PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 2000 **355**, 1627-1635
doi: 10.1098/rstb.2000.0725

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Problems with primate sex ratios

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Birth sex ratios of baboons in Gombe National Park, Tanzania, show an overall male bias of *ca.* 20%, but there is no obvious explanation for this trend. Individual females did not alter their sex ratios according to persistent levels of local resource competition. Sex ratios showed an unexpected relationship between age and rank: subordinate females had more sons when they were young; dominant females had more sons when they were old. The sex ratio of low-ranking females also varied with the severity of environmental conditions during pregnancy. Our findings suggest that mammalian sex ratios might be the product of more complex processes than is generally recognized or that sex-determining mechanisms impose sufficient constraints to prevent adaptive variation in all contexts.

Keywords: sex ratio; local resource competition; primates

1. INTRODUCTION

Sex allocation is one of the most productive and provocative topics in behavioural ecology. Although no one doubts the power of evolutionary theory to predict the optimal sex ratios of haplodiploids, virtually every review of sex ratio variation in birds and mammals has concluded that chromosomal sex determination presents a fundamental constraint against significant deviations from 50:50 (Maynard Smith 1978; Williams 1979; Charnov 1982; Clutton-Brock & Iason 1986; Hiraiwa-Hasegawa 1993). However, a growing list of extraordinary sex ratios has been published in recent years (see, for example, Komdeur *et al.* 1997; Kilner 1998; Sheldon *et al.* 1999) and indirect evidence is also accumulating of selective abortion or resorption of embryos of one sex or the other (see, for example, Kruuk *et al.* 1999). In addition, studies of transgenic mice have shown that a transmission ratio distorter (TRD) can successfully alter the sex ratio: the presence of a TRD on the Y chromosome produces twice as many sons as daughters owing to effects on sperm motility (Herrmann *et al.* 1999).

Even assuming that individuals can adaptively alter their sex ratios, published reports often show striking inconsistencies (see, for example, Clutton-Brock & Iason 1986; Hiraiwa-Hasegawa 1993). However, two important papers have recently provided plausible explanations for these apparent contradictions, focusing on predictions generated by Trivers & Willard's (1973) hypothesis on the effect of maternal phenotype on offspring sex ratio.

First, Van Schaik & Hrdy (1991) re-examined the conflicting relationship between dominance rank and sex ratio in non-human primates. Altmann (1980) had found that high-ranking female baboons gave birth to a preponderance of daughters, whereas subordinate females had more sons (see also Altmann *et al.* 1988; Simpson *et al.* 1982). However, Meikle *et al.* (1984) found that dominant female rhesus monkeys gave birth to a higher proportion of sons than did subordinates. Van Schaik & Hrdy (1991) suggested that these conflicting trends were appropriate for their respective environments. Where matrilines compete intensely against each other, dominant females benefit from recruiting more daughters, whereas the juvenile daughters of subordinate females are vulnerable to harassment (Silk 1983). However, where feeding competition is mild, high-ranking mothers should produce more males because they could endow sons with rapid growth and thereby greater competitive ability (as originally envisioned by Trivers & Willard). Consistent with this argument was the demonstration by Van Schaik & Hrdy that the sex ratio of dominant females changed from female-biased in areas of low population growth to male-biased in rapidly growing populations.

Second, Kruuk *et al.* (1999) followed a similar argument in their long-term study of red deer. On the island of Rum, high-ranking females gain a greater return from sons than daughters (and bias their sex ratio accordingly), but only at low population densities. At high densities, females of all ranks show a sex ratio close to 50:50. Kruuk *et al.* point out that high-ranking ungulates show male-biased sex ratios only in studies in which the population density is below the carrying capacity. Thus their conclusions are virtually the same as Van Schaik & Hrdy (1991), except that high-ranking female primates swing from a female bias to a male bias in richer environments, whereas high-ranking ungulates swing from an unbiased sex ratio to a male bias.

Given the repeated ability of behavioural ecologists to discover individual variations in sex ratio and the consistent pattern in these analyses of primates and ungulates, adaptive sex ratios might well prove to be more widespread than the early sceptics had considered possible. Perhaps environmental variations are more important than anyone had recognized, and the contradictory data

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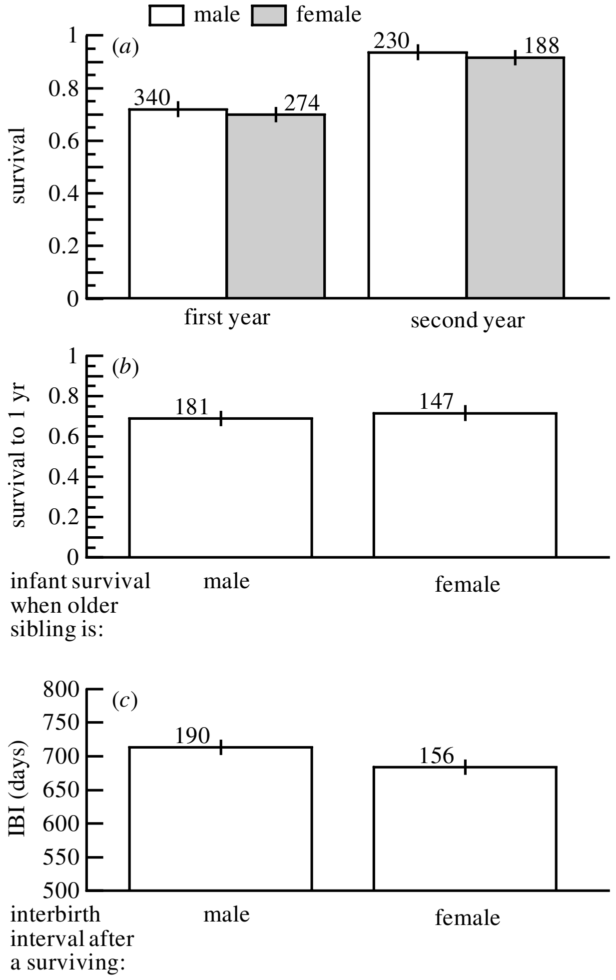

