptive females (Clutton-Brock & Parker 1992; Kvarnemo & Ahnesjo 1996; Reynolds 1996). Accordingly, male excess mortality is viewed as a cost of sexual selection paid for traits that enhance reproductive success (Moore & Wilson 2002).

Proximate hypotheses to explain sex differences in survival include: (1) The costs of growing large and the resulting sexual size dimorphism characteristic for many mammals lead to lower survival in the larger sex (Magalhaes et al. 2007; Promislow 1992; Ricklefs & Scheuerlein 2001). (2) Lower immunocompetence in males, mediated by androgens such as testosterone, renders males more susceptible to parasitic and infectious disease (Hau 2007; Klein 2004; Moore & Wilson 2002; Zuk & McKean 1996). (3) The higher propensity of males to engage in potentially risky behaviours, such as dispersal, physical combat and roaming decreases male survival (Alberts & Altmann 1995; Greenwood 1980; Johnson & Gaines 1990; Owens 2002; Rödel et al. 2004). These hypotheses are not mutually exclusive, and presumably, several processes jointly shape the sex gap in survival in interaction with a given environment. Indeed, sexual size dimorphism, sex-biased parasite load and risky male behaviours seem to be tightly linked across mammals (Brei & Fish 2003; Moore & Wilson 2002).

Male humans are much more likely to fall victim to fatal accidents, homicide and suicide than women, which has led to the conclusion that human male excess mortality is mainly due to risky male behaviour (Owens 2002). The disposition for risky behaviour in males is likely to be a heritage we share with non-human mammals. Behaviours such as dispersal, fighting and roaming can carry substantial costs in terms of survival. In the majority of primates as well as in other mammals males are the dispersing sex (Greenwood 1980; Handley & Perrin 2007; Pusey & Packer 1987), and dispersal has been shown to be a dangerous endeavour (e.g. Alberts & Altmann 1995; Sherman & Morton 1984; Van Vuren &

Armitage 1994). In polygynous mammals, male-male competition over access to receptive females often takes the form of physical combat which can result in injuries or even death. In promiscuous species, where sperm competition plays an important role in male-male competition, males frequently roam widely in search for receptive females and thus not only have higher energy demands, but are also more likely to get killed by a predator (Magnhagen 1991) . Even in monogamous mammals behaviours associated with paternal care can lead to decreased male survival (Sommer 2000).

Due to several idiosyncrasies, Malagasy lemurs (Lemuriformes) provide an excellent model to evaluate several of the hypotheses regarding male excess mortality, particularly to evaluate the importance of risky male behaviours. Firstly, lemurs are sexually monomorphic (Kappeler 1990) and thus, in case they do exhibit male-biased mortality, we can exclude sex differences in growth and maintenance of a larger body size as the proximate cause. Secondly, lemurs are highly seasonal breeders with hormone profiles that parallel reproductive activity and are synchronized by photoperiod (Kraus et al. 1999; Ostner et al. 2002; Perret & Aujard 2001). In several seasonally breeding species males are most susceptible to infections during the breeding season when androgen levels are high (Klein 2004). Consequently, sex differentials in survival due to testosterone mediated differences in immunocompetence should be larger during the time of elevated testosterone levels. Finally, lemur males engage in many of the same supposedly risky behaviours as anthropoid primates and other mammals.

Grey mouse lemurs *Microcebus murinus* are small (~ 60 g), nocturnal and arboreal primates (Cheirogaleidae) that can be classified as solitary foragers (Kappeler & van Schaik 2002). They show a unique seasonally fluctuating sexual size dimorphism, but are overall sexually monomorphic (Schmid & Kappeler 1998). Females and males follow strikingly different lifestyles. Females are philopatric whereas most juvenile males disperse before their first breeding season (Eberle & Kappeler 2004; Fredsted et al. 2005; Radespiel et al. 2003a; Wimmer et al. 2002). Whereas most males sleep alone, most females form stable sleeping groups (Eberle & Kappeler 2006; Radespiel 2000). In the Kirindy Forest population in Western Madagascar the majority of males remain active with only short daily bouts of torpor throughout the dry winter, but most adult females stay inactive for several months (Rasoazanabary 2006; Schmid 1999). During the short annual mating period males roam extensively in search of receptive females. Male home ranges are then more than 4-times larger than those of females, and males travel long distances at night (Eberle & Kappeler

2004; Radespiel 2000). Males also guard and aggressively defend access to receptive females (Eberle & Kappeler 2004).

In this study we firstly aim to verify whether - despite the lack of male-biased sexual dimorphism - sex differences in survival exist in a wild population of grey mouse lemurs and, if they do, to estimate sex differentials. Secondly, we aim to isolate and quantify the survival consequences of two sex-specific behavioural strategies of adult *M. murinus*: female hibernation and male roaming. It has been hypothesized that remaining inactive during the dry winter protects females during periods of low food availability and high predation risk (Rasoloarison et al. 1995; Schmid 1999; Schmid & Kappeler 1998). Similarly, roaming during mate search likely renders males more conspicuous to predators. Accordingly, we tested the prediction that males survive less well than females during both, the non-breeding season, i.e. the dry austral winter, and the breeding season, i.e. the wet austral summer. Lowered male survival during the breeding season would be less straightforward to interpret, however, because it would be consistent with the "risky male behaviour hypothesis" as well as the "adverse effects of androgens hypothesis". In order to tease apart these two hypotheses, we studied the temporal course of sex differentials in survival over the breeding season. If male excess mortality was primarily a direct effect of risky male behaviour, it should be restricted to the period when the behaviour concerned, here roaming, actually occurs, that is the brief mating season within the early austral summer. On the other hand, because male summer testosterone levels are elevated about two months before and beyond the actual mating period (Perret & Aujard 2001), we would expect male survival to be constantly lower than that of females over the entire breeding season (elevated testosterone levels) if males mainly suffer higher mortality due to androgen-mediated decreased immunocompetence.

