

Post-weaning resource competition and sex ratios in spider monkeys

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In this study we examine the applicability of the resource competition hypothesis to explain both the existence of a skewed sex ratio in the spider monkey (*Ateles* spp.) where females disperse, and the variation in sex ratio among geographically separated sites and neighboring sites of varying productivity. The resource competition hypothesis would predict that when females disperse, animals should attempt to reduce the effect of intraspecific competition by limiting the number of male offspring produced by the community. This prediction is in agreement with the observed female biased sex ratio in spider monkeys. The observed variability in sex ratios between populations suggests that when the potential for post-weaning resource competition is high (i.e. in habitats with low productivity), the community will limit the production of the non-dispersing males more than in highly productive habitats.

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Introduction

Several theories have been put forward to provide explanations for skewed sex ratios (Fisher 1958, Hamilton 1967, Trivers and Willard 1973, Clark 1978, Williams 1979, Altmann 1980, Silk 1983, 1984, Clutton-Brock and Iason 1986). Fisher (1958) argued that females should invest equally in both sexes but that a deviation in sex ratio could occur if there were differential costs associated with the different sexes. Hamilton (1967) and Clark (1978) elaborated on Fisher's argument by suggesting that, if the relatives of one sex compete for resources more than the other sex, the best strategy would be to adopt a sex ratio biased in favour of the sex that did not compete for resources. Silk (1984) has constructed a model which demonstrates that through local resource competition a skewed sex ratio can evolve.

The majority of the studies that have examined the applicability of these theories to mammals have studied species where males disperse. Dispersal by males is the

most common pattern of dispersal in mammals (Greenwood 1980). However, since dispersal determines which sex competes for resources subsequent to dispersal, and affects the relative costs of producing infants of a particular sex (differential mortality), it is valuable to study possible factors which may influence sex ratio in a species where females disperse. Once such genus appears to be *Ateles*, where available evidence indicates that males remain in their natal communities, and females disperse (Wrangham 1980, Fedigan and Baxter 1984, White 1986, McFarland Symington 1987, Chapman, unpubl. data). The social organization of spider monkeys is relatively unique in the primate order and may influence many aspects of their demography. Individual spider monkeys associate in loosely organized subgroups that are unstable in size and composition, but which are affiliated at a higher community level (Klein 1972, 1974, Klein and Klein 1977, Chapman 1988).

In this study we first consider if the resource competition hypothesis can predict the direction of sex bias in a species where females disperse. Secondly, we review

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Tab. 1. Sex ratios of spider monkeys at different locations.

Study	Sex ratio (Males: Females)		Methods used	Study period (months)	# of subgroups	Community size
Santa Rosa National Park	Adult	1:5.71	Subgroup Counts	36	1018	42
	Immature	1:5.33				
	Birth (n=8)	1:1.00				
Tikal National Park	Adult	1:1.51	Subgroup Counts	8	...	75
	Immature	1:1.33				
Tikal National Park Cant (1978)	Adult	1:1.31	Transects	11	52	...
	Immature	1:0.89				
Tikal National Park Coelho et al. (1976)	Adult	1:2.23	Subgroup Counts	3	725	70-75
La Macarena Klein (1972)	Adult	1:3.00	Group Composition	13	498	20 adults
	Immature	1:1.75				
Panama Carpenter (1935)	Adult	1:1.65	Subgroup Counts	2	19	...
Manu National Park White (1986)	Adult	1:2.53	Transects	2	60	...
Manu National Park Symington (1987)	Adult	1:2.82	Group Composition	21	...	78
	Birth (n=46)	1:2.67				

sex ratio data available on *Ateles* (*A. geoffroyi*, *A. paniscus*, *A. belzebuth*) from eight studies in five locations and consider the sex ratios in light of the potential for post-weaning resource competition. Finally, we test this hypothesis more directly by documenting the sex ratio of *A. geoffroyi* in Guanacaste National Park, Costa Rica in areas with different levels of productivity. Based on the resource competition hypothesis one would predict that variation in habitat productivity between areas would result in differences in the advantages of producing offspring of one sex over the other as a consequence of post-weaning resource competition. In a situation of intense resource competition, in a species where females disperse, it should be advantageous for females to limit the production and/or survival of male offspring of other females in order to decrease the severity of post-weaning resource competition. Based on this extrapolation of the resource competition hypothesis, we evaluate the prediction that as the productivity of the habitat increases, the proportion of males in the population should also increase.

