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Population trend alters the effects of maternal dominance rank on lifetime reproductive success in yellow baboons (*Papio cynocephalus*)

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Abstract We evaluated the association between dominance rank and lifetime reproductive success of 75 free-ranging female baboons in Mikumi National Park, Tanzania. Data were evaluated over a 22-year period that included a period of troop increase (1975–1987) associated with two troop splits in 1978 and 1979, followed by a precipitous population crash (1987–1996) where the troops successively fused back together in 1989 and 1994. Lifetime reproductive success was significantly greater for high-versus low-ranking females when examined across the entire study period. High-ranking females had a longer reproductive life span (7.4 vs 3.6 years after first birth), reached menarche earlier (4.6 vs 5.2 years), lived longer (12.0 vs 8.8 years), and had more offspring of both sexes (2.25 vs 1.33 for male offspring; 3.25 vs 0.94 for female offspring), with four

times the number of offspring of each sex surviving to 4 years of age compared to low ranking females. Greater offspring production was associated with shorter inter-birth intervals of dominant versus subordinate females (545 vs 723 days), partly owing to lower miscarriage rates (0.05 vs 0.2) and a shorter duration of lactation (244 vs 330 days). Rank effects were then partitioned by mothers experiencing the majority of their reproductive life prior to, versus during, the population decline. The majority of rank effects on measures of lifetime reproductive success were virtually eliminated for mothers reproducing during the troop decline, indicating that the considerable impacts of social status on lifetime reproductive success can be markedly altered by intrinsically and extrinsically mediated demographic events.

Keywords Female lifetime reproductive success · Dominance · Baboons · Predation · Competition

Ramon Rhine is deceased

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Introduction

Much has been written about the matrilineal dominance system in female, terrestrial Old World primates. This system is relatively unique among mammals because of its elaborate pattern of inheritance (youngest daughters inherit the rank just below their mother), the tremendous stability of rank status over the female's lifetime, and the dependence of this stability on matriline size (Hausfater 1975; Cheney 1977; Johnson 1987). Females spend a great deal of time and energy maintaining their lifelong social status, including daily one-on-one dominance challenges, group coalition attacks against others, competition for alliances, and many hours maintaining alliances through grooming (Cheney 1977; Silk et al. 2003). They also compete to increase their relative matriline size, using coalitions to suppress the reproduction of others (Wasser and Barash 1983; Wasser and Starling 1988). High social status is presumed to confer a variety of benefits on females, from priority access to food, safer position in the troop for predator avoidance, social support and

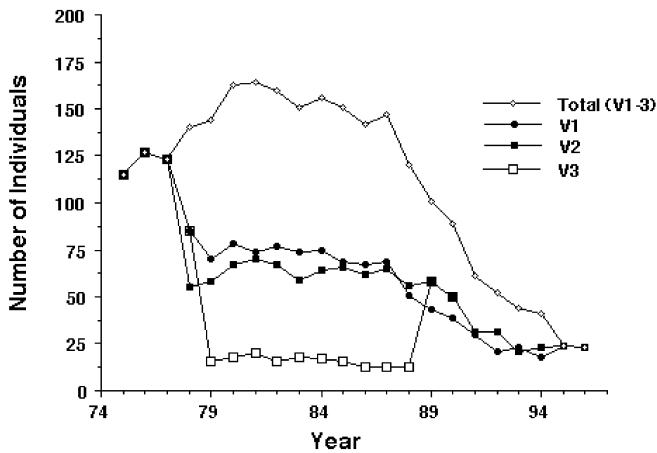


Fig. 1 Change in number of individual baboons in study troops from 1975–1996. Troop V2 split from the original troop in 1978, followed by the split of troops V1 and V3 in 1979. V3 re-fused with V2 in 1989. V1 and V2 re-fused in 1994. Note: All symbols are overlaid for 1975–1977, prior to the troop splits

associated health benefits, and better control of the timing of reproduction (Hausfater 1975; Dunbar 1984; Wasser 1996; Silk et al. 2003). However, given the costs of maintaining one's social position for life, we ultimately expect dominance status to be correlated with lifetime reproductive success. We would also expect a sudden decline in matriline size to result in loss of reproductive advantages inferred on individuals of high social status. We compiled data on lifetime reproductive success of 75 wild female yellow baboons (*Papio cynocephalus*) over 22 years that included a population increase with two troop fissions, followed by a population crash with two fusions of the same troops. We use this unique data set to show for the first time that the considerable impacts of dominance status on lifetime reproductive success can be markedly altered by intrinsically and extrinsically mediated demographic events.

