

Stochastic variation in sex ratios in infant mortality rates due to small samples in provisioned Japanese macaque (*Macaca fuscata*) populations

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Abstract Sex differences in infant mortality in provisioned Japanese macaque populations were examined using 10 data sets from five populations. The results indicate that there was no available data set in which a sex difference in infant mortality was statistically significant. To examine whether the observed sex ratios in infant mortality rates could be the product of stochastic variation in small samples, a correlation between sample size and the magnitude of sex ratios in infant mortality rates was also examined. Notably, the magnitude of sex ratios in infant mortality rates declined significantly as sample sizes increased. These results suggest that previously reported marked sex ratios in infant mortality could be the product of stochastic variation in small samples.

Keywords Sex differences · Infant mortality · *Macaca fuscata* · Stochastic variation

Introduction

Juvenile mortality often has a sex bias among mammals, including primates (Clutton-Brock et al. 1985; van Schaik and de Visser 1990). Though it has been suggested that the most pronounced sex differences in mortality commonly occur after weaning (Clutton-Brock et al. 1985), various trends in sex differences in mortality even before weaning have been found. Infant mortality is higher than juvenile mortality (Dunbar 1987), so that it is a more effective component of lifetime reproductive success than juvenile

mortality. However, few studies on sex differences in infant mortality have been conducted, and they have yielded inconsistent results. For example, statistically significant male-biased (Itoigawa et al. 1992), female-biased (Fukuda 1988), and non-biased infant mortality (e.g., Koyama et al. 1992) have been reported in provisioned Japanese macaque (*Macaca fuscata*) populations, but various sample sizes and statistical tests were employed.

In this study, I collect data on infant mortality for each sex in provisioned Japanese macaque populations—where infant mortality data have been accumulated most abundantly among nonhuman primates—to test the sex difference in each data set using the same statistical test for all data sets and to examine the effect of sample size on the results.

Stochastic processes create variation in small samples, and it is profitable to look at the association between effect size and sample size (Palmer 2000). Using Palmer's idea, Brown and Silk (2002) analyzed relationships between sample sizes and magnitudes of difference in birth sex ratios of high- and low-ranking females in primate groups. They showed that the magnitudes declined as sample sizes increased, and that the mean difference in birth sex ratios among the ranks was zero. These results suggest that observed biases could be the product of stochastic variation in small samples. I examine the correlation between sample size and the magnitude of sex ratios in infant mortality, in order to confirm whether or not reported marked sex ratios in mortality are the product of stochastic variation.

Methods

My literature search for data on the number of births and deaths within the first year of life produced 10 data sets

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from five populations, Katsuyama (KT), Takasakiyama (TK), Arashiyama (AR), Koshima (KS) and Hakone (HK), in provisioned, free-ranging or semi-free-ranging Japanese macaques. I did not use the number of sex-unknown births and deaths for analyses. In cases where the same population was the subject of multiple publications, I dealt with them separately, provided each study period and/or study troop was different.

At KT, whereas Itoigawa et al. (1992) tested sex differences in infant mortality among the offspring of only primiparous, of only multiparous, and of all females, I pooled the offspring of all females to make KT correspond with other populations.

At TK, three data sets were collected (Table 1). Between 1987 and 1993, I used the data that T. Matsui collected on infants from birth until May of the subsequent year. This data set was unpublished as a mortality rate in each sex, although Kurita et al. (2008) used the mortality data in which the data from both sexes were pooled. Matsui's focal animals were 95.5% of all infants (2,010, excluding sex-unknown infants) born for the 7 years because he excluded infants of females that he could not identify adequately. Although Itani et al. (1964) collected data between 1956 and 1962, I did not use data in 1961, because the number of births of each sex was unknown. Sugiyama et al. (1979) collected data on survival only from marked infants at TK. Kurita et al. (2008) showed that, due to decrease of provisioned foods between 1965 and 1980, infant mortality from Matsui's data was much higher than that from Itani et al. (1964).

From AR, 150 macaques were transferred to semi-free-ranging enclosure in U.S.A. in 1972, the AR West population (Fedigan and Zohar 1997). I dealt with the data for AR West separately from that of the original AR by Koyama et al. (1992).

At KS, the study period between 1952 and 1986 was divided into four periods (Watanabe et al. 1992). Data from periods 1 and 2, before any decrease in the amount of artificially fed foods, were dealt with differently from those of periods 3 and 4 because infant mortality rates in periods 1 (19%) and 2 (19%) were much lower than those in periods 3 (43%) and 4 (45%).

