Evolution of Sex Determination in the Conchostracan Shrimp Eulimnadia texana

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American Naturalist, Volume 141, Issue 2 (Feb., 1993), 329-337.

Vol. 141, No. 2 The American Naturalist February 1993

NOTES AND COMMENTS

EVOLUTION OF SEX DETERMINATION IN THE CONCHOSTRACAN SHRIMP *EULIMNADIA TEXANA*

Sassaman and Weeks (1993) describe the unusual mixed mating system of the clam shrimp *Eulimnadia texana* (Packard), in which both selfing and outcrossing occurs. There are three mating types in the system: ss males, Ss hermaphrodites, and SS hermaphrodites, in which the s and S factors are inherited as alternative genetic elements, with s recessive to S in determining sex. Both types of hermaphrodites are capable of selfing and outcrossing with males, but neither are able to fertilize the eggs of other hermaphrodites. Thus, the hermaphrodites only function as females when outcrossing. In the absence of males, Ss hermaphrodites (amphigenics) can, through selfing, produce all three types of offspring (in the approximate ratios of $\frac{1}{4}$ ss : $\frac{1}{2}$ Ss : $\frac{1}{4}$ SS) including male offspring, whereas the SS hermaphrodites (monogenics) breed true. Such a system is analogous to recessive androdioecy with hermaphrodites unable to fertilize one another (Ross and Weir 1976; Gregorius et al. 1983).

In this note we develop a population-genetics model of this breeding system. We derive recursive equations to describe the dynamics at the mating locus under sex-ratio selection, sex-specific viability selection, and inbreeding depression. In this model, only two equilibria are possible: fixation on homozygous hermaphrodites (outcrossing absent) and a polymorphism containing all three mating types. The conditions under which the polymorphism is stable therefore determine the conditions under which we expect to find males in the population. There will be a cost of outcrossing (generally known as the cost of sex) incurred by such a population that produces males as well as hermaphrodites (Williams 1975; Maynard Smith 1978), which must be balanced by some cost of selfing, such as inbreeding depression (Charlesworth 1980; Uyenoyama and Waller 1991*a*, 1991*b*, 1991*c*), in order to account for the continued presence of males. Thus, this system provides a framework in which to study the relative costs of outcrossing and of selfing.

THE MODEL

Our model can be considered an example of a class of models in which mating preferences exist (see, e.g., O'Donald 1980); here, mating for hermaphrodites is

Am. Nat. 1993. Vol. 141, pp. 329–337.

TABLE 1

Overview of the Mating System

Type	Frequency	Sex	Mode of Reproduction
ss	u	Male	Outcrossing with hermaphrodites
Ss	v	Hermaphrodite	Outcrossing with males and selfing
SS	w	Hermaphrodite	Outcrossing with males and selfing

a choice between individuals whose genotype is ss (males) or one's own genotype (Ss or SS) through selfing. This model tracks the adult frequencies (u, v, and w where $u + v + w = 1$) of the three mating types (ss, Ss, and SS, respectively) after selection, as in table 1. We assume that the population has discrete generations that consist of mating, offspring production, and viability selection. We set the viability of males to $1 - \sigma$ with $-\infty \leq \sigma \leq 1$ relative to the viability of hermaphrodites. Furthermore, inbreeding depression reduces the viability of all individuals produced by selfing by an amount, δ. We assume that the fraction of an hermaphrodite's eggs that will be fertilized by outcrossing depends on the probability that an hermaphrodite encounters a male, which will be proportional to the frequency of males in the population (u), specifically, a proportion αu, where $0 \leq \alpha u \leq 1$ of the eggs will be fertilized by the male sperm. Except where explicitly stated, we will further assume that α is a constant ($0 \leq \alpha \leq 1$) that measures the proportion of eggs that a mated hermaphrodite fertilizes with male sperm or, equivalently, α may be the proportion of hermaphrodites that will mate with a male once he is encountered. Of all the remaining eggs, that is, those in hermaphrodites that did not mate and those in hermaphrodites that did mate but were not fertilized by the male sperm, a proportion β, where $0 \leq \beta \leq 1$, will be self-fertilized. If β equals one, then all the remaining eggs will be self-fertilized. If β is less than one, a certain proportion ($[1 - \beta][1 - \alpha u]$) of eggs will remain unfertilized. Thus, as we would expect, the fecundity of an hermaphrodite is increased if she is more likely to outcross (increased αu) or if she is more successful at fertilizing her own eggs (increased β). Before these zygotes reach reproductive age, they experience viability selection, with outbred males having a relative viability of $1 - \sigma$, inbred males having a viability of $(1 - \sigma)(1 - \delta)$, outbred hermaphrodites having a viability set to one, and inbred hermaphrodites having a viability of $1 - \delta$. The parameters in the model are summarized in table 2. We can now derive the adult frequencies in one generation as a function of those in the previous generation:

