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Reconsidering the null hypothesis: Is maternal rank associated with birth sex ratios in primate groups?

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Trivers and Willard hypothesized that vertebrates adaptively vary the sex ratio of their offspring in response to the mother's physical condition [Trivers, R. L. & Willard, D. (1973) *Science* 179, 90–92]. This hypothesis has produced considerable debate within evolutionary biology. Here we use meta-analysis techniques to evaluate claims that nonhuman primate females facultatively adjust the sex ratio of their progeny in relation to their own dominance rank in a uniform way. The magnitude of the difference in birth sex ratios of high- and low-ranking females declines as sample sizes increase, and the mean difference in birth sex ratios of high- and low-ranking females is zero. These results suggest that the observed effects could be the product of stochastic variation in small samples. These findings indicate that presently we cannot reject the null hypothesis that maternal dominance rank is unrelated to birth sex ratios.

Trivers and Willard (1) hypothesized that natural selection might favor the ability to adjust progeny sex ratio in relation to the parents' ability to invest in their offspring. Adaptive variation in sex ratios according to parental condition was subsequently reported for birds (2, 3), primates (4), ungulates (5), and other mammals (6). The status of adaptive explanations of sex-ratio biases in each taxa has been debated (3, 5, 7), and the topic remains highly controversial. In principle this controversy could be resolved, because Trivers and Willard's model seems to generate a straightforward prediction about the relationship between maternal quality and offspring sex. That is, all mothers in good condition are expected to bias their birth sex ratio in favor of sons, whereas all mothers in poor condition are expected to bias their birth sex ratio in favor of daughters. In practice, studies of sex ratios, particularly in birds and mammals, are problematic because they generally are based on small sample sizes. Stochastic variation in small samples is likely to generate considerable apparent variation and complicate efforts to assess adaptive hypotheses. Here we present a meta-analysis of the relationship between maternal condition and offspring sex ratios in primate groups that is designed to test Trivers and Willard's prediction that maternal condition will have a uniform effect on birth sex ratios. This analysis, which takes into account both the magnitude of sex ratio biases and sample size, suggests that we cannot presently reject the null hypothesis that offspring sex is unrelated to maternal rank.

Trivers and Willard's model was based on three assumptions: (i) maternal condition during the period of parental investment would be correlated with offspring condition at the end of this period, (ii) differences in the condition of offspring at the end of the period of parental investment would be maintained into adulthood, and (iii) physical condition would have a greater impact on the reproductive success of one sex than the other sex. For polygynous, sexually dimorphic species, maternal investment was assumed to influence male reproductive success more than female reproductive success, because the reproductive success of males usually is more variable than that of females (8). Thus, Trivers and Willard predicted that natural selection would favor genes that facultatively adjust progeny sex ratio in relation to maternal condition, and they predicted that in polygynous

species, "parents in better condition would be expected to show a bias toward male offspring" (1).

Trivers and Willard assumed that the process that they outlined usually would lead females in good physical condition to skew their birth sex ratio toward males and females in poor condition to skew their birth sex ratio toward females. However, formal models of the relationship between maternal quality and offspring sex ratios produce slightly different conclusions. Leimar (9) considered a situation in which maternal quality is relatively constant over time and is transmitted from mother to offspring with some fidelity. He showed that when maternal condition has a strong effect on offspring quality, it may be more profitable for mothers in good condition to bias investment toward daughters than sons, even if their sons' reproductive success is higher than their daughters' reproductive success. This conclusion was reached because the fitness of sons' offspring depends on the condition of the females that they mate with, whereas the fitness of daughters' offspring depends on their own quality. He noted that "even if it were generally the case in polygynous mammals that a high quality mother could produce a very successful son if she invested in this option, but could only produce a moderately successful daughter, the daughter might still be the better choice" (9). Like Trivers and Willard, Leimar predicts that there will be a uniform relationship between maternal condition or rank and offspring sex.