This study began in 1974 with a single troop of 106 baboons in Mikumi National Park, Tanzania. The troop increased to 130 before splitting into three troops of 60, 49 and 21 individuals. The first split formed V1 and V2 in 1978; then V3 split from V1 in 1979. In 1987, all three troops began to undergo a catastrophic decline (Fig. 1), eventually leading to their fusion back together in 1989 (V2 and V3) and 1994 (V1 and V2). The troop stabilized after the 1994 merger. As of 1996, the total troop size was 23 individuals (11 individuals from V1 and 12 from V2), 7 of whom were adult females. The troop has continued to slowly increase since that time.

The entire baboon population in Mikumi showed a dramatic decline during the period in which our study troops declined. This resulted in an overall lower population size and density but also in fewer troops with a much smaller mean group size (48 individuals in 1984 vs 24 individuals in 1994; G.W. Norton and S.K. Wasser, unpublished data). The catastrophic population decline corresponded with a dramatic rise in known incidences of

leopard predation on our study troops (see Results and Discussion)

We first examine the effects of maternal dominance status on lifetime reproductive success and fecundity of female baboons over the entire study period. Lifetime reproductive success is calculated as: number of offspring surviving to 18 months (~6 months beyond weaning) and 48 months (the earliest recorded onset of female menses). Fecundity is evaluated using: (1) reproductive life span, determined by age at menarche and death; (2) total number of offspring produced; and (3) interbirth interval (IBI), broken down by (a) cycles to conception, (b) percent miscarriages, and (c) lactation duration.

We next examine how the impact of social status on lifetime reproductive success changed during the population increase versus decline. Data are partitioned by mothers according to those experiencing the majority of reproductive life prior to, versus during, the population decline. The former consisted of mothers born a minimum of 10 years (mean age at death) prior to the onset of the decline. The latter consisted of mothers born a maximum of 6 years (mean age at first birth) prior to the onset of the decline (Fig. 1). [All females ($n=17$) born between 1978 and mid-1981 were excluded from these latter analyses.]

Methods

Study site and species

Details of the site, demography and reproductive behavior for the study troops can be found in Rhine et al. (1986, 1988; see also, Norton et al. 1987; Wasser and Starling 1988; Wasser and Norton 1993). The study troops have been followed almost daily at Mikumi National Park as part of an ongoing long-term research project initiated in 1974 (Rhine et al. 1988).

One or more troops were generally observed 5 days per week since 1975, except for three extended periods without fieldwork: 4 November 1977–8 March 1978, 5 January–15 June 1985, and 15 September–1 December 1987. A troop was typically found at one of the sleeping sites within its range in the morning and followed on foot throughout the day. Daily rolls were taken on all animals present, along with reproductive states of all adult females (Wasser 1983). We used the number of missing observation days to estimate the confidence surrounding all reproductive state duration measures. High confidence estimates of a reproductive state duration were those with a combined observational gap immediately preceding and following the first and last observation of that state, respectively, that totaled $\leq 5\%$ of the mean duration (in days) of that state. In this study, we use only high confidence estimates for all reproductive state measures.

Calculating female dominance rank

Relative and absolute dominance rank were calculated using annually constructed win–loss matrices of all female–female agonistic interactions, collected during 30 min of continuous focal animal follows of all adult females (e.g., Wasser 1983; see also Rhine et al. 1988). All hierarchies were essentially linear with very few wins below the diagonal (i.e., subordinates winning against more dominant individuals). Average number of systematically collected agonistic interactions used in these analyses ranged from 200–400 per troop year annually. The highest ranked female was assigned an absolute rank of 1; the lowest ranked female was assigned an absolute rank of n . Relative dominance rank was coded as the fe-

Table 1 Mean lifetime reproductive success measures for adult females of each dominance rank quartile (1–4). Data are shown as mean±SE (sample size in parentheses). Values for *r* and *P* are from simple regression analyses