2. MATERIAL AND METHODS

(a) *Study area and study population*

We have been studying a population of grey mouse lemurs (*M. murinus*) in Kirindy Forest, a dry-deciduous forest located about 60 km north-east of Morondava in Western Madagascar (Sorg et al. 2003) since 1994. The area is characterized by pronounced seasonality with a cool dry season from April/May to Sep (austral winter), a hot dry transitory period in October/November and a hot wet season from December to March (austral summer) (Sorg & Rohner 1996). Reproduction is highly seasonal and starts shortly after female emergence from hibernation in late September. The mating period is limited to a four week period from mid-October to mid-November (Eberle & Kappeler 2004). Mouse lemurs mate promiscuously and most litters are of mixed paternity (Eberle & Kappeler 2004). After a gestation of two months, 1 to 3 young are born and weaned about two months later (Eberle & Kappeler 2006). Females are philopatric and dispersal of juvenile males takes place from April to August; there is no evidence for secondary dispersal in this population (Eberle & Kappeler 2004).

(b) *Capture-mark-recapture*

Captures have been conducted in a 9 ha study area on a monthly basis. The study area is equipped with a rectangular system of foot trails at 25-m intervals. To trap mouse lemurs, we baited Sherman live traps with small pieces of banana and set them near trail intersections in the late afternoon on three consecutive nights per month. A series of three such nights of trapping will be referred to as a trapping session. Captured animals were collected in the early morning, individually marked with subdermal transponders (or re-identified in case of recaptures), subjected to standard morphometric measurements and released at the site of capture in the following late afternoon. From 1999 on, all adult animals inhabiting the study area have been individually marked (some 75 at a time) (for details, see Eberle & Kappeler 2004). Our records of animals present in this area are therefore as complete as possible for a small, nocturnal mammal.

In order to estimate seasonal survival probabilities for the years 1995-2005, we used data from the trapping session conducted at the onset of the dry winter (Apr 9 – May 27) and that after female emergence from hibernation, i.e. at the start of the mating period in the first half of October (Oct 1 – Oct 17), which we define here as the onset of summer. In some years, some of the monthly trapping sessions had to be skipped due to logistic reasons, and in two years (1998 and 2004), trapping sessions were earlier (Aug) or later (Nov) than normal. Including these sessions would have potentially confounded the effects of female hibernation and male roaming. We therefore created "dummy" trapping session (Oct 10) with zero recapture probabilities for these years. The data set comprises a total of 435 individuals (171 females, 264 males) which were caught 796 times (only one capture per trapping session considered).

During three annual mating seasons between 1999 and 2001, we trapped once per week in the 9 ha study area between mid-October and mid-November to determine exact dates for the start and the end of the mating period. These data in combination with the data from regular trapping allowed us to estimate sex-specific survival probabilities before, during, and after the mating period for 1999 and 2000. In 2001, too few animals were captured in the trapping session conducted after the mating period to estimate short term survival. The data sets for these two mating seasons include 486 captures of 78 individuals (36 females, 42 males) in 1999 and 424 captures of 64 individuals (31 females, 33 males) in 2000.

(c) *Modelling outline*

In order to statistically model survival (ϕ) and recapture probabilities (p) we used the Cormack-Jolly-Seber (CJS) approach for open populations (Cormack 1964; Jolly 1965; Seber 1965) implemented in the program MARK (White & Burnham 1999). For model selection and inference we followed the analysis strategies outlined by Burnham & Anderson (2002). This entailed constructing only biologically-plausible models *a priori*, tailored to reflect our hypotheses outlined in the introduction. Model selection was based on Akaike's Information Criterion AIC or one of its appropriate variants (AIC_c, for small samples; QAIC in the presence of overdispersion). We interpreted model selection results in a weight of evidence context based on AIC differences (Δ_i) and normalized Akaike weights (w_i) as described by Burnham & Anderson (2002). Briefly, Δ_i is the difference between the AIC_c of the top model vs. the model considered, and thus reflects the likelihood of a given model relative to the best-supported model which has the lowest AIC. Akaike weights derive from this measure and are normalized so that the weights of all models in the set sum to 1.

The Akaike weights of the top model of each of our 3 data sets (seasonal survival, breeding season survival 1999 and 2000; Tables 2 and 3) were below 0.9, suggesting considerable model selection uncertainty. Therefore, we used multi-model inference techniques to judge the relative importance of model variables (or structural elements), and to obtain model-averaged parameter estimates and standard errors unconditional on a given model (Buckland et al. 1997; Burnham & Anderson 2002). For seasonal survival we averaged estimates only over models in a confidence subset of models (see Table 2). This set included all models for which the relative likelihood was above 0.05 which corresponds to a $\Delta_i = 6$. By doing so, we excluded the negligibly supported models containing a year effect for winter survival, and thus, only one model-averaged maximum likelihood estimate (MLE) for each age/sex-group had to be derived (see Fig. 1a). The relative importance of predictor variables was assessed by summing Akaike weights for all models in which the predictor was present and is given as w_+(predictor) as suggested by (Burnham & Anderson 2002).

