

Maternal rank and local resource competition do not predict birth sex ratios in wild baboons

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We test two models of adaptive adjustment of birth sex ratios that are expected to apply to Cercopithecine primate species. It has been predicted that when maternal investment differentially influences the reproductive success of male and female offspring, females in good condition will bias investment in favour of the sex that gains the greatest fitness returns from additional investment. This hypothesis was subsequently amended to take into account the effects of local resource competition on maternal investment strategies of primate females. This body of theory has been applied to primates with contradictory results, prompting some to question the conclusion that primate females facultatively adjust birth sex ratios in an adaptive manner. Here, we present a meta-analysis of the relationship between maternal rank, birth sex ratios and local resource competition in 36 groups of wild savannah baboons, *Papio cynocephalus*. The results do not support predictions derived from either model of facultative sex ratio adjustment, and we conclude that there is currently no evidence that baboon birth sex ratios are adjusted in an adaptive manner.

Keywords: sex ratio; baboons; local resource competition

1. INTRODUCTION

In 1973, Trivers and Willard predicted that when maternal condition differentially influences the reproductive success of male and female offspring, females in good condition will bias their investment towards the sex that gains the greatest fitness returns from additional investment. For polygynous, sexually dimorphic species in which maternal investment influences offspring condition at weaning, they predicted that females in good condition would bias investment in favour of males. While considerable evidence for adaptive adjustment of sex ratios has accumulated for invertebrates (Godfray & Werren 1996), evidence of adaptive birth sex ratio biases in vertebrates is more highly disputed (Hewison & Gaillard 1999; Palmer 2000; Cockburn *et al.* 2002; Komdeur & Pen 2002; Krackow 2002; West & Sheldon 2002; Cameron 2004; Sheldon & West 2004). Primates provide a particularly inconsistent body of data on sex ratio adjustment (Brown & Silk 2002; Silk & Brown 2004).

Trivers & Willard's (1973) hypothesis was first applied to data on non-human primates (hereafter primates) in the 1980s. The earliest reports indicated that high-ranking female baboons and macaques, who were presumably in good physical condition, produced relatively more daughters than low-ranking females (*Papio cynocephalus*: Altmann 1980; *Macaca radiata*: Silk *et al.* 1981; *Macaca mulatta*: Simpson & Simpson 1982). These species have pronounced sexual dimorphism and polygynandrous mating systems, so the observed patterns did not fit Trivers and Willard's predictions. However, there is reason to hypothesize that high-ranking female baboons and macaques might benefit more from investment in daughters than sons (Silk *et al.* 1981). In these species, females form stable matrilineal

dominance hierarchies and high-ranking females generally reproduce more successfully than low-ranking females (reviewed by Harcourt 1987; Silk 1993). Additionally, social rank is inherited from the mother and female offspring remain in the natal group, while sons do not acquire maternal rank and emigrate when they reach sexual maturity (reviewed by Melnick & Pearl 1987). Thus, high-ranking females may gain higher returns from investment in daughters, who will share their rank and reproductive success, than from their sons whose reproductive prospects are less certain. In contrast, low-ranking females, whose daughters inherit their own low rank and poor reproductive prospects, may gain higher returns from investment in sons than daughters.

This logic was confounded by subsequent reports that demonstrated the opposite trend (e.g. *M. mulatta*: Meikle *et al.* 1984), or found no consistent relationship between maternal rank and birth sex ratio (e.g. *M. mulatta*: Rawlins & Kessler 1986). The inconsistency among these datasets caused some researchers to suggest that the observed patterns could represent stochastic variation in small samples (Rawlins & Kessler 1986; Altmann *et al.* 1988; Rhine 1994), while others have continued to defend adaptive explanations (e.g. Paul & Kuester 1990; Dittus 1998; Schino 2004).

A recent meta-analysis of the primate birth sex ratio literature supports the conclusion that variation in birth sex ratios is the product of stochastic variation in small samples (Brown & Silk 2002; Silk & Brown 2004). The magnitude of the difference between the birth sex ratios of high- and low-ranking females is greatest in studies with the smallest samples and converges to zero as sample sizes become larger. The same pattern was replicated by Schino (2004) using a slightly different set of studies.