	Rank 1	Rank 2	Rank 3	Rank 4	<i>r</i> and <i>P</i>
Age at menarche	4.6±0.1 (15)	4.7±0.1 (16)	5.1±0.06 (23)	5.2±0.12 (21)	<i>r</i> =0.49 <i>P</i> <0.0001
Age at first birth	6.4±0.39 (7)	6.1±0.18 (12)	6.9±0.23 (13)	6.9±0.32 (14)	<i>r</i> =0.27 <i>P</i> <0.07
Age at death	12.0±1.17 (15)	10.6±0.74 (16)	10.74±0.56 (23)	8.8±0.45 (21)	<i>r</i> =0.33 <i>P</i> <0.004
Reproductive age span	7.4 ±1.12 (15)	5.91±0.75 (16)	5.62±0.56 (23)	3.59±0.44 (21)	<i>r</i> =0.4 <i>P</i> =0.0004
Total no. offspring	4.33±0.87 (15)	3.25±0.43 (16)	3.17±(0.43) (23)	1.95±0.33 (21)	<i>r</i> =0.34 <i>P</i> =0.003
No. male offspring	2.25±0.52 (12)	1.87±0.36 (15)	1.48±0.27 (21)	1.33±0.27 (18)	<i>r</i> =0.24 <i>P</i> =0.05
No. female offspring	3.25±0.51 (12)	1.6±0.29 (15)	2.0 ±0.34 (21)	0.94±0.17 (18)	<i>r</i> =0.44 <i>P</i> =0.0002
No. offspring surviving at 18 months	2.8±0.69 (15)	1.94±0.37 (16)	1.70±0.34 (23)	1.10±0.29 (21)	<i>r</i> =0.31 <i>P</i> =0.006
No. male offspring at 18 months	1.4±0.39 (15)	1.06±0.27 (16)	0.7±0.17 (23)	0.57±0.2 (21)	<i>r</i> =0.28 <i>P</i> =0.014
No. female offspring at 18 months	1.4±0.35 (15)	0.88±0.26 (16)	0.96±0.26 (23)	0.52±0.15 (21)	<i>r</i> =0.25 <i>P</i> =0.033
No. offspring at 4 years	2.07±0.51 (15)	1.5±0.33 (16)	1.13±0.26 (23)	0.48±0.18 (21)	<i>r</i> =0.39 <i>P</i> =0.0005
No. male offspring at 4 years	0.93±0.3 (15)	0.81±0.28 (16)	0.52±0.14 (23)	0.29±0.12 (21)	<i>r</i> =0.28 <i>P</i> =0.015
No. female offspring at 4 years	1.13±0.26 (15)	0.69±0.2 (16)	0.65±0.23 (23)	0.24±0.1 (21)	<i>r</i> =0.33 <i>P</i> =0.004
Offspring survivorship to 18 months	0.54±0.09 (12)	0.54±0.09 (15)	0.50±0.08 (21)	0.50±0.09 (18)	<i>r</i> =0.05 <i>P</i> =0.68
Male survivorship to 18 months	0.85±0.50 (9)	0.64±.10 (10)	0.5±0.14 (15)	0.49±0.16 (9)	<i>r</i> =0.26 <i>P</i> =0.055
Female survivorship to 18 months	0.62±0.09 (9)	0.58±0.14 (10)	0.54±0.11 (15)	0.67±0.14 (9)	<i>r</i> =0.07 <i>P</i> =0.63
Offspring survivorship to 4 years	0.41±0.07 (12)	0.42±0.08 (15)	0.33±0.06 (21)	0.21±0.07 (18)	<i>r</i> =0.26 <i>P</i> =0.03
Male survivorship to 4 years	0.57±0.12 (9)	0.37±0.12 (10)	0.28±0.08 (15)	0.29±0.14 (9)	<i>r</i> =0.27 <i>P</i> =0.05
Female survivorship to 4 years	0.5±0.05 (9)	0.48±0.13 (10)	0.26±0.09 (15)	0.28±0.12 (9)	<i>r</i> =0.21 <i>P</i> =0.13

male's absolute dominance rank divided by *n*, the number of adult females in her troop. This method enabled relative rank to be appropriately adjusted with change in troop size (Rhine et al. 1988). Rank quartiles were calculated using the relative ranks. We use quartiles because they (1) better illustrate effects of rank differences by smoothing variance introduced by inter-individual differences and (2) allow comparison with related past work on this population, which also used quartiles (Rhine et al. 1988; Wasser and Norton 1993; Wasser 1995, 1996). Quartiles ranged from 1 (high) to 4 (low), based on relative ranks (0–1), with cut-offs at 0.25, 0.5, 0.75, and 1, respectively.