For HK, I found data on Troops T and P from the Japanese Monkey Malformation Research Group (JMMRG 1979) and data on Troop T from Fukuda (1988). The study period between 1965 and 1977 on Troop T from the former source overlapped the period between 1971 and 1977 of Fukuda's study and had a higher sample size (the number of sex-known births: 237 from the JMMRG and 134 from Fukuda). As the JMMRG literature did not indicate the period over which the infants were traced, I used the data on Troop T from only Fukuda (1988) for analyses. Although, also for Troop P, the JMMRG literature did not show the period over which the

infants were traced, it expressed "infant mortality". I, therefore, used the data for Troop P.

I excluded from analysis cases where infants disappeared with their mothers or were captured (TK between 1987 and 1993, AR between 1954 and 1983, and HK Troop T). In addition, "censored" individuals at the AR West population (Fedigan and Zohar 1997) were excluded from calculations.

For comparison of frequencies between two groups, the chi-square test, the G test, and the Fisher's exact test can be applied (Sokal and Rohlf 1995). The distribution of chi-square or G , however, cannot be approximated suitably by the χ^2 -distribution when sample sizes are small, and an exact test should be employed for 2×2 tables where expected frequencies of at least one cell are less than five (Rees 1985; Sokal and Rohlf 1995). Because the data from Sugiyama et al. (1979) had a cell with an expected frequency less than five, I employed the Fisher's exact test (two-tailed test) to test sex differences in infant mortality for all ten data sets, using SPSS 11.0J (SPSS 1995, 2001). The significance level was set at 5%.

Brown and Silk (2002) calculated a Pearson's correlation coefficient, r , between sample sizes and the absolute value of the differences between the proportion of males produced by high- and low-ranking females, based on Palmer's (2000) idea. In this study, I examined a relationship between sample sizes, sums of the numbers of males and females, and magnitudes of sex ratios in infant mortality rates as in Brown and Silk (2002). I used the absolute value of $\ln(\text{male mortality rate/female mortality rate})$ for each data set to measure the magnitude of the sex ratios in infant mortality rates, where "ln" is the natural logarithm, similar to van Schaik and de Visser (1990) who used the natural logarithm of the ratio between the proportions of males at different ages to measure the sex difference in juvenile mortality. The reason I used an absolute value of \ln was that both male- and female-biased mortality can occur and the test needs to examine not the direction but the magnitude of the bias. I used Kendall's coefficient of rank correlation, τ , because the 10 data sets are unlikely to conform to a bivariate normal distribution because of scarcity of data with a large sample and also the normal approximation for τ is considered more accurate than that for Spearman's coefficient, r_s (Sokal and Rohlf 1995). Because the null hypothesis is that there is no correlation between sample sizes and the magnitudes and the alternative hypothesis is that magnitude declines as sample sizes increase, I adopted a one-tailed test.

Results

The mean and SD of mortality rates from the 10 data sets were $21.2 \pm 15.9\%$ in males and $21.2 \pm 17.4\%$ in females.

Table 1 Sex differences in infant mortality among provisioned Japanese macaque populations

Population	Period that data were collected	Sample size Total (M, F)	Mortality rate (%)		P values ^a	ln(mortality sex ratio) ^b	When infants were traced	References
			M	F				
Katsuyama (KT)	1958–1985	921 (445, 476)	8.8	6.3	0.169	0.33	Within the first 12 months	Itoigawa et al. (1992)
Takasakyama (TK)	1956–1962 ^c	549 (289, 260)	2.8	4.6	0.264	−0.50	Within the first 12 months	Itani et al. (1964)
	1971–1977	33 (20, 13) ^d	50.0	15.4	0.067	1.18	For a year from Sept. of the birth year	Sugiyama et al. (1979)
	1987–1993	1,920 (987, 933)	24.7	21.2	0.074	0.15	From birth to the following May ^e	T. Matsui (unpublished data)
Arashiyama (AR)								
Original	1954–1983	933 (471, 462)	9.3	7.4	0.289	0.23	Within the first 12 months	Koyama et al. (1992)
West ^f	1972–1993	1,209 (598, 611) ^g	9.5	7.9	0.309	0.18	Within the first 12 months	Fedigan and Zohar (1997)
Koshima (KS)								
Periods 1 and 2	1952–1971	155 (84, 71)	11.9	14.1	0.811	−0.17	Within the first 12 months	Watanabe et al. (1992)
Periods 3 and 4	1972–1986	145 (76, 69)	38.2	43.5	0.612	−0.13	Within the first 12 months	Watanabe et al. (1992)
Hakone (HK)								
Troop P	1964–1974	74 (37, 37)	18.9	40.5	0.074	−0.76	— ^h	Japanese Monkey Malformation Research Group (1979)
Troop T	1971–1977	134 (66, 68)	37.9	51.5	0.122	−0.31	From birth to the following March ⁱ	Fukuda (1988)