We assessed the goodness of fit of our global models using the median- $\hat{c}$ approach implemented in program MARK. For the global model of the seasonal survival data set, the variance inflation factor $\hat{c}$ was estimated to be only marginally above 1 ($\hat{c}_{\text{seasonal}} = 1.036$), indicating an appropriate fit of our global model. The estimated $\hat{c}$ for the breeding season data sets were slightly higher (breeding season: $\hat{c}_{1999}= 1.071$, $\hat{c}_{2000}= 1.364$). We adjusted model selection statistics, MLEs and SEs accordingly.

(d) *Candidate set of models*

Table 1 provides a list of candidate models and their biological meaning. Apart from the factor sex (*s*), we considered the factors age (*a*) and time (*t*) in our models for seasonal survival (Table 1a). Age was represented by three age classes, juveniles (*juv*, 3-9 months old, i.e., 1st winter), yearlings (*yrl*: 10-16 months old, i.e. first summer, first breeding season) and adults (*ad*: > 16 months old, i.e. 2nd winter and older). We included yearlings as a separate age class, because first time breeders often fare worse in terms of survival, e.g. due to inexperience and low body condition e.g. (Murie & Dobson 1987). It seems likely that mouse lemurs experience such effects too, because yearlings have a lower body weight than older adults (Eberle, unpubl. data). Weather conditions, especially timing and levels of rainfall differ strongly among years. We therefore expected temporal variation in recapture probabilities and annual survival, at least during summer. However, our sample size was too small to allow a saturated model with all predictors interacting. Hence, our global model includes interactions among age, sex and season, plus an additive effect of year for both survival and recapture probabilities.

All candidate models for winter survival included an age effect, because natal male dispersal in the Kirindy population takes place between April and September (Eberle &

Kappeler 2004). With the CJS-model we cannot separate emigration and mortality, hence estimates for juvenile males are "apparent survival" probabilities. We do know that female dispersal and / or secondary male dispersal are at most very rare events in this population (Eberle & Kappeler 2004) and thus, we feel confident that estimates for these sex-age-classes represent "true survival" probabilities. We were mainly interested in a potential sex effect on winter survival (models 1 vs. 2 and models 4 vs. 5, respectively). Additionally, we considered the idea that hibernation might buffer adult female survival against time variation (model 3). Alternatively, because winter conditions are much more stable across years than summer conditions, we included models without year-variation (models 4 and 5). Candidate models for summer survival again were built to allow the evaluation of an effect of sex (models 2 vs. 3 and models 4 vs. 5). Additionally, we considered the possibility that first time breeders' survival might differ somewhat from that of older individuals (models 1 vs 2).

In order to limit the total number of models, we restricted the candidate set for recapture probabilities to three models per season. Apart from the global model (see above) and an only time-varying one, for early winter recapture probabilities, we added a model including a sex-effect for juveniles only, because juvenile male dispersal might be associated with higher recapture probabilities. Since summer trapping sessions where held usually at the onset of the mating period, we included a recapture model with an additive effect of sex on time.

Modelling breeding season survival (Table 1b), we did not include an age effect, because of the small sample sizes (see above), and, because we knew that the age effect was rather small (see Fig. 1b). Survival between trapping sessions within the periods (*T*) of interest (before, during, and after the mating period) was constrained to be constant. Our main goal regarding breeding season survival was to compare support for the competing hypotheses that male survival was only lowered during the mating period ("risky male behaviour", model 2) versus the hypothesis that male survival was lower than female survival over the entire breeding season ("adverse-effects-of androgens" model 3). The global model (1), allowed a combination of these non-exclusive hypotheses as well as a potential reversal of the sex effect after the mating period due to costs of female reproduction, i.e. gestation and lactation). Finally the time-varying model (4) was included to quantify the relative importance of the sex effect in these two years.

Table 1. Candidate set of models and their biological significance for (a) seasonal survival and (b) breeding season survival of mouse lemurs. Factors considered are age (*a; juv: juveniles, yrl*: yearlings*, ad: adults*), sex (*s, F: females, M: males*) and time (for ϕ*: t: year, T: period, for p: trapping session*). Model notation: * interaction, + additive effect (parallel lines on a logit-scale). The global models are highlighted in bold; see text for further details.