Methods

Sex ratios of geographically separated populations were obtained from eight studies of wild, unprovisioned populations of three species of *Ateles* at five different locations. The five sites are; 1) Tikal National Park, Guatemala (*A. geoffroyi*, Baxter and Fedigan, unpubl. data, Coelho et al. 1976, Cant 1978, Baxter 1979), 2) Santa Rosa National Park, Costa Rica (*A. geoffroyi*, Chapman 1987, 1988, Chapman and Fedigan, unpubl. data), 3) Panama (*A. geoffroyi*, Carpenter 1935), 4) La

Macarena National Park, Colombia (*A. belzebuth*, Klein 1972, 1974, Klein and Klein 1977), and 5) Manu National Park, Peru (*A. paniscus*, White 1986, McFarland Symington 1987).

Although the different studies calculated sex ratio in different ways (Tab. 1), we do not believe that the use of different methods caused any systematic bias. This belief is based on two observations. First, both the least and the most skewed adult sex ratios were obtained using the same method, and secondly, the sex ratio estimated for spider monkeys at Santa Rosa (derived from subgroup encounters; 1:5.71) was similar to an estimate derived from a transect study conducted independently (1:5.44, Chapman et al. 1988) and from an estimate of sex ratio based on the composition of one community (1:4.25, Chapman 1987).

Results and discussion

All of these populations (n=8) had an adult sex ratio biased in favour of females (Tab. 1). The average adult sex ratio in wild populations was 1 male to 2.60 females. However, the estimate of adult sex ratio varied from 1:5.71 at Santa Rosa, to 1:1.31 estimated from Tikal (Cant 1978). In five studies, estimates of the number and sex of the immatures were provided. Using these data, it was determined that the average sex ratio for immatures was 1 male to 2.32 females and ranged between sites from 1:5.33 at Santa Rosa to 1:0.89 at Tikal, as estimated by Cant (1978). In each of these five studies, the bias in sex ratio increased towards females from the immature to the adult stage of life. McFarland Symington (1987) determined the sex ratio from 46 infants

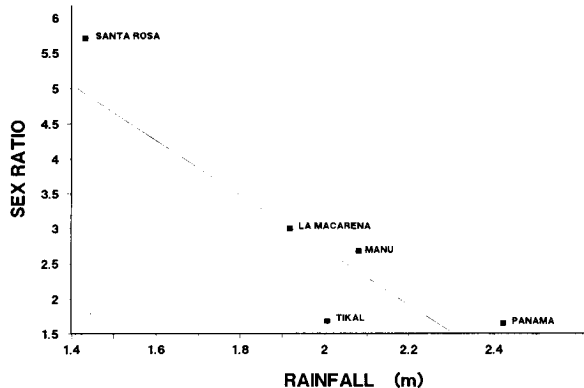


Fig. 1. The relationship between the sex ratio (number of females for each male) of spider monkeys (*Ateles* spp.) and rainfall (a measure of habitat productivity) as measured at five study sites.

born into a community of black spider monkeys (*A. paniscus*) in Manu National Park, Peru as 1:2.67. The sex ratio of adults in this community was 1:2.82. The sex ratio at birth from Santa Rosa was 1:1 (8 births), while the adult sex ratio was highly skewed (1:5.71).

The resource competition hypothesis suggests that for species in which female offspring disperse, females should reduce the effects of intraspecific resource competition by limiting the number of non-dispersing offspring produced by the community (Silk 1983). Following this line of reasoning, it would be predicted that the females in a spider monkey community would limit the number of males produced, since they are the non-dispersing sex. This prediction is in accordance with the observed sex ratios at all field sites.

Females can limit the number of males in a community by either adjusting the sex ratio before birth (Clark 1978) or by decreasing the probability that other females in the community can successfully raise male offspring (Silk 1983). For spider monkeys there is evidence to suggest that both of these mechanisms are operating. McFarland Symington (1987) reported a female biased sex ratio at birth for the spider monkeys at Manu National Park. Thus, it is possible that the sex of offspring is influenced before birth. Sex ratio in spider monkeys may also be facultatively adjusted after birth. At Santa Rosa, immature males were 1.7 times more likely to receive aggression than immature females (Chapman, unpubl. data). Similarly, Fedigan and Baxter (1984) demonstrated that juvenile males were twice as likely to receive aggression than juvenile females. There was evidence that this increased level of aggression directed at immature males had direct consequences on the probability of injury. Six serious injuries have been observed in the spider monkey community at Santa Rosa. An independent male infant received a 10-cm cut on his shoulder which was severe enough to render it non-functional for 3 wk, four small immature

males lost parts of their tails, and one male lost his leg at the hip and survived long enough for it to heal (Chapman and Chapman 1987). However, no such injuries have been observed in immature females who are more numerous at Santa Rosa than males. Also, identifiable immature males were five times more likely to disappear than females (presumably die, since their mothers were always present after their infant disappeared and males do not disperse). In other populations, documentation of wounding similarly suggests that males are more likely to be injured than females (Klein 1974, Carpenter 1935). It seems possible that the sex differences in the level of aggression received and in the probability of injury influences the sex ratio of spider monkey populations. The sex ratios in all populations were closer to unity at early stages of life than in the adult component of the population. From these observations it seems likely that, for spider monkeys, the number of males in the community can be limited both before and after birth.