However, these meta-analyses do not account for the possibility that the relationship between maternal rank and

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birth sex ratios may vary over time or across sites. This possibility was considered by van Schaik & Hrdy (1991), who suggested that the strategy adopted by a high- or low-ranking female may depend on local environmental conditions. They hypothesized that when local resource competition is intense, high-ranking females may gain greater benefits from having daughters, who support them in conflicts and help them to maintain their status and consequent access to resources, than from having sons. In contrast, low-ranking females may have difficulty protecting their daughters from harassment from unrelated females when local resource competition is strong, and may benefit more from investing in sons that eventually emigrate. Thus, van Schaik and Hrdy predicted that high-ranking females would produce a smaller proportion of sons than lower ranking females when local resource competition is intense, with the opposite pattern occurring when local resource competition is relaxed.

To test their hypothesis, van Schaik & Hrdy (1991) collated 11 datasets on maternal rank and birth sex ratio in primates. They relied on an indirect measure of the intensity of local resource competition—the annual population growth rate—because direct estimates of the intensity of local competition for resources were unavailable. Van Schaik and Hrdy reasoned that competition for resources would constrain population growth, so high population growth rates indicate low competition for local resources and vice versa. As they predicted, the difference between the proportion of sons born to high- and low-ranking mothers was positively related to population growth rates (van Schaik & Hrdy 1991).

Although van Schaik and Hrdy's analysis explained much of the observed variation in the relationship between maternal rank and birth sex ratios, a number of criticisms of their analysis have been raised. First, 8 of the 11 studies included in the analysis were based on rapidly growing captive or semi-free-ranging populations. The ecological conditions that females in these groups experienced were probably outside of the normal range of experience for these species (Rhine *et al.* 1992; Packer *et al.* 2000). Among the three wild populations in their sample, no clear pattern was evident. Second, van Schaik and Hrdy's statistical analyses did not take the sample size of each study into account (Silk & Brown 2004). This is problematic because stochastic processes are expected to generate more variation in small samples (Palmer 2000). Third, some data published after van Schaik and Hrdy's original paper was published do not fit their predictions (*Macaca fascicularis*: van Noordwijk & van Schaik 1999; *Lemur catta*: Nunn & Pereira 2000; *P. cynocephalus*: Packer *et al.* 2000; see Silk & Brown 2004).

Some of these shortcomings have been addressed in a recent meta-analysis. Schino (2004) compiled a sample of 19 datasets, including seven unprovisioned wild groups, and employed statistical methods that take into account the size of each sample. Schino reports that the difference in the proportion of males produced by high- and low-ranking females is significantly positively related to population growth rate, thereby replicating van Schaik and Hrdy's results. However, removal of a single data point from Schino's analysis eliminates the relationship between effect size and population growth rate (Schino 2004). The crucial data point comes from one wild group

of baboons in Amboseli (Altmann *et al.* 1988). Although there is no reason to question the validity of these data, there is reason to be cautious about a result that rests on just one data point.

Here we draw on data from 36 baboon groups (*P. cynocephalus*) at 11 sites across Africa to construct a more comprehensive analysis of the relationship between maternal rank, birth sex ratios and local resource competition in wild primate populations. We focus on baboons for three reasons. First, van Schaik and Hrdy's model is expected to apply to species, like baboons, that have matrilineal dominance hierarchies, female philopatry, sexual dimorphism, and are affected by local resource competition. Second, baboons have been studied for many years at a number of sites in the wild generating an extensive demographic database. Third, by focusing on a single taxon we avoid phylogenetic biases.

2. METHODS

In order to test the relationship between population growth rate, maternal rank and birth sex ratios and to weigh the effects of sample size on sex ratio skews, the following data were required for individual study groups:

- (i) number of male and female infants produced by high-ranking females;
- (ii) number of male and female infants produced by low-ranking females;
- (iii) the size of the study group at the beginning of the period in which births were monitored; and
- (iv) the size of the study group at the end of the period in which births were monitored.

We reviewed the primate literature for the necessary data on wild baboon groups. Very few published studies provided all of the necessary information. Therefore, we solicited unpublished data directly from researchers directing all of the ongoing long-term baboon field studies. The response to our requests was uniformly positive, and researchers from all sites who had access to the data that we needed agreed to contribute to the project. The final dataset included information on savannah baboons from 11 study sites in Ethiopia, Kenya, Tanzania, Botswana and South Africa. Data analysis was carried out on 1909 births that occurred in 36 social groups of baboons during a total of approximately 328 group years (table 1).