ϕ	***Survival is…***	*p*	***Recapture is…***
(a) Seasonal survival:			
Winter			
(1) ***a*s+t***	age-, sex-and year-specific	(1) ***a*s+t***	age-, sex-and time-specific
(2) *juv*(*s*+*t*) *ad*(*t*)	as (1), but no sex-effect for adults	(2) *juv*(*s*+*t*) *ad*(*t*)	as (1) but no sex-effect for adults
(3) *juv*(*s*+*t*) *adM*(*t*) *adF*(.)	as (2), but constant over years for adult F	(3) *t*	only time-dependent
(4) *a*s*	age-, and sex- specific; constant over years		
(5) *juv*(*s*) *ad*(.)	as (4), without sex effect in adults		
Summer			
(1) ***a*s+t***	age-, sex-and year-specific	(1) ***a*s+t***	age-, sex-and time-specific
(2) *s*+*t*	sex- and year-specific	(2) *s*+*t*	sex- and time-specific
(3) *t*	only year-dependent	(3) *t*	only time-dependent
(4) *a*s*	age-, and sex- specific; constant over years		
(5) *a*	only age-dependent		
(b) Breeding season survival 1999 and 2000			
(1) ***s*T***	sex-and period-specific, interaction	(1) ***s*t***	sex-and time-specific, interaction
(2) MP(*s*), *T*	only sex-specific during mating period	(2) MP(*s*), *t*	only sex-specific during mating period
(3) *s*+*T*	sex- and period-specific, additive	(3) *s*+*t*	sex- and time-specific, additive
(4) *T*	only period-specific	(4) *t*	only time-specific

RESULTS

(a) *Winter survival (non-breeding season)*

Remaining more active throughout the dry winter did not result in a survival cost for male mouse lemurs (Fig. 1a). The two best supported models (Δ_i<2) suggested constant and equal survival for adults of both sexes (Table 2), and multi-model inference strongly supported this survival model over competing ones ($w_+(\phi_{\mathrm{juv}(s)\ \mathrm{ad}(.)})$ = 0.717). Still, six of the 16 models within the confidence set for the K-L best model (Table 2) did provide some support for a sex-effect on winter survival ($w_+(s)$ = 0.282). Model-averaged MLEs, however, revealed that if survival is sex-biased at all, it is, surprisingly, the males that enjoy marginally higher survival chances (ϕ_{females} = 0.894±0.036; ϕ_{males} = 0.902±0.036). As expected, apparent survival probabilities of juveniles were lower than those of adults and strongly sex-dependent, probably due to natal dispersal of males ($\phi_{\mathrm{juv\ females}}$ = 0.701±0.075, ($\phi_{\mathrm{juv\ males}}$ = 0.506±0.069). None of the models in the confidence set supported between-year variability of winter survival probabilities ($w_+(t)$ = 0.0025).

Table 2. Model selection statistics for the confidence set of models (relative likelihood >0.05) and the global model (*) for seasonal (W: winter, S: summer) survival (ϕ) and recapture (p) probabilities of mouse lemurs (1995-2005). Factors considered are age (*a; juv*: juveniles*, ad*: adults), sex (*s*) and year (*t*).

Rank	Model *i*	*K*	DEV	AIC$_c$	Δ_i	w_i
1	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{t}\ p^{\mathrm{S}}_{a*s+t}$	35	699.55	1484.04	0.00	0.222
2	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{t}\ p^{\mathrm{S}}_{s+t}$	33	704.57	1484.67	0.63	0.162
3	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{a*s+t}\ p^{\mathrm{W}}_{t}\ p^{\mathrm{S}}_{s+t}$	35	701.64	1486.13	2.09	0.078
4	$\phi^{\mathrm{W}}_{a*s}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{t}\ p^{\mathrm{S}}_{a*s+t}$	36	699.46	1486.16	2.12	0.077
5	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{a*s+t}\ p^{\mathrm{W}}_{t}\ p^{\mathrm{S}}_{a*s+t}$	37	697.33	1486.24	2.20	0.074
6	$\phi^{\mathrm{W}}_{a*s}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{t}\ p^{\mathrm{S}}_{s+t}$	34	704.16	1486.46	2.42	0.066
7	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{juv(s+t)\,ad(t)}\ p^{\mathrm{S}}_{a*s+t}$	37	698.14	1487.05	3.00	0.050
8	$\phi^{\mathrm{W}}_{a*s}\ \phi^{\mathrm{S}}_{a*s+t}\ p^{\mathrm{W}}_{t}\ p^{\mathrm{S}}_{s+t}$	36	700.88	1487.58	3.54	0.038
9	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{juv(s+t)\,ad(t)}\ p^{\mathrm{S}}_{s+t}$	35	703.10	1487.60	3.56	0.038
10	$\phi^{\mathrm{W}}_{a*s}\ \phi^{\mathrm{S}}_{a*s+t}\ p^{\mathrm{W}}_{t}\ p^{\mathrm{S}}_{a*s+t}$	38	697.05	1488.18	4.13	0.028
11	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{a*s+t}\ p^{\mathrm{W}}_{juv(s+t)\,ad(t)}\ p^{\mathrm{S}}_{s+t}$	37	699.64	1488.55	4.51	0.023
12	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{a*s+t}\ p^{\mathrm{W}}_{juv(s+t)\,ad(t)}\ p^{\mathrm{S}}_{a*s+t}$	39	695.39	1488.74	4.70	0.021
13	$\phi^{\mathrm{W}}_{a*s}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{juv(s+t)\,ad(t)}\ p^{\mathrm{S}}_{a*s+t}$	38	698.10	1489.23	5.18	0.017
14	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{t}\ p^{\mathrm{S}}_{a*s+t}$	38	698.13	1489.26	5.22	0.016
15	$\phi^{\mathrm{W}}_{a*s}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{juv(s+t)\,ad(t)}\ p^{\mathrm{S}}_{s+t}$	36	702.81	1489.51	5.46	0.014
16	$\phi^{\mathrm{W}}_{juv(s)\,ad(.)}\ \phi^{\mathrm{S}}_{s+t}\ p^{\mathrm{W}}_{a*s+t}\ p^{\mathrm{S}}_{s+t}$	36	703.10	1489.80	5.76	0.012
91*	$\phi^{\mathrm{W}}_{a*s+t}\ \phi^{\mathrm{S}}_{a*s+t}\ p^{\mathrm{W}}_{a*s+t}\ p^{\mathrm{S}}_{a*s+t}$	51	684.76	1505.29	21.25	0.00001

