

POPULATION GENETICS OF A PARASITIC CHROMOSOME:
THEORETICAL ANALYSIS OF PSR IN SUBDIVIDED POPULATIONS

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Abstract.—An assemblage of non-Mendelian sex ratio elements occurs in natural populations of the parasitoid wasp *Nasonia vitripennis*. These include Maternal Sex Ratio (MSR), a cytoplasmic element that causes nearly all-female families, and Paternal Sex Ratio (PSR), a B chromosome that causes all-male families. The PSR chromosome is transmitted via sperm but causes destruction of the paternal chromosomes (except itself) shortly after egg fertilization. Owing to haplodiploidy, this results in the conversion of diploid (female) eggs into haploid (male) eggs. Paternal Sex Ratio is an extreme example of a selfish genetic element. Theoretical analysis shows that subdivided population structures reduce PSR frequency. Paternal Sex Ratio cannot exist in subdivided populations (with temporary mating demes lasting one generation) when foundress number is less than three. The equilibrium frequency of PSR depends strongly on fertilization proportion (x). In populations producing the Hamiltonian evolutionarily stable strategy ($x = [(N - 1)(2N - 1)] / [N(4N - 1)]$), PSR never achieves frequencies over 3% for any deme size. In contrast, if the population produces a high fertilization proportion (i.e., greater than 90%, as produced by MSR), then PSR can achieve frequencies over 90% when deme size is three or larger. Results also show that PSR selects against the MSR cytoplasmic element in populations with small deme size, which results in polymorphic equilibria for both elements.

There is growing evidence that a variety of genetic elements exist that have no function other than their own propagation within the genome and therefore can be considered "genomic parasites" or "selfish genetic elements" (Doolittle and Sapienza 1980; Orgel and Crick 1980; Werren et al. 1988). Parasitic genetic elements illustrate how selection can favor individual genes, even if they are detrimental to the organism. These genetic parasites can also have detrimental effects on populations carrying them. Thus, they can potentially be used to quantitatively study selection operating at different hierarchical levels—for example, gene, individual, and population levels of selection. So far, few studies have investigated the effect of hierarchical selection on parasitic elements.

Paternal Sex Ratio (PSR) is a nonvital supernumerary chromosome that occurs in some natural populations of the parasitic wasp *Nasonia vitripennis* (Werren et al. 1987; Nur et al. 1988; Werren 1991). The PSR chromosome is the most extreme

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example of a selfish genetic element so far described (Godfray and Harvey 1988). Males who carry this chromosome fail to transmit their genetic material (other than PSR) to the next generation because PSR destroys the paternal set of chromosomes, except itself, in the egg shortly after fertilization (Werren et al. 1987). Like other hymenopterans, *Nasonia* has haplodiploid sex determination. Therefore, the result of PSR action is that diploid fertilized eggs, which would have developed into females, are converted into haploid PSR males. The new haploid complement is maternally derived, and it will subsequently be destroyed in the next generation because it is associated with PSR. Thus, PSR "jumps" from one haploid set to another, always destroying the genome with which it is associated. This characteristic imparts a drive to the chromosome under certain population structures, as will be shown below.

Nasonia adjust the sex among their offspring in response to changes in local population structure in ways that are generally consistent with sex ratio theory (Wylie 1966; Walker 1967; Holmes 1972; Werren 1980, 1983; but see Parker and Orzack 1985; Orzack and Parker 1986). Indeed, sex ratio evolution in *N. vitripennis* (and other organisms with subdivided populations) has been a focus of debate in the controversy over levels of selection because it can be interpreted in terms of either individual selection or group selection (Colwell 1981; Charnov 1982; Werren 1983; Wilson 1983; Nunney 1985; Maynard Smith 1987a).

