

Influence of Complex Sex Determination on Demographic Stochasticity and Population Viability

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Introduction

Demographic and genetic factors are often hypothesized to interact to affect population viability (Gilpin & Soulé 1986; Lande 1988; Leberg 1991; Mills & Smouse 1994). Fixation of deleterious mutations and matings between relatives will be more common in small than in large populations. If population growth rate is depressed by these genetic factors, the duration of a population bottleneck will be lengthened. There may be, however, another way in which genetic variation and demography can interact to affect population viability. Rather than affecting the relative fecundity or survival of individuals, the genotypic composition of the population may directly affect a demographic parameter such as sex ratio. If so, genetic drift could increase variation in demographic characteristics and thus the probability that small populations might go extinct.

Populations with multiple-factor sex determination (MSD) segregate for three or more sex factors (Bull 1983). A diverse set of taxa, including fish (Kallman 1984; Wohlfarth & Wedekind 1991; Conover & Van Voorhees 1994), rodents (Fredga et al. 1976; Washburn & Eicher 1983; Bianchi et al. 1993), and insects (McDonald et al. 1978), exhibit MSD. Although thought to be rare, MSD undoubtedly occurs in other taxa; a lack of suitable sex-linked markers has made its true frequency difficult to assess (Bull 1983).

My objective was to use a simple stochastic simulation model to examine the hypothesis that small populations with MSD have an increased probability of extinction due to demographic stochasticity. If genetic drift of sex-determining factors results in increased population extinction, it represents a novel mechanism for relationships between genetic variation and population viability.

Methods

I used simulations to study the effects of three different systems of sex determination on the viability of small populations (Table 1). A simple sex-determination system (SSD) with male heterogamety (XY) was used as a control for comparisons with two MSD systems. In the first MSD system, three major factors, W , X , and Y , interact to determine sex (Table 1). This system is modeled after the WXY system of sex determination observed in platyfish, *Xiphophorus maculatus*; Kallman 1968, 1984). A similar system occurs in several rodents, but the YY genotypes are not viable (Fredga et al. 1976). Linked genes appear to produce small fitness differences among genotypes in *Xiphophorus* (Basolo 1994). The second MSD system is modeled after the F locus in the housefly (*Musca domestica*; McDonald et al. 1978). In this system females are either XX or are heterozygous for the autosomal allele F (Table 1).

I also used simulations to evaluate the viability of populations experiencing bottlenecks of size N . In each simulation initial sex ratios were 1:1, autosomes (F , f) and

Table 1. Genotype-phenotype relationships for three sex-determination systems examined in computer simulation models of population viability.

Sex-determination system	Genotype resulting in*	
	males	females
XY (control)	XY (1.000)	XX (1.000)
WXY	XY (0.828)	XX (0.498) WX (0.208) WY (0.294)
XY with autosomal F factor	$ffXY$ (0.828) $ffYY$ (0.172)	$ffXX$ (0.498) $FfXX$ (0.086) $FfXY$ (0.244) $FfYY$ (0.172)

*Frequencies of genotypes used in simulations examining the effect of population size on viability are provided in parentheses.

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XY factors segregated independently, genotypes had equal survival and fecundity, population size was constant, mating was random, and generations were non-overlapping. For a given N , I compared the proportions of 1000 replicate MSD and SSD populations that survived 10 generations. A short number of generations was chosen as the observation period because pilot studies indicated that the effects of MSD on extinction rates were only large for the first few generations after a population first became small. At the small population sizes for which sex determination affected viability, sex-determining factors were often lost as a result of drift, converting populations with MSD to SSD.

Populations went extinct only when all surviving individuals were the same sex. The effects of different sex-determination systems on population viability were examined for populations of 2–10 pairs of individuals. Males and females were drawn at random from an infinitely large population at the start of the simulated population bottleneck.

If sex-determining factors were rare, they would probably drift out of a population in the first one or two generations, obscuring the effects of MSD on population viability. Therefore, in comparisons of the effects of MSD on population viability at different N , the frequencies of F and W were set at 0.125. This initial frequency of F and W was chosen because it was halfway between their minimum and maximum equilibrium frequencies of 0 and 0.25. The genotypes of the sex-determining factors were also at neutral equilibrium frequencies in the population from which the founders of the simulated populations were chosen. If the initial conditions differed from equilibrium genotype frequencies, the return to an equilibrium condition could affect viability independently of the effects of drift that are of interest here. An iterative computer program was used to determine neutral equilibrium genotype frequencies satisfying equations provided by Bull and Charnov (1977), given that the frequencies of W and F were 0.125. These genotype frequencies (Table 1) were used as starting conditions in all comparisons of viability at different N .