Model notation: * interaction, + additive effect (parallel lines on a logit-scale). The number of estimable parameters (*K*), Akaike's Information Criterion for small samples (AIC$_c$), the difference between the minimum AIC$_c$ of the top model and the model considered (Δ_i) and Akaike weights (w_i) are given for each model.

Recapture probabilities varied among years, but there was little evidence for differences among age-sex classes ($w_+(p_t) = 0.76$), suggesting that activity levels at the onset of the dry season were similar for all animals.

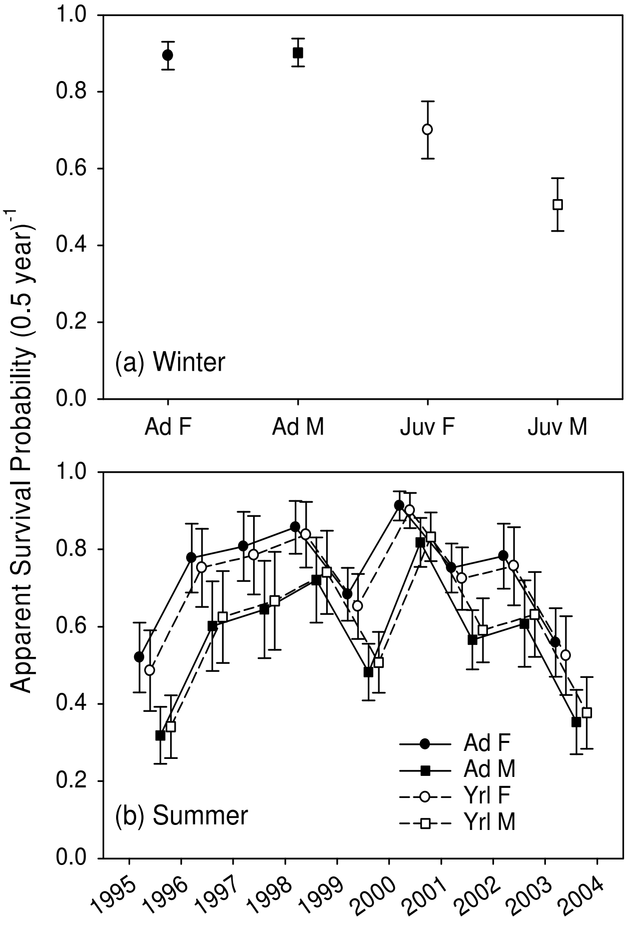

Figure 1. Semi-annual apparent survival probabilities of *M. murinus* during (a) winter (non-breeding season) and (b) summer (breeding season). Depicted are model-averaged MLEs and unconditional SEs (Ad: adult, Juv: juvenile, Yrl: yearling, F: female, M: male).

(*b*) *Summer survival (breeding season)*

Survival patterns in summer differed substantially from those in winter (Table 2, Fig. 1b). Models containing a sex effect were 150-times more likely than those without ($w_+(s) = 0.993$). On average (geometric mean across years), chances of adult male survival over the summer were 16% lower than those of adult females (11% for yearlings). Survival probabilities of first year breeders were similar to those of older consexuals. In general, survival probabilities in summer were lower than those in winter. We found a virtually 100%-support for yearly variation in summer survival ($w_+(t) = 0.99993$), with survival probabilities differing up to 50% between years.

Recapture probability at the onset of the breeding season was substantially higher for males than for females ($w_{+}(s) = 0.993$, geometric means: $p_{\mathrm{ad\ F}} = 0.565$, $p_{\mathrm{ad\ M}} = 0.820$, $p_{\mathrm{yrl\ F}} = 0.584$, $p_{\mathrm{yrl\ M}} = 0.703$), consistent with a higher activity level of males compared to females during the mating period.

(*c*) ***Survival before, during and after the mating period***

For the 1999 and 2000 data sets, we could confirm the existence of a sex gap in survival during the breeding season that we found in the long-term data set, though the relative importance of the effect differed between years (1999: $w_{+}(s) = 0.992$, 2000: $w_{+}(s) = 0.838$). Model selection clearly favoured the hypothesis that the lowered survival of males was limited to the short mating period compared to the alternative of a constantly lowered male survival over the entire breeding season (Table 3). Model $\phi_{\mathrm{MP}(s),\,T}$ was 6.2 times more likely than the competing model ϕ_{s+T} for the 1999 data set and 3 times more likely for the 2000 one. Model-averaging estimated the sex gap in survival during the mating period as 23.6% in 1999 and 13.0% in 2000, respectively (Fig. 2).