$$Tu' = (1 - \sigma)\left[\frac{\alpha uv}{2} + \frac{\beta(1 - \delta)v(1 - \alpha u)}{4}\right],$$

$$Tv' = \frac{\alpha uv}{2} + \alpha uw + \frac{\beta(1 - \delta)v(1 - \alpha u)}{2}, \tag{1}$$

TABLE 2

MATING TABLE

	FREQUENCY	VIABILITY*	OFFSPRING		
			ss	Ss	SS
Mating type:					
Ss with ss	αuv	1	½	½	0
SS with ss	αuw	1	0	1	0
Ss selfed	$\beta v(1 - \alpha u)$	$(1 - \delta)$	¼	½	¼
SS selfed	$\beta w(1 - \alpha u)$	$(1 - \delta)$	0	0	1
Sex			♂	⚥	⚥
Viability†			$(1 - \sigma)$	1	1

* Viability of an individual produced by selfing relative to one produced by outcrossing.

† Viability of males relative to hermaphrodites.

and

$$Tw' = \frac{\beta(1 - \delta)v(1 - \alpha u)}{4} + \beta(1 - \delta)w(1 - \alpha u)\,,$$

where T is a normalizing factor (the sum of the right-hand sides). This model is similar to other models of recessive androdioecy (Ross and Weir 1976; Gregorius et al. 1983) except that in our model the amount of outcrossing depends explicitly on the frequency of males, not all eggs are necessarily fertilized, and viability selection is acting.

The recursions, equation (1), have two equilibria: fixation on monogenic hermaphrodites ($w = 1$) and the polymorphic equilibrium defined explicitly by

$$\hat{u} = \frac{\alpha - 2\beta + 2\beta\delta - \alpha\sigma}{\alpha(2 - 2\beta + 2\beta\delta - \sigma)}, \tag{2a}$$

$$\hat{v} = \frac{2(\alpha + 2\beta - 2\beta\delta - 2\alpha\beta + 2\alpha\beta\delta)(\alpha - 2\beta + 2\beta\delta - \alpha\sigma)}{\alpha(2 - 2\beta + 2\beta\delta - \sigma)f_1}, \tag{2b}$$

and

$$\hat{w} = \frac{\beta(\alpha + 2\beta - 2\beta\delta - 2\alpha\beta + 2\alpha\beta\delta)(2 - \sigma - \alpha + \alpha\sigma)}{\alpha(2 - 2\beta + 2\beta\delta - \sigma)f_1}, \tag{2c}$$

where

$$f_1 = (\alpha\beta\sigma - \alpha\beta\delta\sigma - \beta\sigma + \beta\delta\sigma - 2\alpha\sigma - \alpha\beta + \alpha\beta\delta - 2\beta + 2\beta\delta + 2\alpha).$$

The ratio of hermaphrodites to males at the polymorphism, equation (2), is given by

$$\frac{\hat{v} + \hat{w}}{\hat{u}} = \frac{\alpha + 2\beta - 2\beta\delta - 2\alpha\beta + 2\alpha\beta\delta}{\alpha - 2\beta + 2\beta\delta - \alpha\sigma}. \tag{3}$$