Figure 1. Sex-specific survival and impact on maternal reproductive rate or success. Bars indicate standard errors of the mean; numbers are sample sizes. (*a*) Survival rates do not differ between males and females during the first and second years of life ($p > 0.20$). (*b*) Survival of the next offspring was not significantly influenced by the sex of a surviving older sibling ($p > 0.20$). (*c*) Interbirth interval (IBI) was not influenced by the sex of a surviving offspring ($p > 0.20$).

sets resulted from analyses that were either too coarsely grained or ignored relevant variables. However, sex-determining mechanisms might nevertheless impose serious constraints on individual sex ratios—constraints that can only be overcome under a strong force of selection.

Here we present results from a long-term study of olive baboons at Gombe National Park, Tanzania, comparable in scope with the analyses by Van Schaik & Hrdy (1991) and Kruuk *et al.* (1999). We examine a variety of ecological and demographic factors that have been predicted to influence individual sex ratios in these animals, taking care to determine the interaction between rank and local resource levels. The Gombe population provides an important comparison with earlier analyses because adjacent troops show differences in reproductive rates as high as those included in Van Schaik & Hrdy's review.

We also test the models of Fisher (1930) and Clark (1978) for population sex ratio. Fisher predicted that parents should invest equally in offspring of either sex, so population sex ratios should be inversely related to the average costs of raising each sex. Clark pointed out that members of the philopatric sex are more costly because they eventually compete against their parents for limited resources. Species such as olive baboons with female-biased philopatry should therefore show male-biased population sex ratios due to 'local resource competition' (LRC). Population sex ratios are often skewed in the direction predicted by sex-biased natal philopatry (Clutton-Brock & Iason 1986; Johnson 1988; Gowaty 1993; Hiraiwa-Hasegawa 1993), and LRC is fundamental to the interpretations of individual sex ratios by Silk (1983) and Van Schaik & Hrdy (1991).

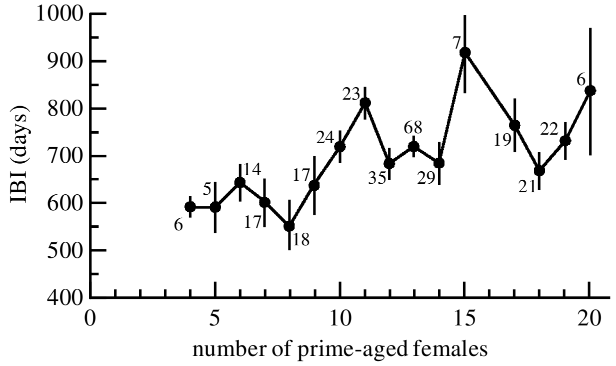

Figure 2. The relationship between troop size and interbirth interval (IBI) after the birth of a surviving offspring. IBI increases significantly with increasing troop size (REML estimation, $F = 10.02$, $p = 0.0018$).

2. METHODS

Gombe National Park covers 40 km^2 of steep valleys running down from the rift escarpment to the shore of Lake Tanganyika. The valleys are filled with semi-evergreen forest, and the slopes and ridge-tops are covered by grassland, savanna woodland and semi-deciduous forest (Goodall 1986). Members of nine different troops are recognized individually from facial features and natural markings. All major demographic events have been recorded since 1967; most deaths are inferred from disappearances. Menarche typically occurs during the fourth year of life; age estimates for females therefore extend to 1963. Dominance ranks are based on the outcome of aggressive and/or competitive interactions. To facilitate comparisons across troops of different sizes, the 'relative rank' was determined for each female. Relative rank is the proportion of females dominated by a particular female, thus the top-ranking female in a given troop has a relative rank of 1.0, and that of the bottom-ranking female is 0.

The duration of post-partum amenorrhoea depends on infant survival (Altmann *et al.* 1978), and the typical birth spacing in this population is two years (Packer *et al.* 1995, 1998). Thus we examine interbirth intervals only after offspring that survived to their second birthday. Offspring older than two years of age are considered to be independent of their mother (see Packer *et al.* 1998). The Gombe baboons show male-biased dispersal: 70% of males leave their natal troops by their ninth birthday and 100% by their 12th birthday (Packer *et al.* 1995), whereas females never move between pre-existing troops (Packer 1979).

Results are available from nine different troops, but four of these split from pre-existing troops in the last few months of the study. Troop-specific growth rates for these four troops are based