For most sites, we were able to divide females into two rank categories: high-ranking and low-ranking. At Gilgil/Chlolo, females were divided into three rank categories (high, medium and low). In this case, following Brown & Silk (2002) and Schino (2004), we omitted data from the middle rank category in our analysis.

The effect size for each study group was calculated as the difference between the proportion of sons and daughters born to high- and low-ranking mothers:

$$\text{effect size} = \left(\frac{\text{HR}_M}{\text{HR}_M + \text{HR}_F} \right) - \left(\frac{\text{LR}_M}{\text{LR}_M + \text{LR}_F} \right),$$

where HR_M is the number of sons born to high-ranking mothers, HR_F , number of daughters born to high-ranking mothers, LR_M , number of sons born to low-ranking mothers, and LR_F , number of daughters born to low-ranking mothers.

Table 1. Summary of data included in the meta-analysis.

study site	number of groups	group years ^a	number of births ^b	growth rate (%) ^c	effect size ^d	source of data
Amboseli, Kenya	8	3.3–13.9(66.6)	13–151(532)	2.4–10.6	–0.25–0.31	J. Altmann & S. Alberts ^e
Awash, Ethiopia	2	1.1–3.3(4.4)	10–39(49)	5.3–10.6	0.17–0.67	J. Beehner & T. Bergman ^e , Nystrom 1992 ^e
De Hoop, South Africa	1	6.4	36	–5.5	–0.18	L. Barrett & S.P. Henzi ^e
Gilgil/Chlolo ^f , Kenya	3	4.0–29.5(51.8)	68–145(283)	–3.1–4.1	–0.13–0.20	S. Strum ^e , Smuts & Nicolson 1989 ^e
Gombe, Tanzania	15	1.2–31.2(156.6)	10–101(605)	–5.7–9.8	–0.25–0.45	C. Packer ^e
Mikumi, Tanzania	4	3.8–6.8(23.8)	17–67(214)	–1.7–7.7	–0.12–0.23	G. Norton & S. Wasser ^e , Rhine ^e <i>et al.</i> 1992
Moremi, Botswana	1	10.3	133	2.4	–0.06	D. Cheney & R. Seyfarth ^e
Mzuki, South Africa	1	3.8	26	15.6	–0.29	S.P. Henzi ^e , Ron 1996
Tana River, Kenya	1	4.0	31	–1.3	–0.17	V. Bentley-Condit ^e

^a For sites with multiple study groups, the range and total number of study years are given.

^b For sites with multiple study groups, the range and total number of births are given.

^c For sites with multiple study groups, the range of growth rates is given; see text for formula for computing population growth rate.

^d For sites with multiple study groups, the range of effect sizes is given; see text for formula for computing effect size.

^e Indicates source of unpublished data.

^f Two study groups were transported intact from Gilgil to Chlolo during the study period.

Following Schino (2004), annual population growth rate (G) was calculated as:

$$P_2 = P_1 \times (1 + G)^N$$

where P_1 and P_2 represent the population size at the beginning and end of the period in which births were monitored and N represents the period of time between the beginning and end of the period in which births were monitored.

The analyses presented here were conducted using the METAWIN software (Rosenberg *et al.* 2000). A random effects model (i.e. one in which effect size is expected to differ between datasets) was used, as such models are generally considered more appropriate for analyses of ecological data (Gurevitch & Hedges 1999). The effect size we defined above is equivalent to the rate difference. We used METAWIN to compute the variance in the effect size. Population growth rate was used as the continuous variable. Weighted mean effects sizes and bias-corrected 95% confidence intervals were calculated. A funnel plot was used to illustrate the relationship between sample size and effect size (Light & Pillemer 1984).