Based on the resource competition hypothesis one could predict a more highly skewed sex ratio (biased towards females) in less productive habitats than in more productive habitats. Unfortunately, there are only limited data on net primary productivity, or plant biomass available from different types of tropical forest. However, the annual net primary productivity for dry forest averages 50–75% that of wet forest (Hartshorn 1983, Murphy and Lugo 1986). Similarly, the total plant biomass in dry forest is estimated to range between 78 and 320 t ha⁻¹, while in wet forest the range is much higher (269–1186 t ha⁻¹, Murphy and Lugo 1986). Santa Rosa contains primarily tropical dry deciduous forest, and the region where the park is located experiences a long severe dry season (mean rainfall 1434 mm). In tropical dry forest 60–75% of the trees are deciduous and lose their leaves in the dry season (Frankie et al. 1974, Hubbell 1979). Such seasonality may create periods of food shortages for specific animal species. Based on the relative productivity of wet and dry tropical forests, and on the seasonality of the forests, one would predict that Santa Rosa should have a sex ratio more strongly biased against males than the other sites. This is the observed pattern, in fact the sex ratio at Santa Rosa is 2.7 times more skewed than the average adult sex ratio of the wetter forest sites.

The floral nature and history of Tikal National Park allows a further refinement of this argument. Tikal is a relatively lush area, dominated by *Brosimum alicastrum* and *Achras zapota* (Coelho et al. 1976). These plants form a major part of the diet of spider monkeys of Tikal. The relatively high abundance of both of these plant species is thought to be a result of Mayan horticultural practices (Baxter 1979). With this in mind, one might expect that the available productivity at Tikal is greater than that at La Macarena or Manu National Parks. Here again, the observed differences in sex ratios, with Tikal (the more productive site) having a sex

Tab. 2. Sex ratios (male: female) of populations of spider monkeys found in different types of habitats in Guanacaste National Park, Costa Rica.

Habitat	Adult sex ratio
Montane Rain Forest	1:1.66
Riverine Forest	1:2.33
Semi-Evergreen Forest	1:4.70
Dry Deciduous Forest	1:5.71

ratio more closely approaching unity than that of either La Macarena or Manu, are in accordance with the predictions of the resource competition hypothesis.

Since net primary productivity has been shown to be related to rainfall (Murphy and Lugo 1986), it is reasonable to use annual rainfall as an index of habitat productivity, which should reflect the potential for post-weaning resource competition. Rainfall estimates for each study were obtained from the original study, or from Wernstedt (1972). As predicted, we found a negative relationship between sex ratio and rainfall ($r = -0.909$, $P = 0.033$, Fig. 1).

As a second more direct examination of the resource competition hypothesis, we documented the sex ratio of neighboring spider monkey (*A. geoffroyi*) populations ranging within a small geographical area (700 km²), but over a diversity of habitats. The areas chosen were within the proposed Guanacaste National Park, Costa Rica (Janzen 1986). Four habitat types were considered (Tab. 2). Based on the work of Murphy and Lugo (1986), we ranked habitat productivity with respect to the potential availability of water. The first habitat type, the montane rainforest (500–1000 m elevation) receives more rain than any of the other habitats (approximately 2239 mm at 600 m; measured outside of the park on adjacent slopes) and is ranked highest for productivity. At this altitude, the length of the dry season is shorter than at lower elevation areas. Guanacaste National Park contains a number of both permanent and temporary rivers and associated strips of riverine forest, the second habitat type. These areas contain relatively lush vegetation, however they represent only thin strips of forest. Also, within the park there are areas of semi-evergreen forest. Semi-evergreen forest contains many trees that either maintain their leaves throughout the dry season, or drop their leaves for only a short period of time. Semi-evergreen forest was considered the third most productive habitat. The fourth and most widespread forest habitat type found in the park is dry deciduous forest. This type of forest receives little rain (1434 mm; measured in Santa Rosa National Park) and the majority of the trees in this type of forest lose their leaves at the start of the dry season and remain bare until the rains begin. The observed sex ratios of spider monkeys in these habitats vary in the direction one would predict based on the resource competition hypothesis (Tab. 2).

Habitats considered to have relatively low productivity contained a greater proportion of females to males than potentially more productive habitats.