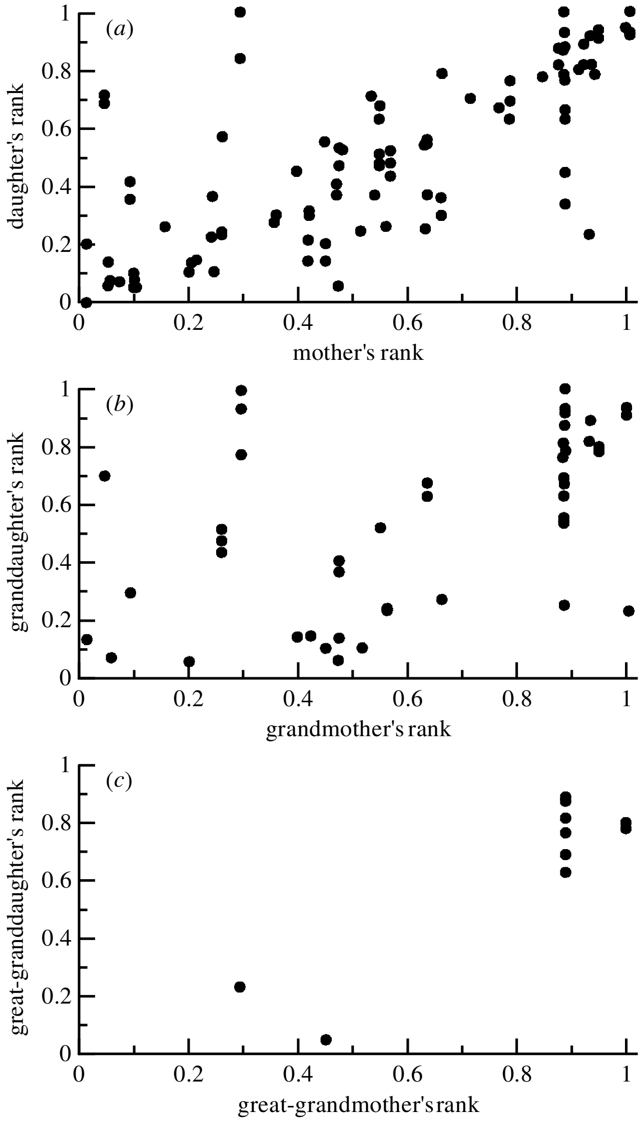

Figure 3. Matrilineal inheritance of female dominance rank. Relative rank is highly correlated between mothers and their (*a*) daughters ($r^2 = 0.555$, $n = 97$, $p < 0.01$, linear regression), (*b*) granddaughters ($r^2 = 0.304$, $n = 50$, $p < 0.01$) and (*c*) great-granddaughters ($r^2 = 0.807$, $n = 12$, $p < 0.01$).

on their respective troops of origin. Analysis is based on 686 live births to 167 females; only one pair of twins has been born in this population.

All analyses on binary outcomes (e.g. male or female offspring, or survival or no survival to first birthday) were performed with marginal generalized linear mixed models (GLMMs) with a logit link. Such models can account for correlation between the multiple observations taken on each mother. Model parameters were estimated with the Generalized Estimating Equations (GEE) approach (Liang & Zeger 1986) in the SAS analysis package. A three-dependent (banded Toeplitz) working correlation structure was used, which allows, for example, for the sex of any offspring to be correlated with the sex of any of the three subsequent offspring of the same mother. Significance of effects was determined by an approximate *Z*-test based on GEE's empirical (robust) estimates of standard error of the mean. Results were robust to other choices of correlation structures.

All analyses on the continuous-outcome interbirth intervals used general linear models (GLMs; Searle *et al.* 1992) and a three-dependent correlation structure to account for correlation between interbirth intervals of the same mother. Interbirth intervals satisfied assumptions of normality. Model parameters were estimated from residual maximum likelihood (REML), and the significance of effects was determined by an approximate *t*-test. Results were robust to other choices of correlation structures.

3. RESULTS

Individuals are expected to gain differing costs and benefits from a son or a daughter according to their specific circumstances. We first consider the environmental and social factors that are likely to influence sex allocation in the Gombe baboons before presenting the results of the sex ratio analysis.

(a) *Effects of environmental and phenotypic factors*

(i) *Inherent attributes of sons versus daughters*

Baboons are sexually dimorphic, so males might be expected to suffer higher mortality than females (Clutton-Brock *et al.* 1985) or to inflict greater costs on maternal reproduction (Clutton-Brock *et al.* 1982). However, the Gombe males do not suffer greater mortality than females in their first two years of life (figure 1*a*), nor do they inflict higher mortality on their mother's next offspring (figure 1*b*) or take any longer to 'fledge' than females (figure 1*c*).

(ii) *Rainfall patterns*

Harsher conditions during pregnancy lowers the sex ratio in red deer (Kruuk *et al.* 1999), possibly because male foetuses are more vulnerable to stress. The dry season at Gombe runs from June to October, and interbirth intervals are longer when lactating females experience below-average rainfall in the dry season (Packer *et al.* 1995). In the following analysis we focus on the effects of a harsh dry season during pregnancy. A stressful pregnancy not only might have a direct influence on the sex ratio but also might affect rates of development in full-term infants.

(iii) *Local resource competition*

LRC has been estimated from reproductive performance (Johnson 1988) and from population growth (Van Schaik & Hrdy 1991) on the assumption that slow growth reflects scarce resources. We examined the possible effects of LRC in three ways. First, the Gombe troops show persistent differences in growth rate, and females in the slowest troop also showed the slowest rate of sexual maturation and the longest interbirth intervals (Packer *et al.* 1995). These inter-troop differences have persisted over decades: the annual growth rate in troop C averaged 1.71% between 1970 and 1996, whereas troop D averaged 9.04% between 1978 and 1996. Second, adding more females to a troop might increase overall levels of feeding competition, as suggested by the fact that interbirth intervals become longer in larger troops (figure 2). Troops can grow only through the recruitment of daughters, so troop size might provide a good estimate of the extent of LRC. Third, the risk of LRC should be greatest for young mothers because they are more likely to survive until their daughters reach maturity (and suffer from the greatest