In addition to this "normal" sex ratio adjustment of *N. vitripennis* (which is presumably under autosomal genetic control), an assemblage of non-Mendelian sex ratio distorters occurs in the wasp, including (1) Son-Killer, a maternally transmitted bacterium that prevents the development of unfertilized (male) eggs (Skinner 1985; Werren et al. 1986; Gherna et al. 1991), (2) Maternal Sex Ratio (MSR), a cytoplasmically inherited agent of unknown etiology that causes female wasps to produce nearly 100% daughters (Skinner 1982, 1983), and (3) Paternal Sex Ratio (Werren et al. 1987; Nur et al. 1988; Werren 1991).

As well as obvious negative effects on the wasp genome, PSR also can have negative effects on populations carrying it. If it becomes common in a population the number of females (and therefore reproductive potential of the population) is severely reduced. In the extreme case in which PSR goes to or near fixation, populations carrying it will go extinct.

Nasonia vitripennis is a small parasitoid wasp that lays its eggs into the pupae of various fly species (Whiting 1967). Evidence indicates that *N. vitripennis* has a subdivided population structure in nature (Skinner 1983; Werren 1983). Thus, the PSR chromosome apparently has antagonistic selective pressures operating on it at different levels; gene-level selection favors its increase but it has negative effects on the fitness of individuals and populations. These characteristics make PSR an excellent system for quantifying the process of selection operating at different levels.

In this article we present a theoretical analysis of the population dynamics of PSR in subdivided populations and discuss how the force of selection may be hierarchically partitioned. Several predictions of the model presented here have been tested experimentally (Beukeboom and Werren 1992).

PATERNAL SEX RATIO IN RANDOM-MATING POPULATIONS

Theoretical dynamics of PSR in random-mating populations are surprisingly simple (Skinner 1987; Werren 1987a). A key feature determining its dynamics is that PSR is transmitted only to fertilized eggs. Therefore, its transmission rate is negatively related to the proportion of unfertilized eggs (males) produced. An increase in the proportion of unfertilized eggs also negatively affects PSR frequency because it results in a greater number of (normal) males who compete with PSR males for mates. These two features are present in the derivation below. If x is the proportion of eggs fertilized by inseminated females (in the absence of PSR these develop into females), t is the proportion of PSR male sperm that carry the chromosome, and w is the mating success of PSR males relative to normal males, and it is assumed that the remaining proportion $(1 - t)$ of eggs fertilized by sperm of PSR males develops into females, then the frequency of PSR in one generation (p) yields the frequency in the next (p') according to the formula

$$p' = pxtw/(pxtw + 1 - x) \quad (1)$$

and equilibrium frequency (p^*) is

$$p^* = [x(tw + 1) - 1]/xtw. \quad (2)$$

Estimates for t are between 0.9 and 1.0, and for w are 1.0 (Werren and Assem 1986; Beukeboom and Werren 1993). If these two parameters are assumed to equal 1.0, then the formula simplifies to $p^* = (2x - 1)/x$. The basic conclusion from the formula is that PSR cannot exist in panmictic populations unless the proportion of fertilized eggs (normal proportion females) is greater than 0.5. These results form a baseline for the following analysis of PSR dynamics in subdivided populations.

PATERNAL SEX RATIO IN SUBDIVIDED POPULATIONS

Assume a "metapopulation" composed of many temporary demes. Each generation, individual demes are formed of N inseminated "foundress" females, which produce progeny and then die. Mating occurs only among progeny of the natal deme, and then inseminated females disperse and randomly assort to form new demes. Therefore each deme lasts only one generation. This population structure was first modeled by Hamilton (1967) in studies of sex ratio selection under "local mate competition" and will henceforth be referred to as a "Hamiltonian" population.

For the purposes of the model it is assumed that females mate only once, or that if they do mate more than once they effectively use the sperm from only one male. This assumption generally holds for *Nasonia* (Assem and Visser 1976). We will further assume that PSR-inseminated and normal inseminated (non-PSR-inseminated) females produce equivalent family sizes, and that PSR and normal males have equal survival, which as an approximation is supported by data (Werren and Assem 1986; Beukeboom and Werren 1993). The metapopulation is composed of a very large (effectively infinite) number of demes.