The modal rank quartile (i.e., most frequent annual rank) was used for analyses of maternal rank effects on lifetime reproductive success. In this study, 5 females switched ranks by more than two rank quartiles over their lifetime, and 43 switched ranks by a single rank quartile (either up or down).

Estimating female age

There were 22 females whose birth dates were unknown. Fourteen of these females were immature at the study onset. We estimated their ages at sexual maturity to be 5 years, which is the mean onset of menarche for all females of known age (Table 1). The remaining eight females already had one offspring at the study onset. We estimated their ages at study onset as 6.5 years (mean age at first birth, Table 1) plus the estimated age in years of their first offspring.

Assessing reproductive failure

We provide a conservative estimate of the percentage of miscarriages per rank quartile, using only cases in which pregnancy was visually confirmed prior to miscarriage. Early pregnancy was visually confirmed by an interval of 10–50 days following detumescence with no observed menses or renewed tumescence, whereby the paracollosal skin changed from shiny black to marbled pink (Altmann 1970). Beyond 50 days gestation, the paracollosal skin turns uniformly pink (visibly pregnant state). Early miscarriages consisted of cases where female paracollosal skin went from marbled pink back to gray, prior to 50 days gestation. Late miscarriages were those where the paracollosal skin went from uniformly pink back to gray with no detectable birth. Both forms of miscarriage were combined in the analyses.

Calculating the interbirth interval

We calculated IBI and the mean for each female while she was 7–10 years old. A 7-year lower limit was used to remove the effect of first reproduction on these analyses. Similarly, a 10-year upper limit was used to control for effects of reproductive aging (Wasser et al. 1998); 10 years was the mean age at death of adult females over the duration of the study, and is lower than the mean age at death prior to the troop decline. Lactation duration analyses were similarly restricted to 7- to 10-year old females. Mean durations per female were used in each of these analyses.

To calculate the number of cycles to conception, we included only high confidence estimates, defined as an observation combined gap of <8 observation days at the beginning and end of the cycle.

Statistics

All data were analyzed using simple and multiple regression analyses. Each female was entered only once into any given analysis. In cases where the dependent variable was a composite of repeated events (e.g. lactation duration across multiple births) the mean of those events was used in the analyses.

Results

Maternal dominance rank had consistent impacts on fecundity and lifetime reproductive success over the entire study (Table 1). Dominant females reached menarche earlier, lived longer, had longer reproductive life spans, produced more male and female offspring and had more surviving offspring at 18 months and 4 years of age. The effect of dominance on offspring survivorship (no. alive/no. born) was significant for survivorship to 4 years but not to 18 months. When partitioned by offspring sex, maternal dominance had significant effects on survivorship to 18 months and 4 years for males only. Thus, throughout the study, rank effects observed on number of female offspring surviving to 18 months and 4 years of age were largely mediated through change in female offspring production and not survivorship (Table 1). Dominant females

also had fewer miscarriages, shorter durations of lactation and shorter IBIs (Table 2).

Effects of maternal rank, troop, and population trend (increasing vs declining) on reproductive success were next examined in multiple regression analyses. The above maternal dominance rank effects remained significant, except for loss of rank effect on number of male offspring produced and male offspring survival to 4 years (Table 3; no male offspring survived to 4 years during the decline). Troop had no effect on reproductive success. However, population trend had a significant effect on all reproductive success measures except female offspring survivorship to 18 months or 4 years. The interaction between dominance rank and population trend had significant effects on age at death, reproductive life span, total number of offspring and number of female offspring produced, number of female offspring surviving to 18 months of age, and number of offspring (and number of female offspring) surviving to 4 years of age. Each of these dependent measures decreased for mothers born during the population decline, with rank effects on their lifetime reproductive success measures disappearing completely (Fig. 2a–d; Table 3). Figure 2a–d clearly shows that the disappearance of rank effects during the decline was primarily due to loss of rank advantage to dominant females. Among the fecundity measures, IBI and lactation duration significantly decreased during the population decline ($F_{1,20}=5.74$, $P=0.03$; $F_{1,30}=4.26$, $P=0.05$, respectively), suggesting some behavioral and physiological compensation. Miscarriage rates also nearly doubled

Table 2 Mean number of cycles to conception, miscarriage rate and duration of lactation and interbirth interval in days per female between the ages of 7–10 years according to their dominance rank quartile (1–4). Data are shown as mean±SE (sample size in parentheses). See results for details on the statistical analyses