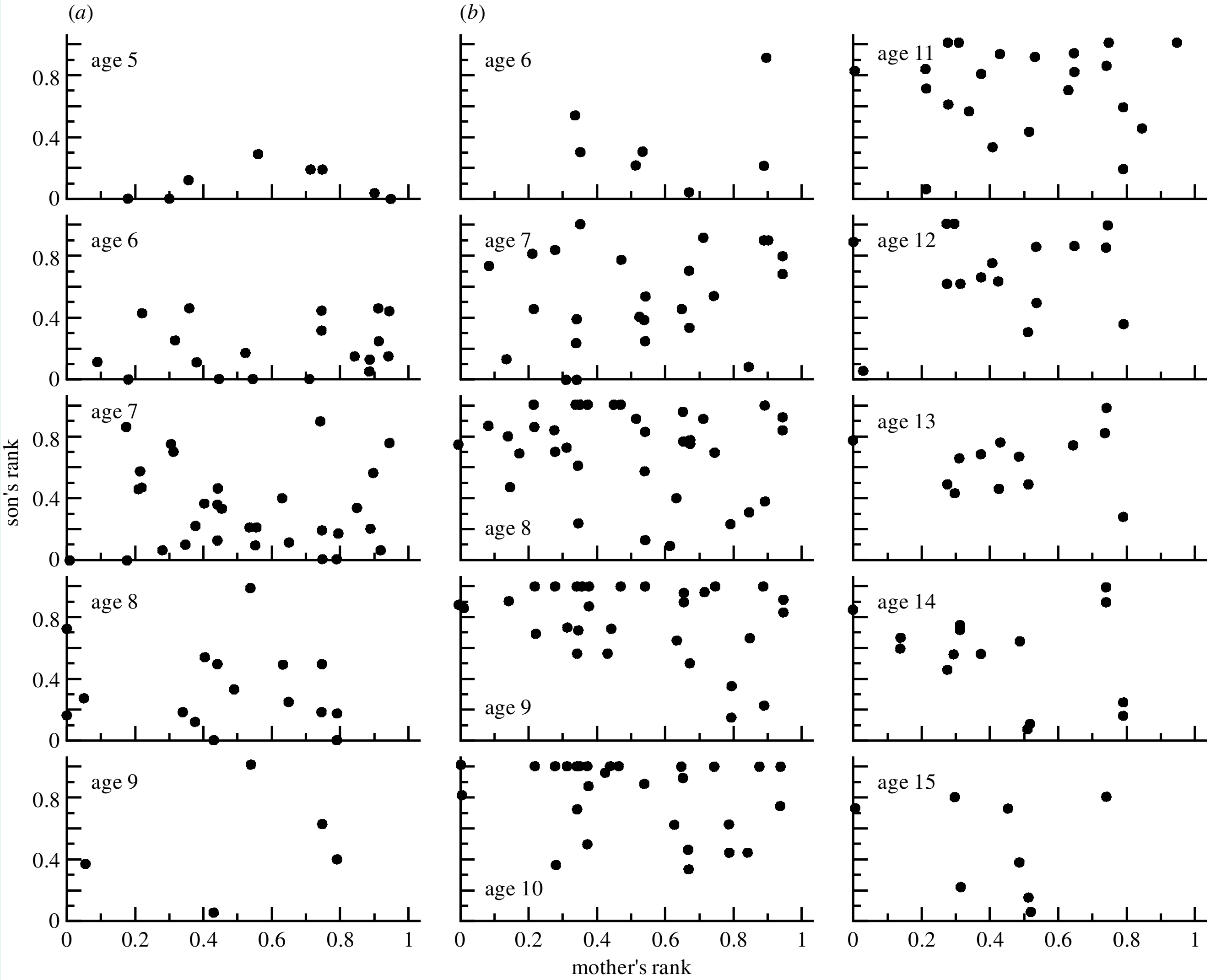

Figure 4. Effect of mother's rank on the dominance rank of sons. (*a*) Males in their natal troop, (*b*) males in their new troop. To control for the effect of male age (see figure 5*d*), each panel presents the relationship between maternal rank and male rank for sons of a particular age. Because male rank is lower for males still resident in their natal troop, data are also separated according to the male's dispersal status. None of these 15 data sets show a significant correlation between the relative ranks of mothers and sons ($p > 0.10$).

cumulative number of daughters) (see Clutton-Brock & Iason 1986). Although the pattern of maternal investment in sons and daughters varies with age (see §3(b)), we could find no strong evidence that adult daughters retarded their mother's reproduction.

(iv) *Maternal rank*

Influence of maternal rank on the fitness of adult offspring

High-ranking females might be better able to influence the fitness of daughters (owing to matrilineal inheritance of rank) than sons (owing to a high degree of sexual dimorphism and male natal dispersal) (Silk 1983). Female rank at Gombe is highly correlated with maternal, grandmaternal and great-grandmaternal rank (figure 3). In contrast, male rank is independent of maternal rank, regardless of age or residence in the natal troop (figure 4). Because maternal rank might influence the behavior of only those males that grew up together, we examined pairs of same-aged males from the same natal troop that resided in the same non-natal troop as adults. However, sons of high-ranking mothers dominated the sons of low-ranking mothers in only six out of 18 pairs.

Gombe females attain adult rank by the age of four years and maintain a similar rank for the rest of their lives (figure 5*a*). However, overall reproductive performance is not strongly correlated with rank in this population: high-ranking females enjoy shorter interbirth intervals and higher infant survival, but they suffer from higher miscarriage rates and more frequent reproductive pathologies (Packer *et al.* 1995). Instead, female reproduction depends on age: females reproduce at a constant rate until senescence (figure 5*c*) (see also Packer *et al.* 1998). In contrast, male rank depends on competitive ability (Saunders & Hausfater 1978; Packer 1979), reaching a peak after full physical development (figure 5*b*). Males compete intensively for temporary 'ownership' of oestrous females, and 'consortships' are highly correlated with reproductive success (Altmann *et al.* 1996). Consorting activity is closely correlated with dominance (Hausfater 1975; Packer 1979) and shows a similar change with age (figure 5*d*).