In some species, a number of the assumptions underlying Trivers and Willard's model have been shown to hold. For example, in red deer (*Cervus elaphus*), adult male body weight is affected by early growth rate, and both birth weight and maternal dominance rank are important components of male, but not female, reproductive success (10–12). According to Trivers and Willard's model, high-ranking female red deer are expected to skew birth sex ratios toward males, whereas low-ranking females are expected to bias birth sex ratios toward females (11). Red deer show the expected biases in birth sex ratios (10, 11). Leimar's prediction that high-ranking females may do better by biasing investment toward daughters may not apply to red deer, because the observed correlations between mother's rank and daughter's rank in red deer are relatively low (9).

Trivers and Willard's model was invoked first by primatologists to explain the empirical observation that high-ranking females produced relatively more daughters than low-ranking females in three different populations of Old World monkeys (13–15). This pattern was thought to be related to the fact that females in these species are philopatric and establish linear, matrilineal dominance hierarchies. Female macaques and baboons acquire their mother's rank, dominance relationships remain stable over long periods of time, and dominance rank is correlated positively with reproductive success (16), which means that high-ranking and reproductively successful females are likely to have high-ranking and reproductively successful daughters, and low-ranking females are likely to produce daughters who become low-ranking and reproduce less successfully. Maternal rank was suggested to have a less consistent effect on

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the fitness of males who disperse from their natal groups and compete for high-ranking positions with males from many different natal groups. Thus, it was hypothesized that high-ranking females might benefit from skewing their birth sex ratio toward daughters, whereas low-ranking females might benefit from skewing their birth sex ratio toward sons. This interpretation is consistent with the results of Leimar's model. He pointed out that the long-term stability of female dominance hierarchies in macaque and baboon groups provided the necessary conditions for high-ranking females to bias investment toward daughters (9).

These reports of biased sex ratios soon were followed by others that showed quite different patterns. Meikle *et al.* demonstrated that high-ranking rhesus macaque females produced more sons than did low-ranking females (17). They explained these findings in terms of Trivers and Willard's original formulation for sexually dimorphic species with the assumption that low-ranking mothers were in poor physical condition. However, as more studies were published, the pattern of results became increasingly variable (4). Although some researchers suggested that the observed patterns might be the product of stochastic variation that arises by chance in small samples (e.g., refs. 18–20), others have continued to support functional explanations (e.g., refs. 21 and 22).

Methods

The variability in the relationship between maternal rank and birth sex ratios in primate groups suggests that it is time to reconsider the null hypothesis that there is no consistent relationship between maternal rank and infant sex. We conducted a meta-analysis of published studies of the relationship between maternal rank and offspring sex by using funnel-graph methods outlined by Palmer (23, 24). Funnel graphs are scatterplots in which effect size is plotted against sample size. The magnitude and frequency of deviations in sex ratio are expected to vary inversely with sample size; effect sizes in small samples will be quite variable, but as sample sizes increase, effect sizes will converge toward a specific value. If strictly random processes are operating, then as sample sizes increase, effect sizes will converge toward zero. Gaps or holes in the funnel can reveal publication biases if investigators tend to avoid publishing non-significant results or results that contravene conventional predictions.

We compiled information from all available studies that reported the number or proportion of male and female infants produced by high- and low-ranking females, and the total number of births was recorded. Our search of the literature produced 35 data sets on 15 species from 23 populations that provided these data (13–15, 17–22, 25–50). The 15 species include 8 genera (*Ateles*, *Cebus*, *Cercopithecus*, *Lemur*, *Macaca*, *Mandrillus*, *Pan*, and *Papio*), but most of the studies were conducted on species in the genus *Macaca* ($n = 24$) and *Papio* ($n = 5$). In some cases, the same group or population was the subject of multiple publications. In the meta-analyses, we included all nonidentical replications based on different samples and enhanced data sets from a single study site.

