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A Re-Evaluation of Factors Influencing the Sex Ratio of Spider Monkey Populations with New Data from Maraca Island, Brazil

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Key Words

Spider monkeys · *Ateles* · Sex ratio · Postweaning resource competition · Infant mortality · Trivers-Willard model · Dominant females

Introduction

Theory suggests that it is advantageous for females to bias the sex ratio of the infants they produce, whenever the sexes yield different fitness returns [1]. There are two principal models that have been used to interpret sex ratio variation in primates. The first model suggests that females should adjust the sex ratio of their offspring in accordance with their own abilities to invest (Trivers-Willard model [2]). Thus, females in good condition should preferentially produce infants of the sex for which future reproductive success is most dependent on the contributions made by the mother [3]. Typically, in primates this means that females in good condition should invest in male offspring, but this is not always the case [4]. The second model suggests that, if relatives of one sex compete for resources more than the other sex, it is advantageous to adopt a sex ratio biased against the sex that competes for the resources (postweaning resource competition hypothesis [5–7]). It seems reasonable to speculate that the selective pressures suggested by both of these models should be able to operate simultaneously, but it is only in species with male residency that these two selective pressures will coincide.

For species of the genus *Ateles*, available evidence suggests that female dispersal and male residency represent the norm [3, 8–10]. Previous studies of spider monkeys have provided support for both of the sex ratio theories outlined above. Symington [3] found a female-biased sex ratio (consistent with the postweaning resource competition hypothesis) in her study of spider monkeys in Peru. She also found that dominant females produced more males than females (consistent with the Trivers-Willard model). Chapman et al. [9] found that variation in sex ratios between populations of spider monkeys was compatible with the predications of the postweaning resource competition hypothesis. However, these findings could not be generalized to other pri-

mate species [10]. This undermines our confidence in the application of the postweaning resource competition hypothesis to spider monkeys and indicates a need for additional data.

In this study, we examine the applicability of the postweaning resource competition hypothesis to a population of spider monkeys living on Maraca Island, Brazil. Furthermore, we add to past observations and explore possible mechanisms whereby sex ratio is altered after birth.

Methods

Study Population

A community of 19–23 individually recognizable spider monkeys (*Ateles belzebuth belzebuth*) were studied on La Maraca Island (35° 25' N, 61° 40' W), Roraima, Brazil. The island receives 225 cm of rain annually, and, as a result, the vegetation on the island is mainly dry upland forest mixed with savanna and *Mauritia flexuosa* stands [11].

Animals were observed to copulate on 8 occasions between June and July 1989. Based on when births were observed in 1990, it is estimated that gestation for this population is approximately 7 months. This is very similar to previous estimates for spider monkeys [12–14].

Documentation of Population Sex Ratio

The study population was observed at various intervals over a 3-year period. Observations were conducted from July to December 1987 and from June 1988 to September 1989 (1,590 h of observations), and a follow-up census was conducted in July 1990. During these periods, all births were recorded, and the sex of infants was determined. When an infant was born during periods when the group was not being observed, the sex of the infant was determined as soon as the observer returned to the island and its age was estimated according to the individual's feeding and locomotor independence. Sex could not be determined for one of the infants born in 1990.

Results and Discussion

In 1987, the group contained 6 adult males, 8 adult females, 1 subadult male, 1 subadult female, 2 juvenile males, 1 juvenile female, 2 male infants and 1 female infant (adult sex ratio = 1:1.33). There were 4 infants or juveniles in the group when they were first observed, and during the course of the study an additional 7 infants were born (5 males, 1 female and 1 sex undetermined).

In 1989, 1 subadult, 3 juveniles and 1 infant (all males) died or disappeared between January and April. The bodies of 2 of these young males were found, and there was no evidence of bites or signs of predation. Violent aggression towards these immatures was never observed.

The observations on the spider monkey community on Maraca Island support the postweaning resource competition hypothesis in that few males reached adulthood. Thus, the sex that does not disperse and remains in the mother's home range competing with her for resources suffered higher mortality than the dispersing sex.

Observations of spider monkeys in Santa Rosa National Park, Costa Rica, suggested that the increased probability of mortality of young males was related to the fact that they were more likely to suffer attacks from females in the community than female infants [9, 15]. Evidence from Maraca Island does not support the notion that aggression directed against immature males was the mechanism leading to the reduc-

tion of the number of males. In contrast, observations in Maraca suggest that early male mortality may be related to different factors, such as the poor physical condition of the immature males.

While supporting the postweaning resource competition hypothesis, the evidence collected from Maraca Island raises an interesting question about the strategies employed by different populations of spider monkeys. There are now 3 published estimates of neonatal sex ratio for spider monkeys: Maraca Island, Brazil – 5 males:1 female [this study]; Santa Rosa National Park, Costa Rica – 1:1 [9]; Manu National Park, Peru – 1:2.7 [3]. It may be that males born into the different populations have such different probabilities of survival that the initial sex ratio must represent a compensatory strategy designed to produce an optimal number of adult males. This raises the question as to why there are such differences between populations in the probability of immature males surviving. The additional data provided by this study on Maraca Island do support the general principles suggested by previous studies, but it illustrates the potential magnitude of the variation in reproductive strategies of different populations and emphasizes the need for further field research.

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