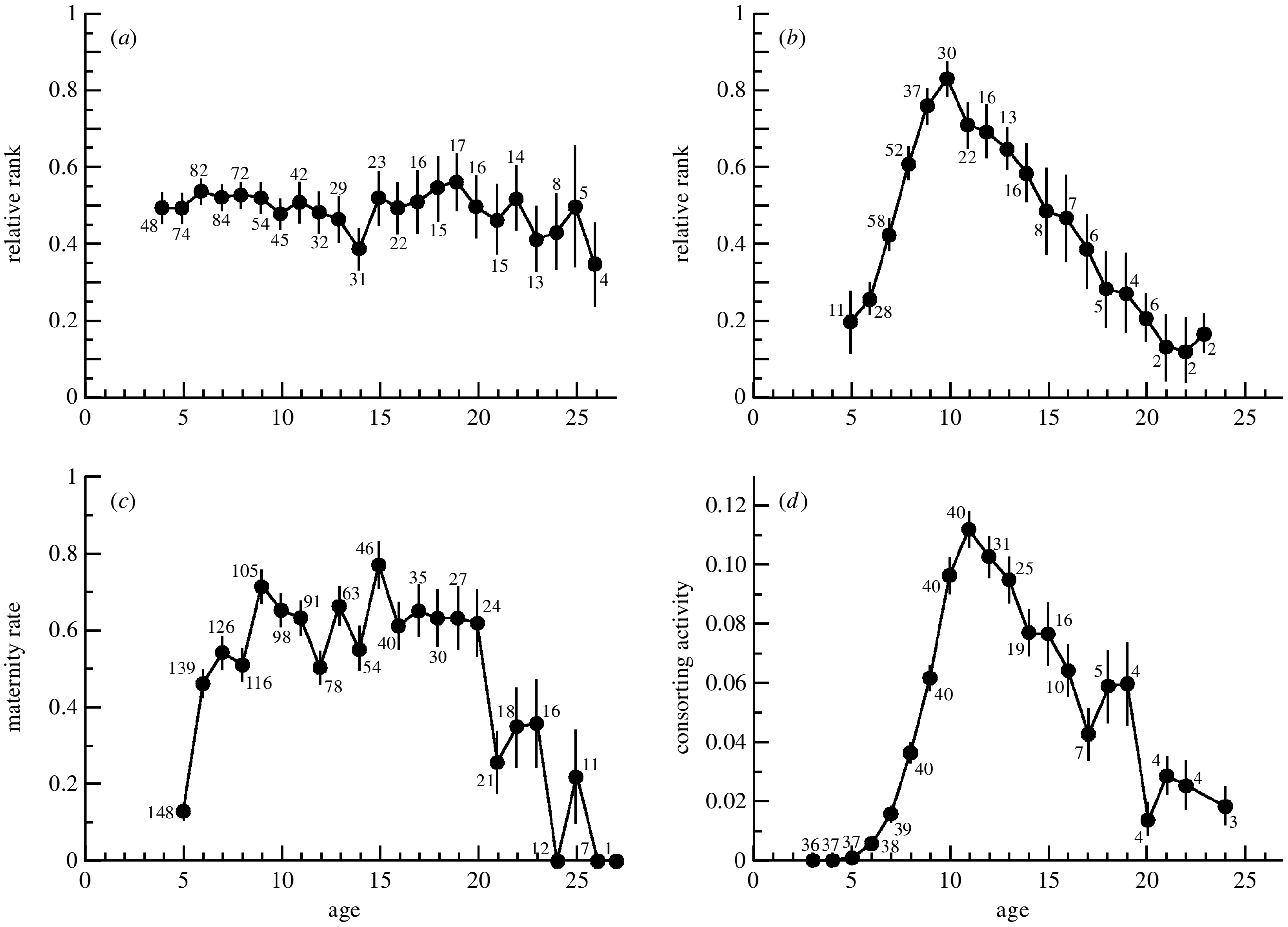

Figure 5. The effect of age on dominance and reproductive rates in females and males. (*a*,*b*) 'Relative rank' is the proportion of like-sexed individuals dominated by each animal, where the top-ranking female is assigned 1.0 the bottom-ranking female is assigned 0. Female rank (*a*) shows no significant change with age; male rank (*b*) reaches a peak at the age of ten years, then declines monotonically ($p = 0.0000$, analysis of variance). (*c*) Gross maternity is the number of live offspring produced at each age (modified from Packer *et al*. 1998). Female reproductive rates remain constant from the age of six to 20 years before declining in old age. (*d*) Consorting activity is the proportion of days per month that each male consorted with an oestrous female. Consorting shows a similar overall pattern to male rank, although it peaks at the age of 11 years.

Thus, whereas female rank is largely inherited (figure 3), female fitness is influenced only slightly by social rank (Packer *et al.* 1995). Although male fitness is strongly influenced by rank (figure 5*b*,*d*), sons do not inherit their mothers' rank (figure 4).