I also examined the influence of variation in initial frequencies of sex-determining factors on population viability. In these simulations $N = 6$ because the effects of demographic stochasticity on population viability are greatest at small population sizes (Gilpin & Soulé 1986). The frequencies of W and F varied from 0 to 0.25 at intervals of 0.025. In these simulations, three pairs of individuals were chosen from an infinitely large population, at neutral equilibrium genotype frequencies, to found each simulated population. For a given frequency of W or F , an iterative computer program was used to determine neutral equilibrium genotype frequencies satisfying equations provided by Bull and Charnov (1977). Other aspects of the simulations were identical to the simulations comparing different population sizes.

The viability of populations that experienced a short but severe founder event was also examined. In these simulations, large populations were reduced to one or two pairs of individuals for a single generation. Each female in the population produced four young, so the population size would double each generation, assuming that the sex ratio was equal. Populations were allowed to grow for four generations, at which point they were sufficiently large to make extinction due to demographic stochasticity unlikely. The proportion of the 1000 replicate populations that became extinct within the four-generation period was compared among the three sex determination systems.

Results

The survival of populations was not significantly different for the two MSD systems at any of the population sizes examined (Table 2). Compared to SSD populations, small MSD populations were less viable (Table 2). The greatest relative reductions of the viability of WXY and $XYFf$ populations occurred when $N = 4$ (20% and 17%, respectively). The relative differences in survival probabilities decreased with increased population size and were different between SSD and MSD populations only when $N < 10$. For larger populations, extinctions due to stochastic variation in sex ratio were rare for all sex-determination systems.

The effect of the sex-determination system on extinction probabilities was not independent of the initial frequencies of the sex-determining factors (Fig. 1). Population viability was highest when the frequencies of F or W were high (>0.225) or low (<0.05). When the fre-

Table 2. Proportions (p) and standard errors (SE) of 1000 simulated populations with different sex-determination systems (XY, WXY, and FfXY) surviving 10 generations.

N^a	XY		WXY			FfXY		
	p	SE	p	SE	RV ^b	p	SE	RV ^b
4	0.262	0.014	0.210	0.013	0.802	0.218	0.013	0.832
6	0.726	0.014	0.664	0.015	0.915	0.660	0.015	0.909
8	0.928	0.008	0.880	0.010	0.948	0.892	0.010	0.961
10	0.976	0.005	0.958	0.006	0.982	0.966	0.006	0.990
12	0.995	0.002	0.991	0.003	0.996	0.987	0.004	0.992
14	0.999	0.001	0.997	0.002	0.998	0.996	0.002	0.997
16	1.000	—	0.997	0.002	0.997	0.999	0.001	0.999
18	1.000	—	1.000	—	1.000	1.000	—	1.000
20	1.000	—	1.000	—	1.000	1.000	—	1.000

^a N is the number of individuals in the populations.

^bThe relative viability (RV) of the MSD populations is the proportion of WXY or FfXY populations that survived 10 generations divided by the proportion of XY populations that survived the same period.

quencies of either W , F , or X were high prior to the bottleneck event, population viability was high and similar to populations that had only one mechanism of sex determination. Relative to populations with SSD, viability was reduced by as much as 14% at intermediate frequencies of F (Fig. 1).

Populations that experienced short bottlenecks also had higher extinction probabilities if they had MSD

