



THE UNIVERSITY OF CHICAGO PRESS JOURNALS

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Source: *The American Naturalist*, Vol. 117, No. 5 (May, 1981), pp. 796-797

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <http://www.jstor.org/stable/2460765>

Accessed: 29-01-2018 17:11 UTC

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SEX RATIO AND LOCAL RESOURCE COMPETITION

Using data from museum collections, zoos, and her own field study, Clark (1978) reported a male-biased secondary sex ratio for an African prosimian, *Galago crassicaudatus*. She suggested that the observed bias is "not satisfactorily explained by existing hypotheses on high sex ratios" (p. 163), but rather that "it results from a social structure which produces sibling and mother-offspring competition for limiting resources that involves only one sex (in this case, female)" (p. 163).

Clark's suggestion is based on three assumptions. (1) "Theoretical explanations for skewed secondary sex ratios derived from social insects are inapplicable to the degree that they depend on haplo-diploid breeding systems" (p. 164). Although Clark's reference (Hamilton 1967) on skewed sex ratios resulting from local mate competition used evidence from haplodiploid insects, effects of local mate competition do not depend on haplodiploidy: Such effects can occur in any sex-determining system (Hamilton 1967; Alexander and Sherman 1977). Further, if mates constitute a resource, then Clark's local resource competition is simply a more general case of Hamilton's (1967) local mate competition. (2) "Since the sex ratio bias applies to all the samples for this species . . ." (p. 164). This assertion may not be true for either the museum sex ratios or the zoo sex ratios. For the museum data, Clark suggested that the tertiary sex ratio represents the secondary sex ratio because "In testing the captive birth data, I found no evidence for differential death before maturity" (p. 163). This reasoning is weak, since zoo conditions must usually be different from those conditions in nature that can lead to differential death of the sexes before maturity. In her interpretation of the zoo sex ratios (table 2), Clark's reasoning is also weak since conditions that might affect sex ratio, such as nutrition of females (Trivers and Willard 1973), population density (Mech 1975), and the variance in male reproductive success (Alexander 1974; Dickemann 1979) are probably unnatural in zoos. (3) ". . . both male and female offspring interact equally with their younger siblings and neither sex acts as classical 'helpers,' so that differential contribution of one sex to the next parental brood does not offer a reason [for the biased sex ratio]" (p. 164). Clark provides no support for this critical assumption.

Finally, contrary to Clark's assertion, existing sex ratio theory may be sufficient to explain the observed biased sex ratio observed in *G. crassicaudatus*. Fisher (1958, not cited by Clark) hypothesized that parents are selected to invest equally in the sexes since, genetically, each sex contributes equally to the next generation. When one sex is more expensive to raise (i.e., when parental investment per offspring is higher for one sex), then parents who produce proportionately fewer of that sex will be favored by natural selection (see also Howe 1977; Maynard Smith 1978). Clark concluded that the tendency of *G. crassicaudatus* daughters to remain longer than sons in their mother's home range leads to "local resource competition" between mothers and daughters. As with other mammals (e.g., Bertram 1976; Hoogland 1981), however, mothers of *G. crassicaudatus* may continue to invest in their daughters following the departure of their sons by ways

such as nonreciprocal grooming, nonreciprocal sharing of knowledge about feeding and sleeping sites, or the giving up of part of their own resource bases (Clark 1978). Whether mothers "willingly" invest in their daughters following the dispersal of their sons or whether such investment is "stolen" by daughters in a process of local resource competition, the effect will be the same: Parental investment per offspring will be higher for daughters (assuming that a son and a daughter are equally expensive to raise prior to the son's departure), and there will be selection for male-biased litters. That is, parental investment does not necessarily involve parental willingness to invest (Trivers 1972, 1974), and benefits gained by daughters through local resource competition are subsumed under parental investment. It follows that the observed male bias in the sex ratio of *G. crasicaudatus* can probably be explained by Fisher's (1958) hypothesis.

ACKNOWLEDGMENTS

The following persons read an earlier version of this manuscript and made helpful suggestions: R. Alexander, D. Baird, G. Barrowclough, G. Borgia, N. Flessness, H. Horn, R. Howard, D. Ligon, R. May, A. Pace, P. Sherman, and G. Williams.

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Submitted January 18, 1980; Accepted August 14, 1980