Maternal rank and sex-dependent productivity of offspring

High-ranking females might be better able to rear daughters (Altmann *et al*. 1988), perhaps owing to selective harassment stemming from LRC (Silk 1983). Various studies have shown that daughters of subordinate females suffer the highest mortality of any juveniles (see, for example, Dittus 1979; Silk *et al.* 1981), and subordinate mothers might also suffer greater costs from raising daughters than sons (Gommendio *et al.* 1990). For dominant females, in contrast, infant mortality might be greater for sons than for daughters (Altmann *et al*. 1988). Thus, subordinate females would often gain a higher productivity through sons, whereas dominants would gain more through daughters. However, Van Schaik & Hrdy (1991) pointed out that these effects are likely to be restricted to populations with extensive female–female competition. Where LRC is minimal, low-ranking daughters should suffer less harassment and high-ranking mothers might be better able to enhance the physical development of their sons (Trivers & Willard 1973).

(b) *Multivariate analysis of infant survival and interbirth intervals*

Tables 1 and 2 present the minimal models of a GLMM analysis of infant survival and a GLM analysis on interbirth interval. In both analyses we tested for effects of offspring sex, rainfall during the mother's pregnancy, whether the infant was conceived during the dry season, troop growth rate, troop size, maternal age and maternal rank. Maternal rank and maternal age were the only two factors that significantly influenced offspring survival (table 1); there were no significant interactions involving the sex of the offspring. The analysis of interbirth intervals revealed two significant interactions with offspring sex (table 2). First, as mothers grow older, they take longer to 'fledge' sons, whereas they fledge daughters more quickly (figure 6*a*). These findings suggest that, whereas mothers become increasingly adept at raising daughters, they find it increasingly difficult to raise sons. Second, although dominance rank does not influence how

Table 1. *Minimal GLMM model for effects on infant survival (survival to first birthday)*

parameter	estimate	s.e.m.	z	p
intercept	0.8491	0.3279	2.590	0.0096
maternal age	−0.0394	0.0203	−1.944	0.0519
maternal rank	1.1341	0.3106	3.651	0.0003

Table 2. *Minimal GLM model for effects on interbirth intervals*

parameter	estimate	s.e.m.	d.f.	t	p
intercept	906.4	120.2	97	7.54	0.0001
maternal age	−24.5	8.1	187	−3.04	0.0027
sex of offspring	−292.1	75.6	187	−3.87	0.0002
maternal rank	−269.8	59.8	97	−4.51	0.0001
rainfall in dry season	4.3	4.0	187	1.07	0.2847
troop size	21.5	5.6	187	3.86	0.0002
troop growth	−5625.9	1472.8	97	−3.82	0.0002
age × sex	−14.8	5.1	187	−2.91	0.0041
rank × sex	−247.3	71.7	187	−3.45	0.0007
rainfall × troop size	−0.7	0.3	187	−2.27	0.0244
age × troop growth	347.2	121.6	187	2.86	0.0048
rainfall × troop growth	120.6	37.5	187	3.21	0.0015

long it takes a mother to rear her son, high-ranking females are able to rear daughters more quickly than are low-ranking females (figure 6*b*), a trend consistent with that found by Gommendio *et al.* (1990). Note that interbirth intervals showed no significant interaction between offspring sex and any of our measures of LRC. This means that low-ranking mothers in large troops (for example) found it no more difficult to raise daughters than sons, compared with mothers in small troops.

(c) *Sex ratio analysis*

The population sex ratio deviated significantly from 50:50; 55% of 662 live-born infants were male ($\chi^2 = 6.187$, $p < 0.02$). Five of six stillborn or miscarried offspring were male, suggesting that the primary sex ratio might be even more male biased than at birth. Although no factor significantly influenced sex ratio in a univariate analysis, the GLMM model revealed that maternal rank interacted significantly with age and with dry-season rainfall (table 3). The sex ratio of high-ranking mothers became male biased as they grew older, whereas the sex ratio of subordinate mothers was male biased when they were young (figure 7*a*). The sex ratio of high-ranking mothers was unaffected by dry-season rainfall, but low-ranking mothers shifted their sex ratio from female biased during harsh years to male biased during mild years (figure 7*b*).

4. DISCUSSION

None of these data are easy to interpret. The population sex ratio is significantly male biased, but sons and daughters do not differ in infant mortality nor in their impact on the survival of younger siblings or on their mother's subsequent reproductive rate. If we assume a population-wide effect of LRC from additional females in each troop (figure 2), each female adds only 10.4 days to an average interbirth interval of 670 days; this is far too small to account for the 22% excess of males.

Contrary to the assumptions of Van Schaik & Hrdy's (1991) meta-analysis, the relative costs of raising sons and daughters did not vary with changes in LRC as measured by troop growth rates or by troop size. The relative costs of daughters and sons did change with maternal age, but the relationship between age and sex ratio was complex. Young mothers take longer to rear daughters than to rear sons, whereas older mothers take longer to rear sons (figure 6*a*), predicting that mothers should have sons when they are young and daughters when they are old. Although young subordinate females did have more sons, their sex ratios became unbiased as they grew older, whereas dominant mothers had increasingly male-biased sex ratios as they aged (figure 7*a*). It is therefore unclear whether these sex ratio variations are in any way adaptive.

Daughters are costlier to low-ranking females (figure 6*b*), but subordinate females produce excess daughters after the harshest dry seasons (figure 7*b*). The interaction between rainfall and rank is analogous to the results of Kruuk *et al.* (1999), in which red deer (of all ranks) showed female-biased sex ratios after harsh winters, possibly owing to higher foetal mortality in males. However, miscarriages are more common in high-ranking Gombe females than in subordinates (Packer *et al.* 1995), and low-ranking females show male-biased sex ratios after mild dry seasons (which would require the selective abortion of daughters when conditions were exceptionally good). Regardless of the mechanism, rainfall patterns are highly erratic at Gombe, with a lag_1 (i.e. one year lag) correlation of only 0.097 ($n = 27$ years). A harsh dry season should therefore be viewed as a stressor rather than a predictor of future conditions, and the variation in figure 7*b* is unlikely to be adaptive.