Clearly, the adult sex ratio will generally not be even. In fact, the sex ratio is always biased toward hermaphrodites unless males are sufficiently more fit than hermaphrodites. It is straightforward to show that the polymorphism defined by equation (2) exists and is locally stable whenever

$$\alpha(1 - \sigma) > 2\beta(1 - \delta) . \tag{4}$$

When the inequality in condition (4) is reversed, the polymorphic equilibrium is unstable and the fixation point $\hat{w} = 1$, where only selfing monogenic hermaphrodites are present and there is no outcrossing, is locally stable. Presumably, global convergence occurs to the equilibrium that is locally stable using a given set of parameters; numerical iteration (of 10,000 randomly chosen parameter sets and starting conditions) bears this out, but it has not been proved analytically. Condition (4) has an intuitive interpretation. The left-hand side represents the advantage of producing males (and outcrossing), which is high if the fecundity through outcrossing (α) is high and if the relative viability of males ($1 - \sigma$) is high. Similarly, the right-hand side represents the advantage of selfing, which is high when the fecundity through selfing (β) is high and the viability of selfed offspring ($1 - \delta$) is high. There remains the factor of two, which arises from the intrinsic twofold advantage of selfing (a twofold cost of outcrossing). This advantage follows from the fact that, in the absence of viability and fecundity differences, a selfing hermaphrodite will produce the same total number of offspring as a couple composed of an hermaphrodite and a male and will therefore produce twice as many offspring per individual parent. As expected, inbreeding depression aids in the maintenance of males, whereas viability selection against the males hinders their maintenance.

The above results corroborate the analysis performed by Lloyd (1977) on phenotypic models of selection. According to Lloyd (1977), the average equilibrium fitness of a male must equal that of an hermaphrodite in a one-locus model such as ours. Using table 2 and the method of Lloyd (1977), the relative fitness of a male is

$$(1 - \sigma)(v + w)\alpha = (1 - \sigma)(1 - u)\alpha , \tag{5}$$

while the relative fitness of an hermaphrodite is

$$\alpha u + 2\beta(1 - \delta)(1 - \alpha u) . \tag{6}$$

These fitnesses will equal one another (eq. [5] = eq. [6]) only at the equilibrium defined by equation (2a). Note, however, that since the analysis of Lloyd (1977) is based on phenotypic fitnesses and explicitly ignores the underlying genetics, it cannot be used to determine the different genotypic frequencies within a sex (eqq. [2b] and [2c]) and is not, generally, a replacement for the specific dynamics of the model (eq. [1]).

THE DATA

Our model makes both qualitative and quantitative predictions regarding the breeding system of *Eulimnadia texana*. Its accuracy may be measured by whether those predictions are reasonable in light of the biology of these shrimp. When collecting data, it will often be easier to determine the mating type frequencies than the parameters for this model. Therefore, we can rewrite equation (2), assuming that the system is at equilibrium, as

$$\sigma = \frac{2\hat{u}\hat{v} + \hat{v} + 4\hat{u}^2 - 4\hat{u}}{\hat{v}(1 - \hat{u})} \tag{7}$$

and

$$\alpha = \frac{\beta(1 - \delta)\hat{v}}{\hat{u}[2\hat{w} + \beta(1 - \delta)\hat{v}]},$$

which may be rearranged to give

$$\beta(1 - \delta) = \frac{2\alpha\hat{u}\hat{w}}{\hat{v}(1 - \alpha\hat{u})}.$$

These formulas may now be used to fit the data already provided by Sassaman and Weeks (1993).

