

# Facultative parthenogenesis and sex-ratio evolution

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## Summary

Phenotypic models of selection are used to determine the effect of facultative parthenogenesis on the production of males in a spatially variable environment when (i) sex determination is under strict genetic control, and (ii) when sex may be environmentally determined. The results show that when sex is under strict genetic control and there is some chance of maturing in isolation, selection favors a female-biased sex ratio. When sex can be environmentally induced by cues which indicate high density, selection favors a mixture of genetic and environmental control, such that half the individuals always become female and the other half become females when isolated and become males when not isolated.

*Keywords:* Environmental sex determination; mixed control; nematodes; parthenogenesis; sex ratio.

Assuming panmixia in a large population, Fisher (1930) suggested that natural selection should favor equal expenditures on male and female offspring. Hence, if males and females are equally expensive to raise to independence, the sex ratio is selected to come to and remain at 1:1. Hamilton (1967) was the first to consider situations where the panmixia assumption is violated, and he found that local competition among males for access to mates favors a female-biased sex ratio (see also Charnov, 1982). In the present study, I consider an additional departure from the panmixia assumption: facultative parthenogenesis. I also consider selection in facultative parthenogens when environmental sex determination is a possibility, as in some nematodes.

The model assumes a simple dichotomy in population structure: individuals either mature and reproduce in isolation, or they find themselves in a large mating aggregation (perhaps drawn together by a concentration in resources). Open competition for mates within the large mating aggregations is assumed. Let the probability of being isolated at reproduction be  $p$  and the probability of maturing in a dense mating aggregation be  $(1 - p)$ . Isolated females reproduce by parthenogenesis, while females in the large mating aggregations reproduce sexually. Let the fitness of a sexually produced offspring relative to parthenogenetically produced offspring be  $x$ , and assume that  $x$  is less than  $1/2$ , so that obligate parthenogenesis is not favored by selection (see Williams, 1975; Maynard Smith, 1978).

I first consider strict genetic control of sex expression. Let  $r$  and  $(1 - r)$  be the frequencies of males and females in the population, respectively. I assume that the population is large enough so that the sex ratio of a single female's brood does not significantly affect the population sex ratio. I also assume that males and females are equally expensive to produce. Under these assumptions, the fitness of a rare individual ( $W_i$ ) is closely approximated by:

$$W_i = 2xp(1 - r_i) + (1 - p)[(1 - r_i) + r_i(1 - r)/r],$$

which gives the relative genetic contributions to grandchildren that come from isolated daughters, plus crowded daughters, plus crowded sons, respectively.

The fate of random mutations, which either increase or decrease the sex ratio of an individual's brood, is calculated by finding the partial derivative of  $W_i$  with respect to  $r_i$  (which gives the effect of changing the brood's sex ratio on individual fitness):

$$\frac{\delta W_i}{\delta r_i} = (1 - p) \left[ \frac{1 - r}{r} - 1 \right] - 2px.$$

Mutations that increase the number of males in a brood are favored when the derivative is positive [i.e. when  $p < 1$  and  $(1 - r)/r > 1 + 2xp/(1 - p)$ ], and mutations that decrease the number of males in a brood are favored when the derivative is negative [i.e. when  $p = 1$  or when  $(1 - r)/r < 1 + 2xp/(1 - p)$ ]. Hence, for  $p < 1$ , selection on individuals results in the population becoming as close as possible (see Maynard Smith, 1982) to the stable equilibrium,  $r^*$ , (where  $\frac{\delta W_i}{\delta r_i} = 0$ ) at

$$\frac{1 - r^*}{r^*} = 1 + \frac{2px}{1 - p} = \frac{1 - p + 2px}{1 - p}. \quad (1)$$

The production of  $r^*$  males by a single, heritable phenotype is, therefore, an ESS (evolutionarily stable strategy, in the sense of Maynard Smith, 1982). Note that, if the probability of being isolated at maturity is zero (i.e.  $p = 0$ ), the sex ratio is selected to become as close as possible to 1/2, which is consistent with Fisher's argument. As the probability of becoming isolated increases (i.e.  $p$  increases from 0 to 1), the sex ratio is selected to become increasingly female-biased. This result (Equation 1) is directly parallel to the Charlesworths' (1981, p. 61) result that allocation to female function in hermaphrodites is selected to increase with increases in enforced selfing.