Table 3. Model selection statistics for breeding season survival of mouse lemurs in (a) 1999 and (b) 2000. Given are rank, number of parameters (K), the quasi-likelihood adjusted deviance (QDEV), the quasi-likelihood adjusted AIC (QAIC_c), the difference between the minimum QAIC_c of the top model and the model considered (Δ_i) and Akaike weights (w_i) for the best supported models ($\Delta_i<2$) of the candidate set, the highest ranked model for each survival hypothesis and the global model(*).

Rank	Model *i*	*K*	QDEV	QAIC_c	Δ_i	w_i
Breeding Season 1999						
1	$\phi_{\mathrm{MP}(s),\,T}\ p_{\mathrm{MP}(s),\,t}$	16	177.03	506.79	0	0.361
2	$\phi_{\mathrm{MP}(s),\,T}\ p_{t}$	12	186.64	507.82	1.027	0.216
3	$\phi_{s*T}\ p_{\mathrm{MP}(s),\,t}$	18	175.08	509.20	2.413	0.108
6	$\phi_{s+T}\ p_{\mathrm{MP}(s),\,t}$	16	180.83	510.59	4.77	0.054
11	$\phi_{T}\ p_{\mathrm{MP}(s),\,t}$	15	188.15	515.75	8.965	0.004
14*	$\phi_{s*T}\ p_{s*t}$	22	174.17	517.14	10.352	0.002
Breeding Season 2000						
1	$\phi_{\mathrm{MP}(s),\,T}\ p_{\mathrm{MP}(s),\,t}$	16	178.49	333.55	0	0.271
2	$\phi_{\mathrm{MP}(s),\,T}\ p_{s+t}$	14	183.18	333.89	0.336	0.229
3	$\phi_{T}\ p_{\mathrm{MP}(s),\,t}$	15	182.66	335.54	1.986	0.100
4	$\phi_{s+T}\ p_{\mathrm{MP}(s),\,t}$	16	180.62	335.67	2.123	0.093
5	$\phi_{s*T}\ p_{\mathrm{MP}(s),\,t}$	18	176.44	335.90	2.346	0.084
16*	$\phi_{s*T}\ p_{s*t}$	24	175.15	348.094	14.54	0.0002

Concurrent with decreased male survival probabilities, recapture probabilities of males were higher than those of females during the mating period in both years (Table 3).

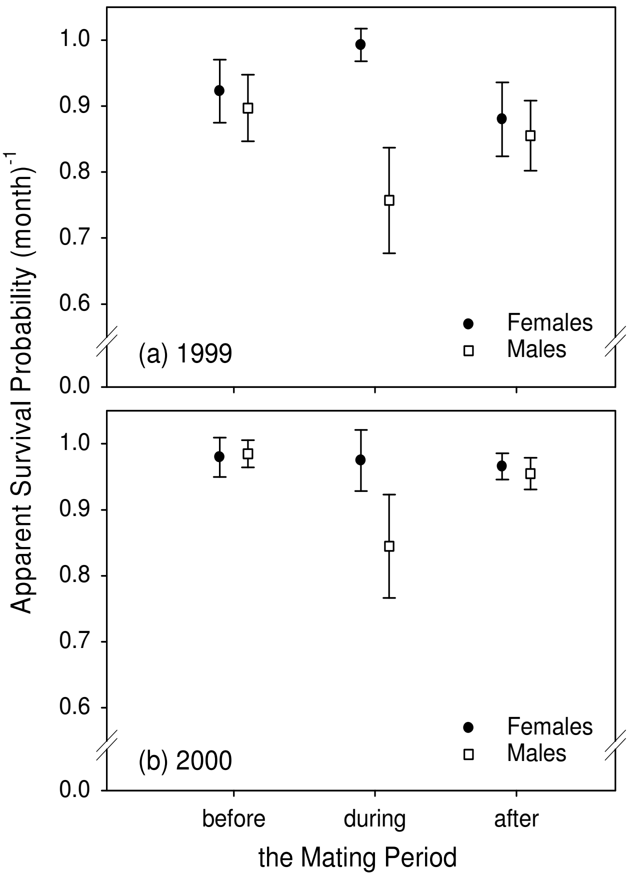

Figure 2. Sex differentials in apparent survival probability of *M. murinus* over the breeding season: before, during and after the mating period in (a) 1999 and (b) in 2000. Depicted are model-averaged MLEs and unconditional SEs.

4. DISCUSSION

Seasonal survival in our study population of grey mouse lemurs was characterized by high constant winter survival and lowered summer survival that varied substantially among years. We found clear evidence for a sex difference in survival in this sexually monomorphic primate. Surprisingly, sex-specific activity patterns during the dry winter did not contribute to the female survival advantage – adult winter survival did not differ between active males and hibernating females. Instead, males incurred higher mortality during the breeding season, consistent with the hypothesis that intrasexual selection imposes a survival cost on males. We could show that at least in two years lowered male survival was restricted to the 4-week mating period when males roam widely in search for receptive females. Our findings provide strong support for the hypothesis that male roaming behaviour is indeed risky in terms of survival.