	Rank 1	Rank 2	Rank 3	Rank 4	<i>r</i> and <i>P</i> values
Cycles to conception	3.11±0.26 (19)	3.3±0.26 (20)	3.89±0.45 (18)	3.17±0.51 (18)	<i>r</i> =0.20 <i>P</i> =0.46
Miscarriage rate	0.05±0.03 (14)	0.07±0.04 (17)	0.12±0.05 (20)	0.20±0.07 (20)	<i>r</i> =0.25 <i>P</i> =0.04
Lactation duration	243.75±20 (10)	346.5±19 (11)	385.8±25 (10)	330.2±23 (13)	<i>r</i> =0.35 <i>P</i> <0.02
Interbirth interval	545.4±18 (16)	598.4±23 (19)	690±26 (19)	723±34 (20)	<i>r</i> =0.52 <i>P</i> =0.0001

Table 3 Results of multiple linear regression analyses on effects of rank, population trend [increasing (*I*) or declining (*D*)] and their interaction on measures of lifetime reproductive success for 58 adult females

	Overall <i>r</i>	Overall <i>P</i>	Rank	I/D	Rank*I/D
Age at death	0.68	0.0001	0.0001	0.0001	0.004
Reproductive life span	0.71	0.0001	0.0001	0.0001	0.005
Total no. offspring	0.70	0.0001	0.0002	0.0001	0.024
No. male offspring	0.45	0.005	0.11	0.007	–
No. female offspring	0.66	0.0001	0.0001	0.002	0.05
Total no. offspring at 18 months	0.68	0.0001	0.002	0.0001	0.11
No. male offspring at 18 months	0.59	0.0001	0.016	0.0001	–
No. female offspring at 18 months	0.56	0.0001	0.01	0.0006	0.05
No. offspring at 4 years	0.70	0.0001	0.0001	0.0001	0.03
No. male offspring at 4 years	0.58	0.0001	0.04	0.0001	–
No. female offspring at 4 years	0.59	0.0001	0.0004	0.0002	0.009
Offspring survivorship to 18 months	0.48	0.002	0.41	0.0008	–
Male survivorship to 18 months	0.50	0.003	0.06	0.006	–
Female survivorship to 18 months	0.18	0.54	0.68	0.30	–
Offspring survivorship to 4 years	0.58	0.0001	0.035	0.0001	–
Male survivorship to 4 years	0.61	0.0001	0.16	0.0001	–
Female survivorship to 4 years	0.34	0.09	0.07	0.28	–