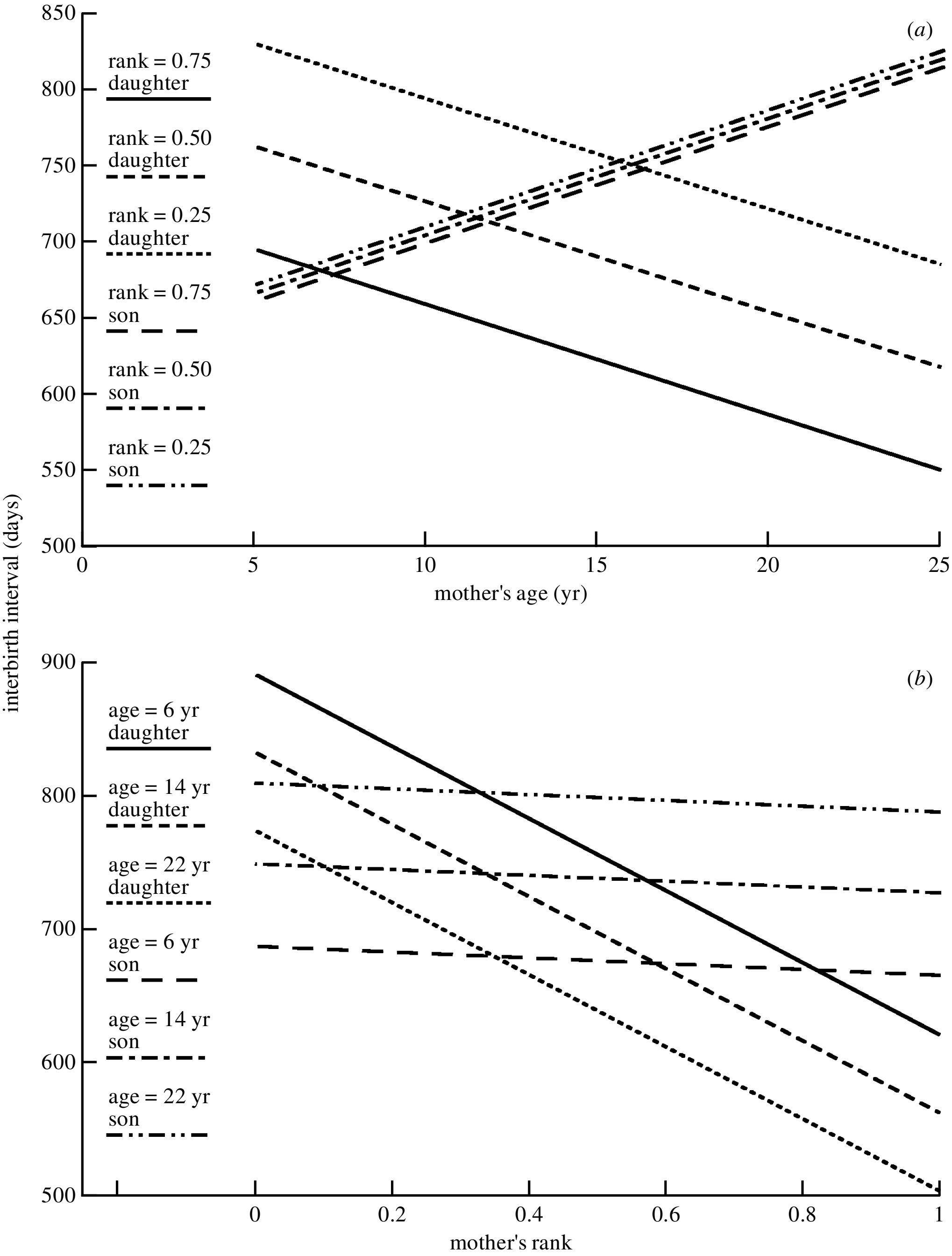

Figure 6. Significant interactions on interbirth intervals that include offspring sex. (*a*) With increasing maternal age, interbirth intervals become shorter after the birth of a daughter but longer after the birth of a son. (*b*) After the birth of a daughter, high-ranking mothers have shorter interbirth intervals than subordinates, but there is no effect of rank after the birth of a son.

It is hard to reconcile our data with the clear advantages of sex ratio variation reported for birds (Komdeur *et al.* 1997; Sheldon *et al.* 1999) and red deer (Kruuk *et al.* 1999). One possibility is that the Gombe baboons gain important advantages from factors that we have overlooked in our analysis. Perhaps young subordinates and older dominants gain unsuspected benefits from sons; or perhaps the results in figure 7 are misleading and the Gombe baboons are unable to alter their sex ratios adaptively. It is possible that these females gain fewer advantages from altering their sex ratios than other populations. Although the interbirth intervals in figure 6 would translate into an advantage of 10–25% to any female who could control her sex ratio, there is no strong effect of maternal rank on offspring fitness in this population (see, for example, figure 4). In contrast, high rank confers strong fitness effects on adult sons in red deer (Clutton-Brock *et al.* 1986); and high-ranking Amboseli baboons might impart high fitness to their adult daughters as well as gain a higher productivity from a female-biased sex ratio (Altmann *et al.* 1988).