For each study, the effect size was calculated as the difference between the proportion of males produced by high- and low-ranking females. A standard procedure was used for weighting the samples (ref. 51; see *Appendix*). Weighted average sex ratios are presented for all studies together for studies of macaques only and for studies of wild and captive/semi-free-ranging populations separately. The results also were recalculated with studies with the largest sample sizes removed (i.e., those over 1,000); because removal of these data points did not alter any of the results significantly, they are included in the analyses.

Not all researchers categorized females into rank categories in the same way. In the majority of cases, investigators divided

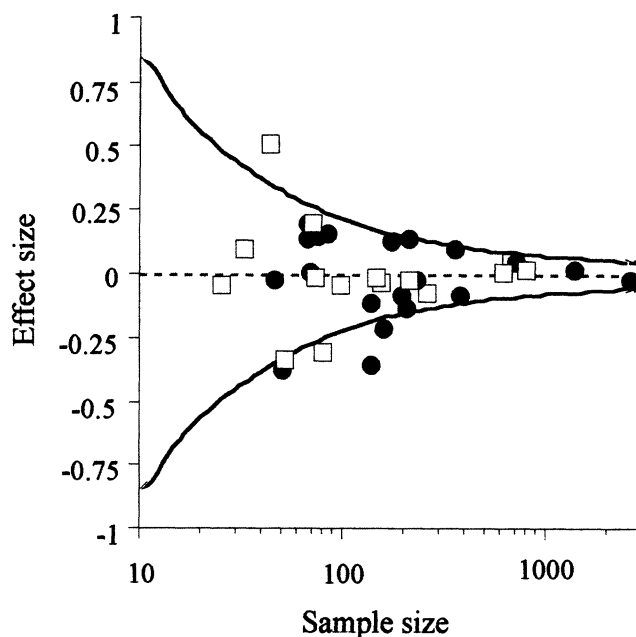


Fig. 1. Effect size is plotted against sample size. The effect size is the difference between the proportion of male infants produced by high- and low-ranking females. The sample size is the total number of infants produced by high- and low-ranking females. Open squares denote studies of wild populations; closed circles denote studies of captive or semi-free-ranging populations. The dotted line indicates an effect size of zero; curved lines are binomial significance levels ($P = 0.05$, two-tailed) from table Q in ref. 52 (23).

females into high- and low-ranking categories and provided aggregate progeny sex-ratio values for the two rank classes. However, in some cases, investigators divided females into three rank categories (high, middle, and low; refs. 21, 27, 32, 39, and 46); in these situations, we excluded mid-ranking females from the analyses. Some investigators compared top-ranking females with all others (15, 34, 36); here, we categorized the top-ranking females as high-ranking and all other females as low-ranking. In other cases, investigators presented sex-ratio information by matriline (17, 19, 50); in these cases, we categorized the top half of the matriline as high-ranking and the bottom half of the matriline as low-ranking. If the number of lineages was odd, we dropped the mid-ranked lineage from the analysis, and if only one lineage was in a group, we excluded the data for that group. In a few cases, necessary values were not included in published reports; we obtained the missing information from the authors.

Results

We plotted the sample size (total number of births) against the effect size (difference in the proportion of males produced by high- and low-ranking females) to assess the shape of the distribution (Fig. 1). Effect sizes vary considerably when samples are small but converge toward zero in larger samples. The weighted mean effect size for all populations is -0.0008 (*Macaca* only = -0.0083). To obtain sufficient power to reliably detect an effect size even 10 times as large as this one, the sample size would need to be at least 1,500 (53). The weighted mean effect size for wild populations is 0.0139 ($n = 15$), and the weighted mean for captive and semi-free-ranging populations is -0.0086 ($n = 20$), which means that, on average, there is no difference in the proportion of males produced by high- and low-ranking females. The absolute value of the effect size is correlated negatively with sample size ($r = -0.397$, $P = 0.018$, $n = 35$; *Macaca* only: $r = -0.491$, $P = 0.015$, $n = 24$). Together, these