Sex differences in survival in a monomorphic primate

Sexually monomorphic species are expected to show a small sex differential in survival compared to dimorphic species e.g ((Moore & Wilson 2002; Promislow 1992). Combining seasonal survival estimates resulted in a (geometric) mean sex gap of 16% (ϕ_{females}=0.65, ϕ_{males}=0.49) in annual adult survival (11% in yearlings: ϕ_{females}=0.62, ϕ_{males}=0.51) over the ten year study period. Assuming no age-dependence in survival after age 2, our estimates translate into a sex differential in life expectancy at first reproduction (*e*) of 0.9 yrs (e_{females} = 2.0 yrs, e_{males} = 1.1 yrs). Sex differences in life expectancy at birth are likely to be even higher due to survival costs of natal dispersal in males. Hence, sex differences in survival can be substantial even in the absence of sexual dimorphism. The magnitude of the sex differential in survival ($\Delta\phi_s$) in *M. murinus* is within the range of those found in some of the sexually dimorphic squirrels which share several aspects of mouse lemur life history, in particular hibernation/torpor and a promiscuous mating system characterized by competitive male mate searching (*Spermophilus citellus*: $\Delta\phi$ = 18%, Millesi et al. 1999; *S. townsendi*: $\Delta\phi_s$ = 13%, Smith & Johnson 1985). Sex-biased survival has been reported for several other monomorphic small mammals (*S. columbianus*: $\Delta\phi$ = 9%, Neuhaus & Pelletier 2001; *Zapus hudsonicus*: $\Delta\phi_s$ = 15%, Meaney et al. 2003; *Tamias amoenus*: $\Delta\phi_s$ = 21%, Schulte-Hostedde et al. 2002). On the other hand, no evidence for sex-differential survival was found in a number of promiscuous monomorphic small mammals (*Dipodomys spectabilis*, Skvarla et al.

2004; *Sciurus vulgaris*, Wauters et al. 2004; *Eliomys quercinus*, Schaub & Vaterlaus-Schlegel 2001), documenting that there is large variability within this group.

The survival patterns in our study population partially diverge from those published for the Ampijoroa population of *M. murinus.* (Lutermann et al. 2006) also reported high mortality in their study population in north-western Madagascar. However, they concluded that males do actually outlive females on average. Unfortunately they did not account for recapture probabilities. If, as in our study, males have higher capture probabilities during mating periods, male survival estimates will be inevitably biased towards higher values. Thus, comparative inference drawn from these studies has to be regarded as preliminary. If these distinct patterns in sex-specific survival at the two study sites are real, they would provide a unique opportunity to study behavioural and, ultimately, environmental conditions shaping intraspecific sex differences in survival. Population differences may be due to the fact that females do not hibernate in the Ampijoroa population and that they produce up to two birth cohorts per year which might entail an increased survival cost of reproduction (Radespiel et al. 2003a; Radespiel et al. 1998; Schmelting et al. 2007).

There is only limited information on sex differences in survival in other wild lemur populations. Due to the fact that males are usually the dispersing sex in lemurs, estimating unbiased male mortality rates in the wild remains a challenge and therefore, only life tables for females have been published so far (*P. diadema*: Pochron et al. 2004, *L. catta*: Gould et al. 2003). Observational data of marked animals in the wild suggest that at least in two species females might enjoy a longer lifespan (*P. verreauxi*: Richard et al. 2002, *L. catta*: Gould et al. 2003). Further circumstantial evidence comes from studies on the adult sex ratio in primates (Clutton-Brock & Iason 1986; Kappeler 2000; Mitani et al. 1996). Whereas in anthropoid primate groups the adult sex ratio is usually strongly female-biased suggesting excess male mortality, the adult sex ratio in lemur groups is balanced or even slightly male-biased (Kappeler 2000; Ostner & Kappeler 2004). Two main scenarios are conceivable: Either mortality and sex ratio at birth are male-biased or both are unbiased. The latter scenario would be consistent with the hypothesis that sexually monomorphic species should show low sex differentials in mortality. There is, however, some evidence for a male-biased sex ratio at birth in captive and wild lemur populations (Debyser 1995; Kappeler 1997). Our results also support the first scenario of male-biased sex ratios at births and clearly show that sex ratio estimates, especially if derived without accounting for a potential bias in the detection process, can easily lead to erroneous inference regarding sex differences in survival.

Winter survival: safe sleeping?

Contrary to our prediction, hibernating adult female mouse lemurs did not survive better than males which only undergo daily torpor bouts of <24 h throughout the dry winter. Thus, remaining active does not seem to impose an additional survival risk on males. Equal or even male-biased winter survival has been reported for other small mammalian species with annual male-biased mortality (e.g. Michener & Locklear 1990; Millesi et al. 1999; Neuhaus & Pelletier 2001). Juvenile mouse lemurs of both sexes had substantially lower survival chances (age differential: $\Delta\phi_{\text{females}}$ = 19%, $\Delta\phi_{\text{males}}$ = 40%). Unfortunately, it is not possible to estimate unbiased sex differentials for juvenile survival without additional information on natal dispersal rates in males.

Various potential benefits have been proposed to explain tropical torpor and hibernation in general and female hibernation in the Kirindy mouse lemur population in particular (Schülke & Ostner 2007). Since females actually emerge from hibernation with a lower body mass than males (Schmid 1999) as Schülke & Ostner (2007) already pointed out, resource scarcity (food and/or water) is unlikely to be the ultimate cause why females choose to sleep through a large part of the dry season. Indeed, a constant and high level of overwinter survival relative to breeding season survival has been reported for many species were both sexes undergo obligate hibernation (Meaney et al. 2003; Michener & Locklear 1990; Millesi et al. 1999; Neuhaus & Pelletier 2001; Schaub & Vaterlaus-Schlegel 2001; Sendor & Simon 2003; Smith & Nichols 2003).