In order to determine whether the results were influenced by patterns at particular study sites, we repeated the analyses with different subsets of the data (i.e. without data from Gombe, Amboseli, Mikumi or Gilgil/Chlolo). To deal with concerns about the appropriate time-period for evaluating responses to population growth rates, we compared the results based on groups observed for less than 5 years with results based on groups observed for more than 20 years. We also repeated the analysis without the two groups from the Awash, which were composed of both *P. c. anubis* and *P. c. hamadryas*. None of the analyses based on subsets of the original sample generated results that differed substantially from results based on the full sample. Below we present results based on the full sample of 36 study groups.

3. RESULTS

The Trivers and Willard hypothesis predicts that effect sizes will differ significantly from zero. The most extreme positive and negative values of effect size were from the groups with the smallest numbers of births (Spearman $\rho = -0.443$, $p = 0.004$, $n = 36$), and effect size converged towards zero in large samples (figure 1). The weighted mean effect size was not significantly different than zero (weighted mean = 0.0354, 95% CI = –0.0364 to 0.1072, $n = 36$; table 1). These results indicate that there was no consistent difference between the birth sex ratios of high- and low-ranking females.

The van Schaik and Hrdy hypothesis predicts that effect sizes will be positively related to rates of population growth. As population growth rates rise, effect sizes are expected to increase as high-ranking females produce relatively more males than low-ranking females. There was considerable variation in the rates of annual population growth across groups, but this variation was not consistently related to effect size (figure 2). Neither the slope of the regression ($b = -0.2163$; s.e. = 0.8088, $p = 0.7892$) nor the intercept ($a = 0.0438$, s.e. = 0.0472, $p = 0.3535$) was significantly different from zero. Thus, differences between the birth sex ratios of high- and low-ranking females are not consistently linked to population growth rates.

4. DISCUSSION

These analyses indicate that wild female baboons do not adjust birth sex ratios in relation to their own condition in a uniform way, as Trivers & Willard (1973) originally proposed. These results are consistent with two previous analyses of birth sex ratios in primates that found that the magnitude of the difference in birth sex ratios of high- and low-ranking female primates declines as sample size increases, and that the weighted mean difference in birth sex ratios of high- and low-ranking females is zero (Brown

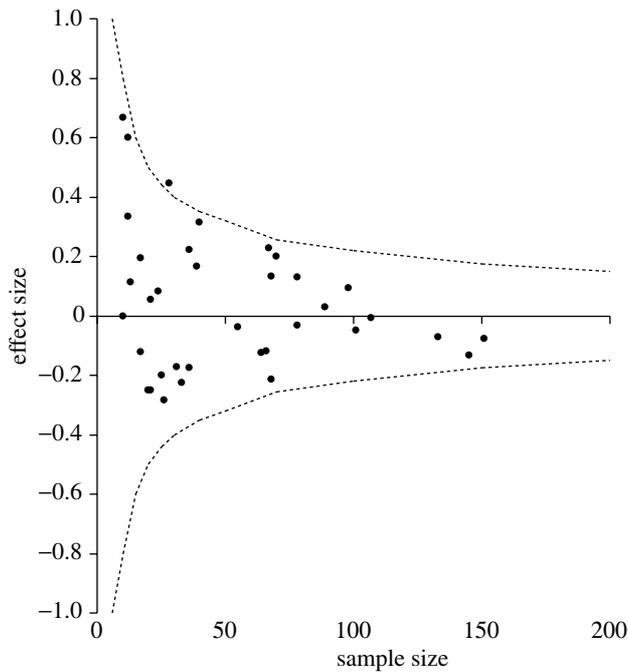


Figure 1. The relationship between sample size and effect size. As sample size increases, effect sizes decline. Each point represents a single study group. Effect size is defined as the difference between the proportion of male offspring produced by high- and low-ranking females. The sample size is the number of births in the study group.

& Silk 2002; Schino 2004). In addition, our results indicate that local resource competition, as measured by population growth rate, does not modulate the relationship between maternal rank and birth sex ratios in wild baboon groups. Thus, our results do not support predictions derived from van Schaik & Hrdy's (1991) model of sex ratio adjustment. Taken together, the results suggest that baboons do not facultatively adjust birth sex ratios in an adaptive manner. This conclusion rests on certain assumptions that need to be more critically considered. We turn to these issues below.