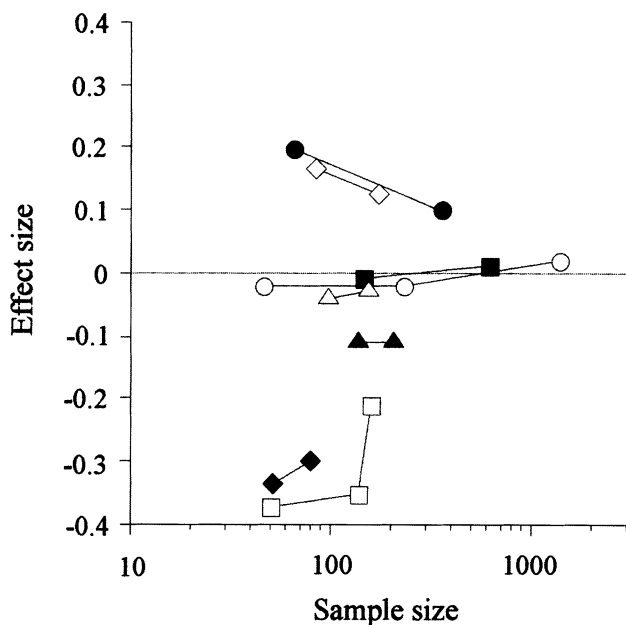


Fig. 2. Effect size is plotted against sample size for sites from which more than one study has been published. Symbols indicate studies from the same sites as follows. \blacklozenge , Amboseli, Kenya (13, 18); \blacktriangle , Davis, CA (14, 43); \square , Madingley, U.K. (15, 31, 36); \bullet , Salem, Germany (21, 39); \circ , Cayo Santiago, Puerto Rico (19, 26, 27); \triangle , Ketambe, Indonesia (47, 48); \diamond , Rome, Italy (25, 41); \blacksquare , Arashiyama, Japan (32, 46). For other definitions, see the legend for Fig. 1.

findings suggest that the variation in effect sizes at low samples is the result of stochastic variation.

At several sites, researchers have published multiple reports of the relationship between maternal rank and birth sex ratios by using successively larger samples. These studies do not represent true replications, because later studies include data from earlier studies. However, these reports are useful, because they allow us to evaluate the relationship between sample sizes and effect sizes within populations. Fig. 2 indicates that, at most of these sites, the effect sizes of larger sample sizes are closer to zero than for small samples.

Fig. 1 shows no conspicuous holes, suggesting that researchers have been equally likely to publish results with positive and negative effects. To determine whether investigators also were equally likely to publish significant and nonsignificant results, we computed χ^2 values for all the populations from which we could extract the number of male and female offspring produced by high- and low-ranking females. When multiple studies of the same population were available, we calculated χ^2 values for only the first study published. Only 3 of the 23 studies (13%) showed significant interactions between maternal rank and offspring sex, which is not significantly higher than chance ($\chi^2 = 3.13$, $df = 1$, not significant).

Discussion

Our analyses indicate that the data are distributed much as we would expect by chance and that maternal rank is not associated consistently with biased birth sex ratios in this data set on nonhuman primates. The weighted mean effect size is zero, consistent with the null hypothesis that maternal rank is not related to birth sex ratio in a uniform manner. If there had been a stable relationship between maternal rank and birth sex ratio, the mean effect size would have a specific, nonzero value and would have been observed across all sample sizes. The significant negative relationship between absolute effect size and sample size and the weighted mean effect size of zero suggest that the

pattern of results could have been produced by chance. These results mean that we can rule out the hypothesis that there is a simple and uniform effect of dominance rank on birth sex ratios that holds across the sampled primate populations.

Although some researchers have been concerned about the possibility that significant sex ratio skews are more likely to be published than nonsignificant distributions (54), this does not appear to be the case with the primate sex ratio literature. Researchers seem to have been willing and able to publish nonsignificant results. Additionally, investigators have seemed equally likely to publish results that indicated that high-ranking females produced a higher fraction of sons than lower-ranking females did as they were to publish results that showed the opposite pattern.