Escaping or at least lowering a high predation pressure has been hypothesized as the decisive benefit of prolonged female inactivity (Goodman 2003; Schmid & Kappeler 1998; Schülke & Ostner 2007). Differences in activity level have often been causally linked to selective predation (e.g. Norrdahl & Korpimaki 1998; Roth & Lima 2007) and in Kirindy Forest, gray mouse lemurs are regularly preyed upon by various predators, including owls and snakes, carnivores (Eberle & Kappeler in press-b) and a lemur, Coquerel's dwarf lemur *Mirza coquereli* (Eberle & Kappeler, unpubl. obs). However, the high overwinter survival in both sexes argues against an increased predation risk due to higher levels of activity at this time of the year. Hence, with respect to direct survival consequences, our findings suggest that daily torpor and hibernation are equivalent alternative strategies to cope with energetic hazards and hungry predators during the dry winter.

So why do female mouse lemurs in Kirindy Forest doze away a good part of the year, or the other way round, why do males forego a good winter’s sleep? Even if female hibernation does not result in a direct survival benefit, delayed effects, i.e. a later onset or a reduced pace of the aging process are conceivable (Clutton-Brock & Isvaran 2007). Hibernation has been theoretically and empirically linked to a long lifespan (Brunet-Rossinni & Austad 2004; Calder 1985; Holliday 2006), e.g. in captive Turkish hamsters lifespan was shown to be directly correlated with the length of hibernation (Lyman et al. 1981). The answer to the second question might be that males have to prepare themselves for the mating season by accumulating fat reserves for roaming and direct male-male competition (Schülke & Ostner 2007). Studying survival patterns in the closely related *Cheirogaleus medius* where both sexes hibernate (Dausmann et al. 2004; Fietz & Ganzhorn 1999) and in *M. murinus* populations where both sexes either hibernate (possibly Mantadia, Randrianambinina et al. 2003) or remain active (Ampijoroa, Radespiel et al. 1998; Radespiel et al. 2003b) could shed light on the puzzling phenomenon of sex-specific wintering strategies in the Kirindy mouse lemur population.

Summer survival: risky roaming?

Male mouse lemurs in our population seem to pay a high price for reproduction. High breeding season mortality in males has been reported in many small mammals, but only few studies have used a temporal scale fine enough to explore the potential proximate causes of this phenomenon in more detail (e.g. (Boonstra et al. 2001; Neuhaus & Pelletier 2001). We could not detect an effect of sex on survival outside the short mating period, which strongly supports the "risky male behaviour hypothesis" over the "adverse-effects-of-androgens" hypothesis, since roaming and physical male competition only occur during the short mating period (Eberle & Kappeler 2002; Eberle & Kappeler 2004), while testosterone levels are increased over a much longer period of time than the brief mating season (Perret & Aujard 2001). However, the balance between these processes might differ across years, e.g. dependent on yearly survival ("good years" vs. "bad years") and parasite dynamics. Our estimates of sex-specific survival after the mating period also suggest that, despite the high demands of pregnancy and lactation, females do not suffer direct survival costs of reproduction (see also Michener & Locklear 1990; Murie & Dobson 1987; Neuhaus & Pelletier 2001). However, as in the case of female hibernation, we cannot exclude delayed survival costs due to decreased immunocompetence and an increased parasite load in males.

Sperm competition plays a large role in male-male competition in mouse lemurs (Eberle & Kappeler in press-a) and competitive mate searching leads to higher activity levels which were reflected in increased male recapture probabilities during the mating period. Predation pressure might actually reach its maximum when both prey and predator are active and breed. The dangers of increased activity combined with reduced vigilance might render males especially vulnerable to predation. (Hoogland et al. 2006) documented that predation risk in Utah prairie dogs was higher for roaming males than for any other functional category during the mating period. Additionally, the body condition of male mouse lemurs deteriorates substantially over the mating period (Schmid & Kappeler 1998), which might further increase their susceptibility to predation and possibly disease.

Conclusion

Many studies have investigated the reproductive benefits of risky male behaviours and invoked their survival costs, but few have quantified these costs using robust statistical methods. In general, seasonal patterns of sex-specific survival in mouse lemurs resembled those found in other small mammals with a similar life history strategy rather than those typical for their larger primate relatives. Despite sexual monomorphism and an observed equal or even male-biased population sex ratio, we found strong support for male-biased mortality in grey mouse lemurs. Our study emphasizes that in order to understand what drives sex differences in survival we need to dissect annual survival into time slots which correspond to distinct processes and events in the life cycle of the population. By estimating sex differentials at sequential times of the year, we could reject the hypothesis that female hibernation in the Kirindy population results in female survival benefits. We could also track the phase of sex-biased survival down to the short mating period providing strong circumstantial evidence that roaming behaviour carries a high survival risk for male mouse lemurs. Experimental approaches and multi-state modelling of long-term data-sets of marked individuals will be needed to detect delayed survival costs of sex-specific behavioural strategies.

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