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Ed.

Sex ratio in primates: a test of the local resource competition hypothesis

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Introduction

Fisher (1930) argued that parental investment should be equally divided between male and female offspring. However, if the offspring of one sex are more expensive to produce than offspring of the other sex, fewer of the expensive sex should be found when parental investment ends. Clark (1978) advanced this hypothesis by suggesting that since members of the non-dispersing sex compete with their parents longer than the dispersing sex, they are more costly, and the parents should limit the number of non-dispersing infants that are produced or survive in the group. This hypothesis has been labelled the "local resource competition hypothesis" and has been further developed and formalized by Silk (1984). In support of these theoretical developments, habitat productivity (which may reflect the level of local resource competition) has been shown to be related to sex ratio in spider monkeys (Chapman et al. 1989) and kangaroos (Johnson and Jarman 1983). The sex ratio differed between areas such that more of the non-dispersing sex were produced in habitats with higher productivity and thus, potentially less local resource competition.

The objective of this study was to examine the generality of the local resource competition hypothesis by considering relationships between sex ratio and habitat productivity and to discuss these findings in relation to the assumptions of the hypothesis. To meet this objective we chose to examine the adult and birth sex ratios of well-studied primate species. We predict that birth sex ratio should be male-biased when daughters are philopatric and female-biased when daughters disperse. Secondly, we examine predictions as to how sex ratio should vary between areas characterized by different levels of productivity. If we assume that in productive habitats, the potential for intense competition is lower than in less productive habitats, then the potential of resource competition between mothers and the non-dispersing sex should decrease as habitat productivity increases. If this occurs, more offspring of the non-dispersing sex should be produced or survive. Thus, for species in which males disperse one would predict that the proportion of females produced or surviving should increase with habitat productivity. For species in which females disperse, the proportion of males produced or surviving should increase with habitat productivity.

Methods

We reviewed the literature for studies which reported the sex ratio of a number of primate groups of a given genus or species over a range of habitat types. We found six genera for which a number of sex ratio estimates were available from a variety of habitats (mean number of studies in different locations = 12, range 5–19), and for which the dispersal pattern of the species was known (baboons-*Papio* spp., vervets-*Cercopithecus aethiops,* langurs-*Presbytis entellus* males disperse; howlers-*Alouatta* both sexes disperse; chimpanzees-*Pan* spp., spider monkeys-*Ateles* spp. female offspring disperse) (Pusey and Packer 1987). Sex ratio was reported as the number of females per one male and was calculated from all the groups within a small geographical region. If possible, birth sex ratio was calculated at the time of birth. If this information was not provided, the sex ratio of the infants was considered to represent birth sex ratio. Birth sex ratio for howlers was not estimated,

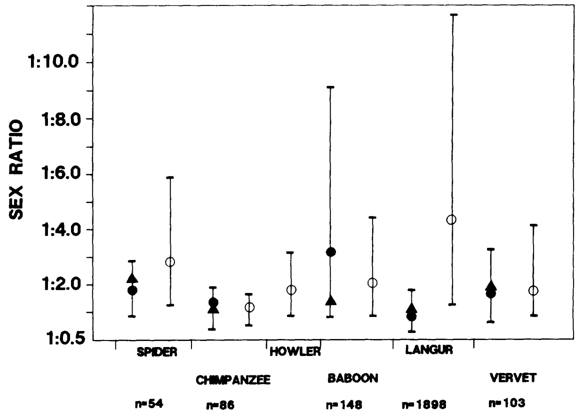

Fig. 1. The birth and adult sex ratio for six groups of primates calculated from studies of free-ranging populations. The bars represent the range in the sex ratios reported for different studies, the clear circles represent the mean of the sex ratios reported in the different studies, the triangle represents the mean birth sex ratio calculated as the total number of female infants reported from any study divided by the number of male infants, and the solid circle represents the mean birth sex ratio averaged between studies. The n values represent the number of births recorded from wild populations used in the calculations.

since in some species of howlers it is extremely difficult to determine the sex of infants.

Recent work in a number of tropical environments has demonstrated that habitat productivity is related to annual rainfall (Murphy and Lugo 1986). Thus, we used annual rainfall as an index of habitat productivity. Annual rainfall was determined from either the original study, subsequent publications by the same authors, by different authors studying in the same area, or from Wernsteadt (1972). Since the references for the studies used consist of over 116 citations we have not referred to each study separately, however a listing of the studies can be obtained from any of the authors.

Results

Birth sex ratio

The local resource competition hypothesis would predict that sex ratio should be male biased when sons disperse and female biased when daughters disperse. The sex ratios at birth (cumulative from all studies) for spider monkeys (1:2.25) and chimpanzees (1:1.21), where females disperse, were female biased as predicted. However, considering baboons (1:1.37), vervets (1:1.77), and langurs (1:0.93) where males disperse, only the langurs were male biased as predicted (based on 2289 births, Fig. 1).