The results described above do not necessarily mean that primates do not vary their sex ratios adaptively. Other models of sex ratio adjustment consider the asymmetries in the value of sons and daughters as influenced by helpers in communally breeding species (55, 56), the effects of mate attractiveness on offspring fitness (57, 58), and the degree of local competition for mates (59) or resources (60, 61). Among nonhuman primates, it has been suggested that local resource competition may produce global biases in population sex ratios in favor of the dispersing sex (60, 62), and that there may be an interaction between maternal dominance rank and the extent of local resource competition (43, 61, 63). Our findings do not rule out any of these hypotheses, but they do demonstrate that it is essential to take sample size into account when testing predictions about sex ratio adjustment. Leimar's (9) formal treatment of Trivers and Willard's (1) model also demonstrates that verbal models of sex ratio evolution may not be sufficient to provide meaningful insight about evolutionary processes. It is important also to recognize that consistent, replicable skews in birth sex ratios may not necessarily reflect adaptive strategies.

The failure to reject the null hypothesis does not mean that Trivers and Willard's model is invalid, because primates may not meet the assumptions. For example, maternal condition during lactation may not correlate with offspring condition at weaning, differences in condition at weaning may not be maintained into adulthood, or maternal resources may have equivalent effects on sons and daughters. Attempts to assess the underlying assumptions for primate groups are surprisingly limited, and the results are inconsistent (4).

We evaluated published claims that high- and low-ranking female nonhuman primates facultatively adjust the number of males and females that they produce. It is possible, of course, that females do not manipulate the number of males and females that they produce, but do skew investment in sons and daughters. Females could do this before birth by differentially provisioning male and female fetuses or after birth by allowing infants of one sex to suckle more frequently, shifting weaning times in relation to infant sex, or providing more protection and support to one sex. However, there is little regularity in investment patterns reported in the literature (4). For example, male macaques are larger than females through infancy and later in life (26), but sons do not appear to be suckled more frequently or weaned later than daughters (4). Maternal interbirth intervals, which may provide a measure of the costs of raising offspring, are not consistently related to maternal rank, infant sex, or the interaction between maternal rank and infant sex (4).

One of the most frequent and persistent criticisms of evolutionary theory is that it generates untestable and unfalsifiable predictions. For example, difficulties in assessing the fitness costs and benefits of behavioral acts make it difficult to test predictions derived from kin-selection theory, particularly in long-lived animals such as nonhuman primates. However, the sex ratio models evaluated here generate straightforward predictions about the relationship between maternal rank and birth sex

ratios, and metaanalysis techniques provide a means for constructing rigorous tests of these predictions. In nonhuman primates, the distribution of the data suggests that much of the observed variation in birth sex ratios of high- and low-ranking females, which often has been interpreted in adaptive terms, actually may be the product of stochastic variation in small samples. The null hypothesis that nonhuman primate females do not adjust the sex ratio of their offspring in relation to their own rank remains in play.

Appendix

The variance v_i for study i was calculated as

$$v_i = \frac{p_{i1}(1 - p_{i1})}{n_{i1}} + \frac{p_{i2}(1 - p_{i2})}{n_{i2}}, \quad [1]$$

where p_{i1} is the proportion of sons born to high-ranking mothers, p_{i2} is the proportion of sons born to low-ranking mothers, n_{i1} is the number of offspring born to high-ranking mothers, and n_{i2} is the number of offspring born to low-ranking mothers. The weighting w_i for study i was calculated as

$$w_i = \frac{1}{v_i}. \quad [2]$$

The weighted average effect size \bar{e} was calculated as

$$\bar{e} = \frac{\sum_{i=1}^k w_i e_i}{\sum_{i=1}^k w_i}, \quad [3]$$

where e_i is the effect size for study i and k is the total number of studies. Eqs. 1, 2, and 3 are taken from ref. 51, equations 18-12, 18-2, and 18-1, respectively.

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