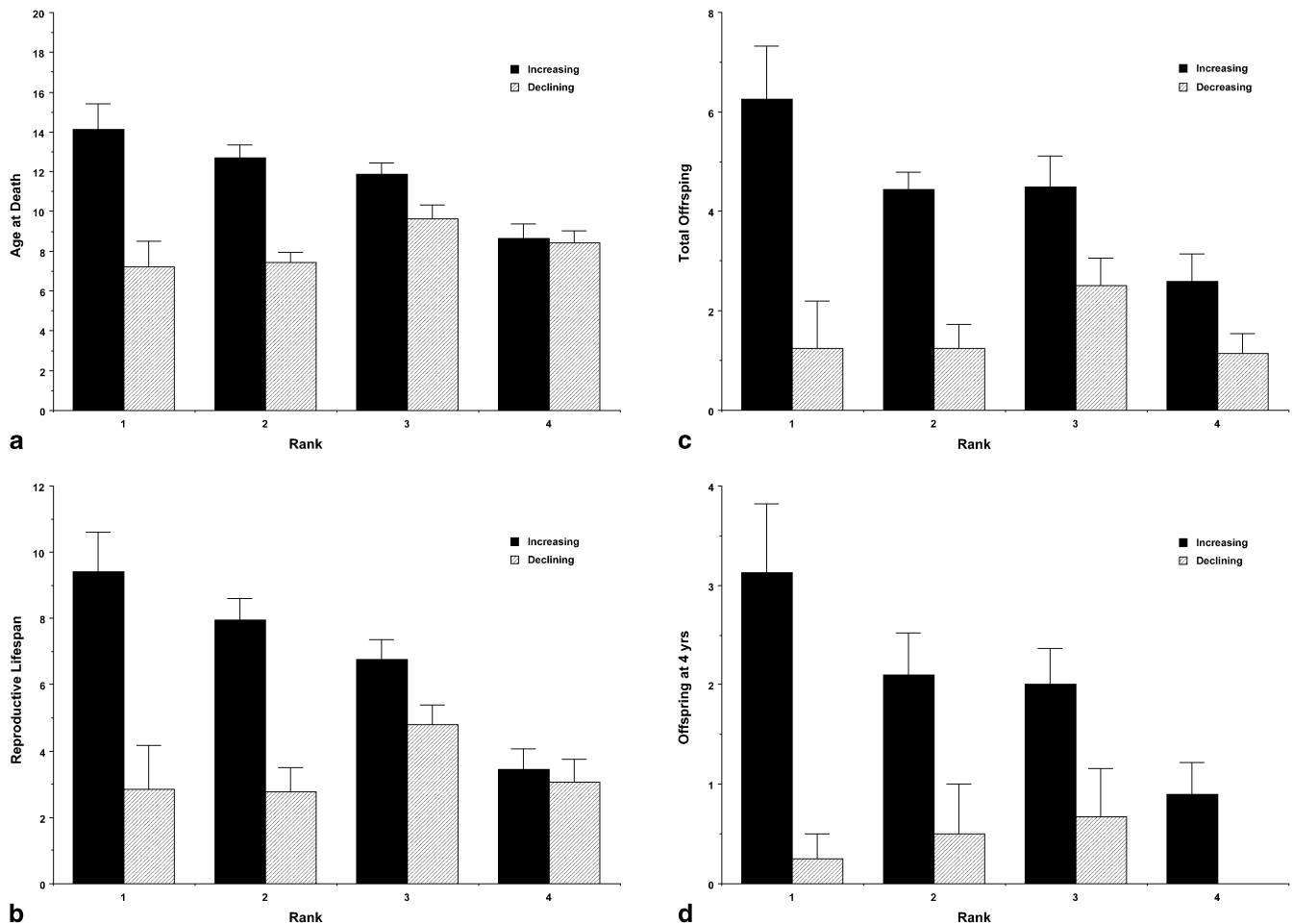


Fig. 2 Effects of maternal dominance rank for adult female baboons born during the period of population increase (*I*) or decline (*D*) on **a** age at death, **b** reproductive life span, **c** total number of offspring produced over the female's lifetime, and **d**

offspring still alive at 4 years of age. [$n=8, 9, 10,$ and 10 , for rank quartiles 1–4, respectively, in the increasing (*solid black*) condition and $4, 4, 7,$ and 6 in the declining condition (*shaded*)]

during the decline but this difference was not significant ($F_{1,54}=1.55, P=0.28$).

There was a notable, but not significant effect of population trend on the ratio of male to female offspring survivorship to 4 years of age only ($F_{1,18}=3.8, P=0.06$). Survivorship was slightly (but not significantly) higher for male than female offspring during the period of population increase. However, only female offspring survived to 4 years during the period of population decline (Fig. 3b). While the within-sex variance is high, survivorship to 18 months also became lower for male versus female offspring during the decline (Fig. 3a). These sex differences in survivorship implicate predation as a cause of the decline since male but not female offspring increasingly position themselves on the troop periphery with age, presumably making them more vulnerable to predation (Rhine et al. 1981, 1984; Wasser and Norton 1993). Leopard predation was also visually confirmed in 21% ($n=21$) of all cases of missing adult females. The majority of these losses occurred during the period of population decline. By contrast, we could not confirm illness, or death due to illness, in any case of

adult female loss ($n=102$ adult female deaths; but see Cheney et al. 1988).

Discussion

This study demonstrates a clear effect of maternal dominance rank on lifetime reproductive success in unprovisioned free-ranging baboons (Table 1). High-ranking females produced on average 2.07 ± 0.51 offspring that survived to 4 years of age, compared with 0.48 ± 0.18 offspring for low-ranking females. High-ranking females had a longer reproductive life span, reached sexual maturity earlier and lived longer. They also produced more offspring of both sexes (Table 1) through shorter IBIs, including shorter lactation and lower miscarriage rates (Table 2). The dramatic effects of maternal rank on lifetime reproductive success in this study were primarily the result of differences in production rather than long-term survivorship of offspring, particularly for female offspring. This contradicts the suggestion by Silk et al. (2003) that infant survival is arguably the most important