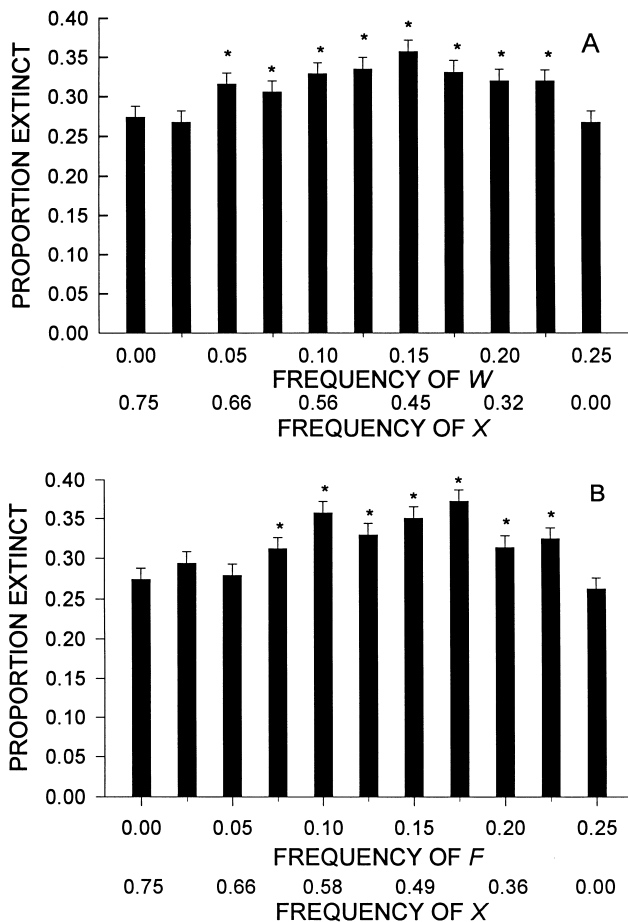


Figure 1. Probability of extinction for populations with WXY (a) and XYFf (b) sex determination at different initial frequencies of sex-determining factors. The frequencies of each pair of sex-determining factors on the horizontal axis are in neutral equilibrium at the start of the simulations. The frequency of X changes as a function of F and W at neutral equilibria. Probability of extinction is measured as the proportion of 1000 simulated populations with six individuals that did not survive 10 generations. Bars represent standard errors. Asterisks denote initial frequencies of sex-determining factors that resulted in higher probabilities of extinction than observed for populations with XY sex determination, based on empirically derived 99% confidence intervals.

rather than SSD. Populations founded by a pair of individuals from an WXY or FfXY population had about a 75% higher probability of extinction than if they were founded from an XY population ($\bar{x} \pm \text{SE} = 0.270 \pm 0.014$, 0.272 ± 0.014 , and 0.155 ± 0.011 , respectively). Although extinction probabilities were lower for populations founded with two pairs, if the founders were from an WXY or FfXY population the new population had an extinction probability of more than 150% higher than if they were from a SSD population ($\bar{x} \pm \text{SE} = 0.049 \pm 0.007$, 0.034 ± 0.006 , and 0.014 ± 0.004 , respectively).

Discussion

There are many MSD systems that could theoretically occur (Bull 1983); generalizing my results to these other systems would be risky. The effects on population viability of the two MSD systems I examined were remarkably similar.

Very small populations with MSD can experience large decreases in their viability relative to populations with SSD; relative differences decrease rapidly with increasing population size. The lack of effect of MSD on the viability of larger populations is not surprising because demographic stochasticity has its strongest effects on population viability at small population sizes (Gilpin & Soulé 1986, Lande 1988). In the case of variation in sex ratio, once $N \geq 10$ it was very uncommon for all the offspring produced by a generation to be the same sex, regardless of the sex-determination system being modeled. There is also frequency-dependent selection against biased sex ratios (Fisher 1930; Bull 1983). Severe drift, such as experienced in the smallest populations examined, is needed to overcome this selection and cause the population to go extinct.

Loss of genetic diversity is generally thought to have negative effects on a population's viability (Allendorf & Leary 1986; Gilpin & Soulé 1986). In the case of MSD, the greater the diversity of sex-determining factors, the lower the viability of small populations. Because the negative effects of MSD on population viability appear to be largest when all of the sex-determining factors are relatively common, it becomes pertinent to examine the frequency of these factors in natural populations. There is considerable variation in the frequencies of both X and F , as well as of several autosomal alleles that promote maleness, among populations of houseflies (Denholm et al. 1985; Tomita & Wada 1989), and many have multiple factors present in sufficient frequencies to affect viability at small population sizes. Although the data are less complete, frequencies of X and W vary widely among populations of *X. maculatus* (Kallman 1965).

Associations of genetic diversity and extinction are usually attributed to genotypic variation in individual

survival or fecundity (Gilpin & Soulé 1986; Mills & Smouse 1994; Lande 1995). In the MSD systems I modeled, the fecundity and viability of individuals of the same sex are not influenced by genotype. Rather, the viability of populations is reduced by the effects of genetic drift on demographic stochasticity.

Outbred populations experiencing severe bottlenecks are often thought to be more threatened by the loss of genetic variation and accumulation of deleterious mutations the longer they remain small (Gilpin & Soulé 1986; Lande 1988; Lande 1995). But the relative effects of MSD on extinction probabilities were strongest in populations that experienced a bottleneck for only one generation. The relative difference in viabilities of the MSD and SSD populations was greatest for short bottlenecks because genetic drift did not have sufficient time to cause loss of sex-determining factors before extinction occurred. Once one of their sex-determining factors is lost, the MSD populations would have the same extinction probabilities as SSD populations.

The sex-determination systems I modeled are characteristic of species that are not of particular concern to conservation biologists. It is likely, however, that some endangered species have MSD. For example, complex sex determination is found in several poeciliid fishes (Kallman 1984; Angus 1989), and many species in this family are threatened with extinction (Deacon et al. 1979). Unfortunately, except for the few species that have appropriate phenotypic markers, it is likely that for most taxa of concern to conservation biologists the intricacies of sex determination will remain poorly understood. But because the effects of MSD on population viability occur only in very small populations, my findings do not suggest a need for new management prescriptions. In general, the best defense against extinction resulting from all forms of demographic and genetic stochasticity is to increase the size of small populations.

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