All-Female Litters as a Reproductive Strategy: Defense and Generalization of the Trivers-Willard Hypothesis

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In her recent article, Myers (1978) discussed explanations for an unequal sex ratio in litters. She stressed the plausibility of Fisher's suggestion that, in dimorphic species, it is advantageous to produce more young of the cheaper sex if the population is resource-limited. She elaborated the hypothesis to include the costs of raising young and demonstrated its applicability to redwing blackbirds.

Trivers and Willard (1973) proposed an alternative hypothesis based on the idea that males born in adverse times are likely to remain handicapped in reproductive competition. In such times, females bearing all-female litters thus ought to have a selective advantage. This hypothesis was strongly criticized by Myers.

Myers showed weaknesses in Trivers and Willard's data base. She also tried to demonstrate flaws in the logic of the hypothesis by means of a model based on the following assumptions: (1) The sex ratio of litters can be manipulated only by decreasing the number of male offspring without compensatory change in the number of females; (2) the reduced litter size does not enhance the survival of the mother or her female offspring. Myers found that, given these conditions, low survival of male offspring is not a sufficient reason for deviation from an equal sex ratio.

The reasons for making these assumptions are not obvious. It is especially hard to match assumption (2) with the situation the model attempts to simulate. If reproduction is limited by resource shortage then, by definition, the size of the litter and the survival of the mother and/or the offspring must be inversely related to each other.

There is also a counterexample that raises questions about the universal validity of assumption (1). There does not seem to be a significant difference in the litter sizes of wood lemmings bearing only females and those bearing litters with normal 1:1 sex ratio. (For possible mechanisms, see Kalela and Oksala [1966], Maynard Smith and Stenseth [1978].) Such blind manipulation (occurring irrespectively of external factors) differs from the conditional manipulation of Trivers and Willard, but the existence of the female-bearing genotype demonstrates that this strategy must be occasionally advantageous. If the Fisher-Myers hypothesis could account for the biased sex ratio in wood lemmings, one would expect wood lemmings to be especially dimorphic rodents. However, according to the data provided by Siivonen (1976), the index of dimorphism (maximum body length of species: minimum body length of pregnant females) is 1.54 for the wood lemming, whereas the average value for all Finnish microtines is 1.61 (range 1.49–1.72). Stenseth (1978) proposed that females with all-female litters are favored by periodic inbreeding, but a mechanism related to the Trivers-Willard hypothesis appears to be another possibility.

Whatever the causal mechanism responsible for the population cycles in wood lemmings, diseases and carnivory are probably most intense during decline (see

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Hörnfeldt 1978; Fitzgerald 1978). Because of their greater activity and aggressiveness, males are likely to be most severely affected by these factors. If recruitment continues during the decline, the males maturing in the peak phase will be at a disadvantage. They will be subjected to the strongest discriminatory male mortality, and younger ones will profit.

In a more general form, this can be stated as follows: Whenever the risks and rewards of being a male are unevenly distributed in time, there are periods when bearing all-female litters is the optimal strategy. In principle, this generalized form of the Trivers-Willard hypothesis is symmetrical, and so is the original one. Each offspring has a father and if males of some cohorts are at a disadvantage, those of other cohorts must be correspondingly favored. Hence, periods when all-male litters are the optimal strategy must exist, too. However, it is possible that these periods are not preceeded by clear signs which could trigger conditional manipulation of sex ratios, and neither of the genetical mechanisms proposed for the wood lemming could readily be modified to produce all-male litters.

The usefulness of this generalization is arguable as long as the critical data from the wood lemming are missing. (Is the discriminatory male mortality in declining populations especially strong? Does the recruitment continue during the decline?) A further problem is that there are very few cases which might be covered by the broader version of the hypothesis but not by the original. (Stenseth [1978] discussed the collared lemming of Siberia and the root vole of Alaska as additional cases of correspondingly biased sex ratios.)

Aside from these problems, the original Trivers-Willard hypothesis appears to be firmly based on logic and seems to complement—rather than compete with—the interesting ideas of Myers. Any animal whose juveniles are less stress-tolerant than the adults should reduce its reproductive effort when facing adverse times (Goodman 1979). The optimal allocation of the reduced reproductive effort between young of different sexes depends on the individual costs of raising the offspring, as proposed by Myers, and on the ability of the young to compete with those born in better times. This is not an either-or question.

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