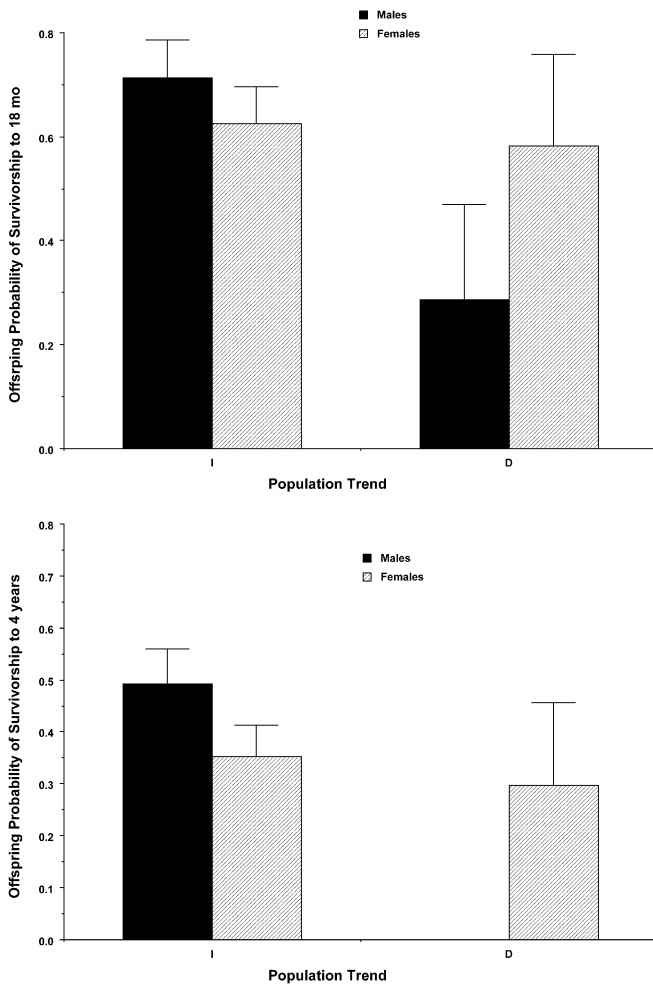


Fig. 3 Sex-specific offspring survivorship to **a** 18 months and **b** 4 years, during the period of population increase (I) and decline (D) ($n=27$ and 6 mothers in the increasing and declining conditions, respectively)

source of variation in lifetime reproductive success. It also speaks to the importance of socially mediated reproductive suppression as a competitive strategy to suppress the matriline sizes of other females (Wasser and Barash 1983; Wasser and Starling 1988).

Table 1 shows the effect of dominance on lifetime reproductive success, independent of the impact of the troop decline. When population trend was taken into account, rank effects on lifetime reproductive success virtually disappeared during the troop decline (Table 3), demonstrating that this relation is tightly linked to environmental conditions. This is inconsistent with the untested assumption by Silk et al. (2003) that social status effects on lifetime reproductive success are independent of environmental conditions. Loss of rank effects on lifetime reproductive success in our study was largely due to loss of rank advantage to high-ranking females (Fig. 2a–d). Female–female attack coalitions, employed in both reproductive competition (Wasser and Starling 1988) and rank maintenance (Cheney 1977), greatly declined during the population crash as well (S.K. Wasser, unpublished data).

These combined results suggest that the disappearance of rank effects on lifetime reproductive success may have been exacerbated by loss of one's social network (Silk et al. 2003), especially close kin, making it more difficult to reinforce rank status. It further suggests that relative matriline size is an important vehicle for capitalizing on the lifetime reproductive success advantages of rank. Increased offspring production (this paper) and timing births to occur under optimal social and ecological conditions (Rhine et al. 1988; Wasser and Norton 1993) are key components of maintaining matriline size and hence sustaining a relatively high lifetime reproductive success. Reproductive competition ties directly into this since females can improve offspring survival from birth by suppressing the reproduction of others, simultaneously increasing their relative matriline size (Wasser and Starling 1988; Wasser and Norton 1993). However, when the ability to maintain matriline size is challenged by other factors (e.g., excessive predation), reproductive competition is diminished and females appear unable to maintain the reproductive advantages of high dominance rank.

Longer reproductive life span is also vital to lifetime reproductive success. In fact, Rhine et al. (2000) found that most variance in lifetime reproductive success among the Mikumi baboons was explained by variance in reproductive life span, and the present study showed that this too is highly correlated with dominance status. Females appeared to compensate for their decreased reproductive life span during the decline by reducing lactation duration and IBI. This response is consistent with Ricklefs' (1998) model of aging, which predicts that females will reduce parental investment (lactation duration and IBI) to restore reproductive life span owing to the overall importance of the latter to lifetime reproductive success.