I now consider the outcome of selection when sex can be environmentally determined. Facultative parthenogenesis is especially interesting in this context because it meets one of the important conditions of the Charnov and Bull (1977) model for selection favoring ESD (environmental sex determination): male and female fitnesses must be different in different environments (see also Bull, 1983). This condition is clearly met by facultative parthenogens, because only females reproduce when they are isolated.

There are three potential types of individuals in the population: (i) unconditional males in frequency  $r$ , (ii) unconditional females (all facultative parthenogens) in frequency  $q$ , and (iii) conditional males in frequency  $(1 - r - q)$ . Conditional males are induced by environmental cues associated with high density to become males; in the absence of such cues, they become females and reproduce parthenogenetically. The variables  $p$  and  $x$  are as defined above. Assuming a large population, and that all three types of individuals are equally expensive to rear, a rare individual's fitness ( $W_i$ ) is closely approximated by:

$$\begin{aligned} W_i &= p[2xq_i + 2x(1 - r_i - q_i)] + (1 - p) \left[ q_i + \frac{(r_i + (1 - r_i - q_i))q}{r + (1 - r - q)} \right] \\ &= 2px(1 - r_i) + (1 - p) \left[ q_i + \frac{(1 - q_i)q}{(1 - q)} \right], \end{aligned}$$

which gives the relative genetic contributions of isolated females and conditional males, plus crowded females, unconditional males, and conditional males.

Working as before, the partial derivative of  $W_i$  with respect to  $r_i$  is taken to determine the equilibrium frequency of unconditional males:

$$\frac{\delta W_i}{\delta r_i} = -2px, \quad (2)$$

so there is selection to eliminate unconditional males, unless either  $p$  or  $x$  is zero. Similarly, the partial derivative of  $W_i$  with respect to  $q_i$  is calculated to determine the fate of random mutations, which affect the production of unconditional females:

$$\frac{\delta W_i}{\delta q_i} = (1 - p) \left[ 1 - \frac{q}{1 - q} \right].$$

Hence, mutations that increase the production of unconditional females increase in the population when the derivative is positive (i.e. when  $p < 1$ , and  $q < 1/2$ ); and mutations that decrease the production of unconditional females increase in the population when the derivative is negative (i.e. when  $p < 1$ , and  $q > 1/2$ ). The equilibrium ( $q^*$ ) is, therefore, reached when the probability of being isolated is less than one, and

$$\frac{q^*}{1 - q^*} = 1. \quad (3)$$

Hence, a heritable phenotype that produces  $q^*$  unconditional females is an ESS. Because  $r = 0$  at equilibrium (from Equation 2), the frequency of conditional males ( $1 - r - q$ ) is equal to  $1 - q$ ; and because  $q^* = (1 - q^*)$  at equilibrium (from Equation 3), the frequency of unconditional females is equal to the frequency of conditional males. This result is analogous to Fisher's rule, the only difference being that males are environmentally induced, rather than genetically determined. It also suggests that a stable mixture of genetic and environmental control of sex expression should exist at equilibrium. Such mixtures of control [called 'mixed control' by Lloyd and Bawa (1984)] may also exist for morphological characters independent of sex (Lively, 1986).

There is evidence for mixed control of sex expression in the facultative parthenogen *Diplen-teron potohikus*, a free-living nematode. Yeates (1970) and Clark (1978) showed that sex determination is density dependent in this species: individuals reared alone became female (and reproduced parthenogenetically), while cultures of multiple individuals yielded 5.5–15.9% males depending on density (Clark, 1978). Clark also showed that the male-inducing factor is probably a metabolite produced by the nematode, and he suggested that the capacity for response to the metabolite is restricted to a fraction of the population by selection. The actual frequency of conditional males (about 16%), however, differs from that expected by the present model (50%). This difference between observation and expectation might be due to sampling error in the establishment of the original nematode cultures, or to simplifying assumptions in the model.

In conclusion, the models show that when ESD is not an option, a female bias is selected as an increasing function of the probability of being isolated. When ESD is an option, selection favors an equal mixture of females and conditional males independent of the probability of being isolated, provided this probability is between zero and one.

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