First, population growth rate may not provide an accurate indicator of the extent of local resource competition. The measure that we used to estimate population growth is very similar to measures used in previous analyses, but these measures might not accurately reflect the demographic or ecological cues that influence females' investment patterns. However, direct measures of the extent of local resource competition are not available from these study sites. Moreover, we do not know what cues females might use as proxies to assess the extent of local resource competition and adjust investment in male and female offspring.

Second, our analysis is based on a single measure of the population growth rate for each study group. The same problem applies to previous analyses conducted by van Schaik & Hrdy (1991) and Schino (2004). These estimates may not provide sufficiently detailed information about the selection pressures acting on mothers at specific time-points. In other words, the time-scale of our analysis may be different from the time-scale that affects females' investment decisions. In our dataset, the duration of observations ranged from 1.2 to 31.2 years. Although the exclusion of the shortest and

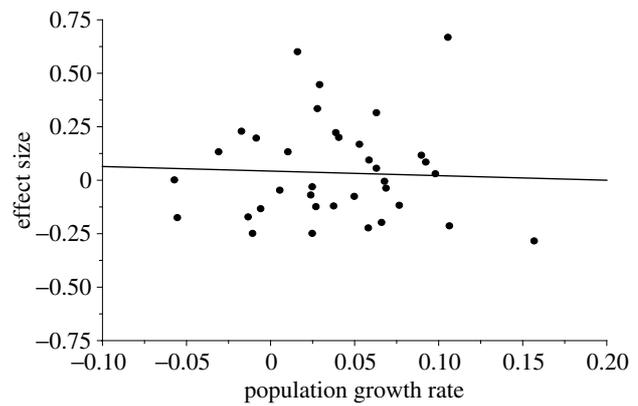


Figure 2. The relationship between population growth rate and effect size. Each point on the graph represents a single study group. Effect size is defined as the difference between the proportion of male offspring produced by high- and low-ranking females. The formula for computing population growth is given in the text.

longest studies had no substantive impact on the results, we cannot exclude the possibility that our measures of population growth are not based on the relevant time-scale.

Third, maternal rank may not be a good indicator of female physical condition. While higher ranking females typically obtain priority of access to resources (Barton 1993), there is relatively limited evidence that social rank influences physical condition in free-ranging baboons. Nonetheless, in some wild populations, dominance rank is associated with the growth rate of offspring and age of maturation (Altmann & Alberts 2003; Johnson 2003) and with components of reproductive success in females (Smuts & Nicolson 1989; Barton & Whiten 1993; Packer *et al.* 1995; Altmann & Alberts 2003 but see also Cheney *et al.* 2004). Thus, in species like baboons, maternal rank may provide a meaningful measure of a mother's ability to influence the reproductive prospects of her offspring.

Fourth, our data come from studies of a single species and we cannot assume that our results apply to other species. Nine of the 11 studies in van Schaik and Hrdy's original analysis were derived from studies of macaques, raising the possibility that their model applies to macaques, but not baboons. However, this possibility is not supported by Schino's analysis. While 12 out of the 19 studies included in the meta-analysis were based on macaques, the significant relationship that he reports between population growth rates, maternal rank and birth sex ratios rests on the Amboseli baboon sample. When this data point is removed, no consistent pattern emerges.

The meta-analyses presented here provide little support for the prediction that female baboons facultatively adjust the sex ratio of their progeny in relation to their own rank or local environmental conditions. We cannot exclude the possibility that observed variation in birth sex ratios of high- and low-ranking female baboons is the product of stochastic biases that arise in small samples. We hope that our work will encourage others to continue conducting similar comparative analyses on a range of taxa and to consider critically the sources of variation in birth sex ratios in vertebrate species.

These analyses rest on the dedicated efforts of scores of researchers who spent countless hours in the field collecting these data. We acknowledge all those who carried out the fieldwork this paper is based on and are especially grateful to those who provided us with unpublished information: Jeanne Altmann, Susan Alberts, Louise Barrett, Jacinta Beehner, Thore Bergman, Dorothy Cheney, Peter Henzi, Craig Packer, Vicki Bentley-Condit, Guy Norton, Pia Nystrom, Robert Sapolsky, Robert Seyfarth, Barbara Smuts, Shirley Strum and Samuel Wasser. We are also grateful to Sarah Blaffer Hrdy and Carel van Schaik for their support for this project and their open-mindedness about the endeavour.

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