In summary, the female-biased sex ratio observed in spider monkeys is in accordance with predictions derived from the resource competition hypothesis (Clark 1978). Evidence from eight studies of spider monkeys and from a census of Guanacaste National Park, suggests that when habitat productivity is low, and thus the potential for post-weaning resource competition is high, the spider monkey community will limit the production of non-dispersing males more than in productive habitats.

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References

- Altmann, J. 1980. Baboon mothers. – Harvard Univ. Press, Cambridge.
- Baxter, M. J. 1979. Behavioural patterns relating to age and sex in free-ranging spider monkeys (*Ateles geoffroyi*) in Tikal National Park, Guatemala. – Masters Thesis, Univ. of Alberta, Edmonton.
- Cant, J. G. H. 1978. Population survey of the spider monkey *Ateles geoffroyi* at Tikal, Guatemala. – *Primates* 19: 325–335.
- Carpenter, C. R. 1935. Behaviour of red spider monkeys in Panama. – *J. Mammal.* 16: 171–180.
- Chapman, C. A. 1987. Foraging strategies, patch use, and constraints on group size in three species of Costa Rican primates. – Ph.D. Dissertation, Univ. of Alberta, Edmonton.
- 1988. Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. – *Behaviour* 105: 99–116.
- and Chapman, L. J. 1987. Social responses to the traumatic injury of a juvenile spider monkey (*Ateles geoffroyi*). – *Primates* 28: 271–275.
- , Fedigan, L. M. and Fedigan, L. 1988. A comparison of transect methods for estimating population density of Costa Rican primates. – *Brenesia* in press.
- Clark, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. – *Science* 201: 163–165.
- Clutton-Brock, T. H. and Iason, G. R. 1986. Sex ratio variation in mammals. – *Quart. Rev. Biol.* 61: 339–374.
- Coelho, A. M., Bramblett, C. A., Quick, L. B. and Bramblett, S. 1976. Resource availability and population density in primates: a sociobioenergetic analysis of energy budgets of Guatemalan howler and spider monkeys. – *Primates* 17: 63–80.
- Fedigan, L. M. and Baxter, M. J. 1984. Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). – *Primates* 25: 279–294.
- Fisher, R. A. 1958. The genetical theory of natural selection. – Dover Publ., New York.
- Frankie, G. W., Baker, H. G. and Opler, P. A. 1974. Comparative phenological studies in tropical wet and dry forests in the lowlands of Costa Rica. – *J. Ecol.* 62: 881–919.

- Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. – *Anim. Behav.* 28: 1140–1162.
- Hamilton, W. D. 1967. Extraordinary sex ratios. – *Science* 156: 477–488.
- Hartshorn, G. S. 1983. Plants. – In: Janzen, D. H. (ed.), *Costa Rican Natural History*. Univ. of Chicago Press, Chicago, pp. 118–157.
- Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. – *Science* 203: 1299–1309.
- Janzen, D. H. 1986. Guanacaste National Park: Tropical, ecological, and cultural restoration. – Editorial Univ. Estratal a Distancia, San José, Costa Rica.
- Klein, L. L. 1972. The ecology and social organization of the spider monkey, *Ateles belzebuth*. – Ph.D. Dissertation. Univ. of California, Berkeley.
- 1974. Agonistic behaviour in neotropical primates. – In: Holloway, L. (ed.), *Primate aggression, territoriality, and xenophobia*. Academic Press, New York, pp. 77–122.
- and Klein, D. D. 1977. Feeding behaviour of the Colombian spider monkey. – In: Clutton-Brock, T. H. (ed.), *Primate ecology*. Academic Press, New York, pp. 154–181.
- McFarland Symington, M. 1987. Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. – *Behav. Ecol. Sociobiol.* 20: 421–425.
- Murphy, P. G. and Lugo, A. E. 1986. Ecology of tropical dry forest. – *Ann. Rev. Ecol. Syst.* 17: 67–88.
- Silk, J. B. 1983. Local resource competition and facultative adjustment of sex ratio in relation to competitive abilities. – *Am. Nat.* 121: 56–66.
- 1984. Local resource competition and the evolution of male-biased sex ratio. – *J. Theor. Biol.* 108: 203–213.
- Trivers, R. L. and Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. – *Science* 179: 90–92.
- Wernstedt, F. L. 1972. World climatic data. – Climate Data Press, Lamont, PA.
- White, F. 1986. Census and preliminary observations on the ecology of the black-faced black spider monkey (*Ateles paniscus chamek*) in Manu National Park, Peru. – *Am. J. Primatol.* 11: 125–132.
- Williams, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. – *Proc. R. Soc. Lond.* 205: 567–580.
- Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. – *Behaviour* 75: 262–300.