The magnitude, abruptness and far-reaching consequences of the population decline beg speculation about the complex ecological factors that precipitated it. Several lines of evidence point to a rise in leopard predation as an important proximate cause of mortality during the population decline in our study. These include: relatively high incidences of visually confirmed predations during the population decline; lack of evidence for other causes of mortality (e.g., illness); greater male versus female offspring mortality with increasing age during the decline; and possibly the loss of rank effects on reproductive success. Baboon food resources may have also been limited and constrained during the decline: Despite fewer troops and number of individuals per troop competing for resources, the baboons continued to work long and hard over large areas and distances to find food; range sizes, distances traveled, diet diversity, time spent feeding and intertroop encounters at food patches and sleeping refugia each remained comparable to those seen in larger troops before the decline (Norton, unpublished data). While resource limitation may have contributed to the population decline, we would have expected effects of maternal rank on lifetime reproductive success to have increased, not decreased, if the decline were driven by increased re-

source competition. This assumes that priority of access to resources is a principal advantage of dominance.

The extent to which extrinsic events may have precipitated the sudden and sustained elevation of predation and associated crash is also of interest. The timing of the decline corresponded with an abrupt and sustained crack-down on poaching in Mikumi that may have elevated the importance of baboons as a primary food source of leopards. Extremely heavy poaching for elephant ivory and game meat in the Mikumi/Selous ecosystem (Dublin et al. 1997) increased the number of fresh carcasses available to the scavenger–predator populations during the late 1970s to mid-1980s. This was abruptly curtailed in Mikumi by the appointment of a new chief park warden in 1986, whose policies led to an unprecedented crack-down on poachers (Gordon 1989). This was followed by a joint, country-wide anti-poaching campaign by Tanzania's military, police and wildlife authorities in late 1988–1989, reinforced by the CITES ivory ban in 1989. The resultant abrupt and sustained cessation of poaching in our study area appears to have produced a ripple effect that precipitated the elevated leopard predation and associated baboon mortality: A dramatic reduction in the availability of fresh carcasses may have led to a shift to baboons as a primary food source of leopards. At the same time, a reduction in dry season fires (frequently set by poachers) and associated increases in grass height, shrubs and wooded habitats (Norton, unpublished data) likely increased baboon vulnerability to predation by providing better cover for leopards as well as a shift in baboon ranges as they tried to avoid areas of high cover. These same changes may have also limited and constrained baboon food resources. Additionally, most old females (>15 years) and females approaching old age (>10 years) died immediately prior to and during the first 2 years of the decline. This loss of experienced older females, resulting in an entirely young, less experienced adult female population, could have reduced the foraging skills and available knowledge of rarely used foraging areas, further increasing baboon vulnerability to predation, as well as exacerbating the disruption of social networks.

What we find most striking about the above chain of events is the magnitude of impacts that seemingly unrelated macro-ecological events and management practices appear to have had on the relation between social structure and lifetime reproductive success in the Mikumi baboons. The abrupt and sustained cessation of poaching instigated by management authorities in Mikumi, coupled with associated changes in fire patterns, habitat and faunal densities, appears to have precipitated and sustained an increase in leopard predation and predation risk. Baboon ranging, foraging patterns and food resources were also affected. These combined events led to a population crash, the fusion of troops that were separated for up to 16 years, and a breakdown of the relation between social status and lifetime reproductive success in free-ranging yellow baboons.

The dynamic changes that occurred during this study also have broad implications for behavioral ecology and sociobiological theory. They suggest that predation and resource competition are tightly linked, and that their relative importance (Wrangham 1980; Isbell 1990) in the evolution of sociality is likely to be highly dependent on environmental conditions. The high variance we found in female lifetime reproductive success suggests that mate choice by males may be a more important component of sexual selection in baboons than previously appreciated, just as female–female reproductive competition was previously found to be more important than expected (Wasser and Barash 1983). At the same time, the relative importance of these forms of sexual selection are likely to vary with environmental conditions. As the baboon population crashed in Mikumi, so did variance in female (and probably male) lifetime reproductive success. Reproductive competition decreased, at least among females. Parental investment also decreased. We have yet to examine whether mate choice by both sexes varied under such conditions, as sexual selection theory (Williams 1966; Trivers 1972) would also predict.

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