Habitat productivity and adult sex ratio

We found no relationship between sex ratio and rainfall for any of the three species in which males disperse from their natal areas (Fig. 2; Tab. 1). As predicted, with howlers, where both sexes disperse, there was no relationship between rainfall and sex ratio. For chimpanzees and spider monkeys, where females leave their natal area, results were contradictory (Fig. 2). As predicted for spider monkeys there was a negative relationship between rainfall and adult sex ratio, however the

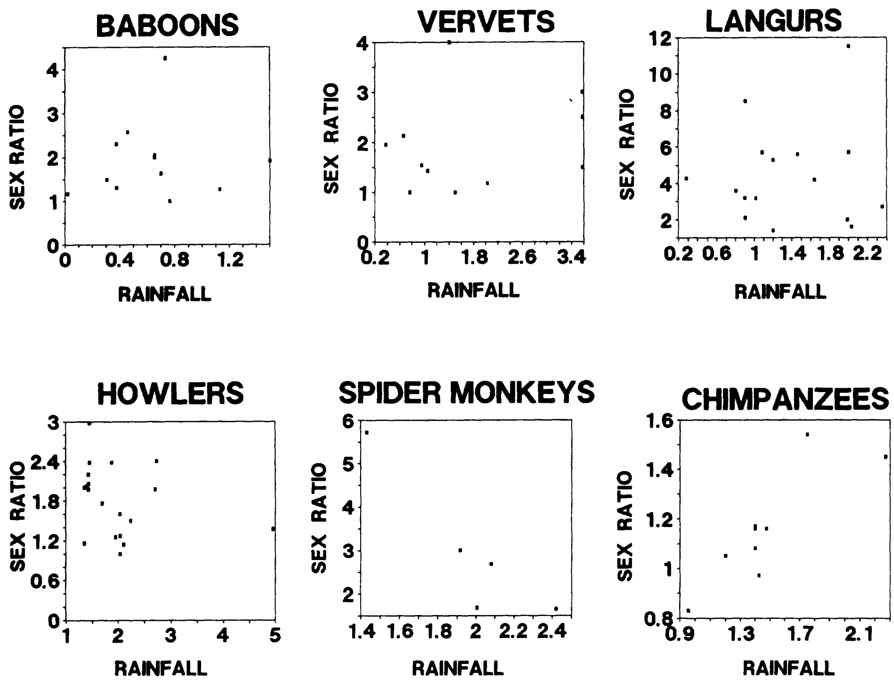

Fig. 2. The relationship between sex ratio (females/males) and rainfall (in meters; our measure of habitat productivity) for baboons, vervets, langurs, howlers, spider monkeys, and chimpanzees.

Tab. 1. The relationship between sex ratio and habitat productivity (rainfall) for primate species where males disperse, both sexes disperse, and females disperse. Birth sex ratios are only reported for combined groups where sample sizes are large (birth sex ratio was calculated as the total number of female infants in any population divided by the total number of male infants).

Taxon	Adult sex ratio	Birth sex ratio	Predicted/Observed
Papio	1:2.02 r=0.126, P=0.71	1:1.37 – – –	+/NS
Cercopithecus aethiops	1:1.81 r=0.242, P=0.47	1:1.77 – – –	+/NS
Presbytis entellus	1:4.35 r=0.002, P=0.99	1:0.93 – – –	+/NS
Combined male dispersers	1:2.76 r=0.088, P=0.60	1:2.17 r=−0.137, P=0.74	+/NS
Alouatta			
Both sexes disperse	1:1.79 r=−0.272, P=0.26	– – –	NS/NS
Ateles	1:2.84 r=−0.909, P=0.03	1:2.25 – – –	–/–
Pan	1:1.16 r=0.850, P=0.01	1:2.21 – – –	–/+
Combined female dispersers		1:1.42 r=0.564, P=0.24	–/NS

sample size for this species was small (n=5 populations). For chimpanzees, we predicted a negative relationship between adult sex ratio and rainfall, however a positive relationship was found.

One possible explanation for the generally negative results obtained could be that as rainfall and habitat productivity increases, the density of primate populations increases, such that the level of competition realized by the individual does not change. Statistically removing the effect of population density did not alter the significance of the relationships found (partial correlations between sex ratio and rainfall removing the effect of population density; baboons r = 0.077, P = 0.440, vervets r = 0.218, P = 0.678, langurs, r = −0.076, P = 0.787, howlers r = −0.320, P = 0.244, chimpanzees r = 0.767, P = 0.044). Similarly, removing the effect of group size did not change the significance of the relationships.

Discussion

The findings presented here suggest that with the exception of the spider monkeys, and possibly the howlers, variation in sex ratio among populations cannot be explained by the local resource competition hypothesis. It is possible that either the basic premises of the model are not entirely correct, that our measure of habitat productivity is inaccurate, or that the assumptions of the model are not valid. The local resource competition hypothesis assumes: 1) that if there is a decrease in the production or survival of the non-dispersing sex, levels of resource competition will decrease, and 2) that the costs of having non-dispersing offspring present in the group are not offset by benefits that the offspring provide. Considering the general behavioural characteristics of many primate species, it seems likely that the second assumption may be violated. The presence of adult kin in a group has been shown to provide additional predator warning (Cheney and Seyfarth 1985), increase the number of individuals for which alliances can easily be formed (Gouzoules and Gouzoules 1987), and increase the number of grooming partners (Walters and Seyfarth 1987).

This investigation illustrates the difficulties of assessing the relative costs and benefits of producing sons and daughters. We suggest that although variables such as habitat productivity may be important in determining the sex ratios in some species, they may play a small role in others. In these species other costs or benefits may override the influence of increased feeding competition with the non-dispersing sex.

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