In contrast, Gombe might have undergone such profound ecological perturbations that the baboons are not yet adapted to current circumstances. Gombe became

Table 3. *Minimal GLMM model for effects on offspring sex*

parameter	estimate	s.e.m.	z	p
intercept	0.1412	0.6778	0.208	0.8349
maternal age	−0.0912	0.0475	−1.919	0.0550
maternal rank	−0.5276	1.1681	−0.452	0.6515
rainfall	0.0578	0.0197	2.931	0.0034
age × rank	0.1787	0.0766	2.334	0.0196
rank × rainfall	−0.0736	0.0331	−2.222	0.0263

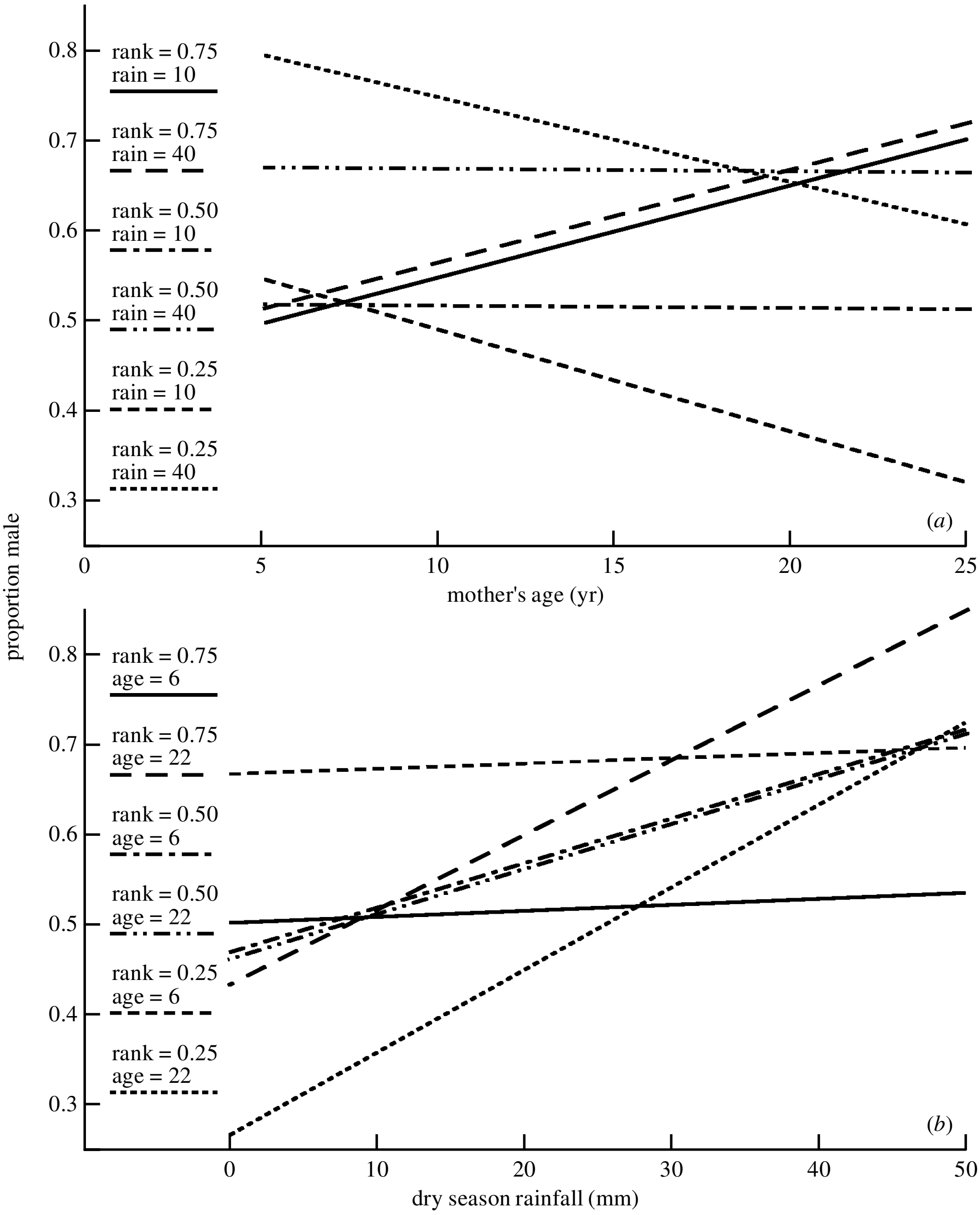

Figure 7. Interactions between maternal rank, maternal age and dry-season rainfall on offspring sex. (*a*) Daughters have more daughters when they are younger, whereas dominant females have more sons as they grow older. (*b*) Subordinate females are more likely to have sons after a mild dry season and are more likely to have daughters after a harsh dry season.

a reserve in 1943 when the human inhabitants were relocated (Kjekshus 1977), and the amount of vegetation has increased continuously in the absence of cultivation and fire. Consequently the 90 individuals in the original study increased to 260 animals between 1967 and 1996. The male-biased population sex ratio might reflect an ancestral adaptation to a harsher environment (with a concomitantly higher mortality of male foetuses), which would have resulted in a 50:50 sex ratio at birth. Under current conditions, the relative costs to high- and low-ranking females of producing sons and daughters might have been abnormal. However, most of the data in Van Schaik & Hrdy's review came from captivity, in which 'ecological conditions' were totally outside the experience of any species, and the study by Kruuk *et al.* (1999) was conducted in a novel environment.

We can conclude only that primate sex ratios remain problematic, even after a fine-grained and ecologically sensitive analysis. It remains mysterious why some populations modify their sex ratios according to precise evolutionary predictions whereas others do not. A more serious consideration of the significance of 'non-significant' results is overdue.

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