M Males, F females

^a P values were calculated for sex differences in infant mortality rate using Fisher’s exact test (two-tailed test)

^b ln(male mortality rate/female mortality rate), where “ln” is the natural logarithm

^c Because the number of births of each sex in 1961 was unknown, data from 1961 were excluded

^d Marked infants were traced

^e Births were concentrated in the period from May to August

^f Macaques were transferred from Arashiyama in Japan to Texas in the U.S.A.

^g “Censored” individuals (Fedigan and Zohar 1997) were excluded from the calculations

^h Information was not given

ⁱ Births were concentrated in the period from April to October

Although some data sets seemingly exhibited sex-biased mortality, none displayed a significant sex difference (Table 1).

Next, I investigated the relationship between sample sizes and the magnitudes of sex ratios in infant mortality rates. I dealt with each value from the 10 data sets independently for the following reasons. For the TK, KS, and HK populations, mortality rates in each sex were not similar among periods or between troops of the same populations (Table 1). Although the two data sets in the AR population show similar mortality rates for each sex (Table 1), the West macaques lived in an entirely different habitat from the original AR macaques (see “Methods”).

The absolute values of ln(male mortality/female mortality) significantly declined as sample sizes increased ($n = 10$, $\tau = -0.467$, $P < 0.05$, Fig. 1). For the four populations, TK, AR, KS, and HK, where multiple data sets were collected, I could evaluate the relationship within each population. Fig. 1 indicates that smaller samples had larger

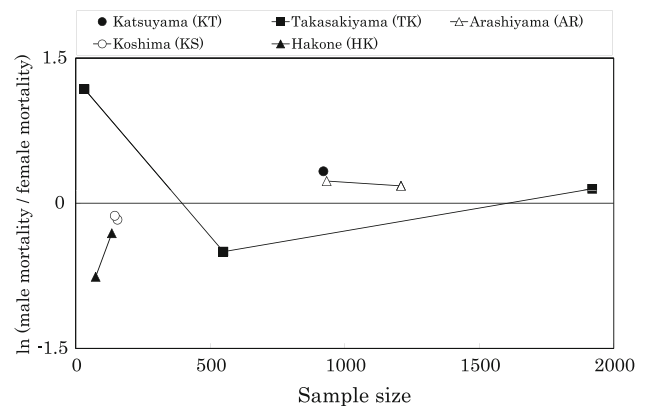


Fig. 1 Sample size and sex ratio in infant mortality. *Sample size* is a sum of the numbers of males and females; *ln* is the natural logarithm absolute values than larger samples within each population, except for KS where the two data points occur close to each other.

Discussion

The findings of this study can be summarized in two points: (1) There is no available data set showing significant sex-biased infant mortality in provisioned Japanese macaque populations. (2) Previously reported marked sex ratios in mortality (e.g., TK between 1971 and 1977 or HK Troop P) could be the product of stochastic variation in small samples. A significant negative correlation between sample size and magnitude of sex ratios in mortality was first found in this study, and it indicates that it is essential to take notice of sample size when markedly skewed sex ratios in mortality are found.

Among juveniles in female-bonded species such as macaques, female-biased mortality is more common than male-biased mortality (van Schaik and de Visser 1990). The most influential cause of female-biased mortality is aggression toward juvenile females by group members (e.g., Silk et al. 1981). In Japanese macaques, however, there are few reports of fatal attacks toward immature individuals (see Watanabe et al. 1992), and infanticide is extremely infrequent (Yamada and Nakamichi 2006). The lack of fatal attacks toward infants, regardless of sex, may be reflected in the result that all of data showed nonsignificant sex bias, although sex differences in some factors such as nutrition intake need to be studied.

Using the Fisher's exact test, Takahata et al. (1998) examined sex differences in infant mortality in two non-provisioned Japanese macaque populations and found slightly female-biased mortality in Yakushima and significantly male-biased mortality in Kinkazan. Their sample sizes were small (62 and 49), and directions of sex bias in the two were opposite. Thus, their result does not contradict the finding of the present study that conspicuous sex ratios in infant mortality could be the product of stochastic variation due to small samples.

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