Sassaman and Weeks (1993) characterized the frequency of genotypes in a population (Portal 1) from southeastern Arizona. Of 308 individuals reared from the site, 20% were male ($u = 0.2$). Among a subsample of 49 hermaphrodites genotyped by rearing their selfed progenies, 37 were amphigenic (Ss) and 12 were monogenic (SS). Thus, of the total population, we estimate that 60% were Ss hermaphrodites ($v = 0.6$) and 20% were SS hermaphrodites ($w = 0.2$). Unfortunately, these estimates reflect the extent of viability selection under laboratory conditions rather than selection under natural conditions (the latter might be measured in an appropriate study). Further, these estimates are based on a fairly small number of hermaphrodites. Nevertheless, we demonstrate how the model can be tested by inserting these values into equation (7), assuming that the population is near equilibrium. Hence, we estimate that $\sigma = 0.42$ and that $\alpha = [15\beta(1 - \delta)]/[2 + 3\beta(1 - \delta)]$ or equivalently that $\beta(1 - \delta) = 2\alpha/(15 - 3\alpha)$. Several other lines of evidence suggest that viability selection may act against males. Strenth (1977) has documented higher male mortality than hermaphrodite mortality in natural populations of *E. texana,* and Sassaman and Weeks (1993) have inferred a slightly higher male mortality among selfed progeny even under laboratory conditions. In order to compensate for this male mortality and ensure the maintenance of males, $\beta(1 - \delta)$ must be about an order of magnitude smaller than α, as shown in figure 1. Thus, most eggs must be fertilized by males when males are present (and many eggs must go unfertilized when males are absent) or inbreeding depression must be rather high. That hermaphrodites outcross when males are available appears to be the case from the data of Sassaman and Weeks (1993) and from the dependence on male frequency of the apparent inbreeding levels in natural populations (Sassaman 1989).

These inferred parameter values suggest that while there may be strong viability selection acting against males, the tendency of hermaphrodites to use male sperm rather than their own, in combination with inbreeding depression, compensates

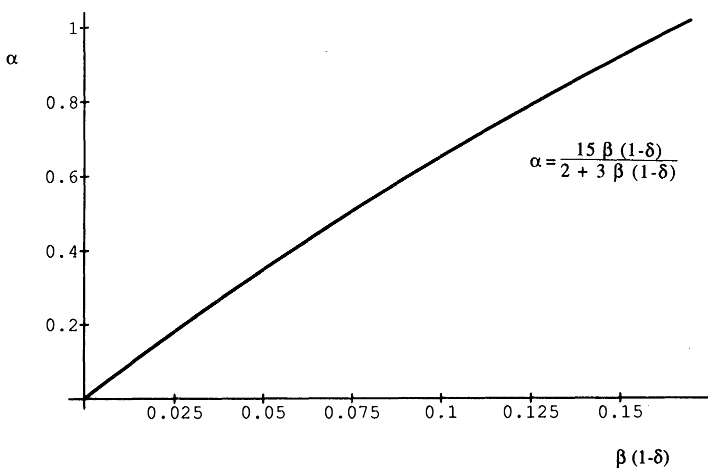

FIG. 1.—The values of α and $\beta(1 - \delta)$ that are consistent with the data and the model (using eq. [7]).

for both the cost of outcrossing and the lower viability of males. That inbreeding depression promotes the maintenance of males in this system helps to explain this androdioecious system. In other androdioecious systems in which hermaphrodites are cross-fertile, inbreeding depression is avoided even in the absence of males, and other factors must suffice to maintain males (Lloyd 1975; Charlesworth and Charlesworth 1981).

FREQUENCY-DEPENDENT MALE FERTILITY

We have assumed above that α is a constant that is less than one in value, to reflect the probability that an hermaphrodite fertilizes her eggs with male sperm once a male is randomly encountered. In reality, α need not be constant but might be a function of the population composition. Hermaphrodites may be more likely to accept sperm from males when males are rare (or common). Furthermore, males may actively seek out hermaphrodites so that the proportion of hermaphrodites that encounter males is greater than the frequency of males (u). In fact, α may be quite arbitrary as long as (αu) is always less than or equal to one so that the proportion of eggs fertilized by males is never greater than one. At one extreme, all of the hermaphrodites' eggs may be fertilized through outcrossing as long as there is at least one male in the population ($\alpha u = 1$ for all u). In this case, the population will become dioecious with no selfing and with heterozygotic females the generation after a male appears. We do know, however, that not all hermaphrodites outcross when males are present (Sassaman and Weeks 1993, table 4). Consider, then, that when males are rare ($w \sim 1$), they mate with $\alpha_{w\sim 1}$ hermaphrodites on the average ($\alpha_{w\sim 1} > 1$) but that this amount decreases according to some unspecified function (subject to $\alpha u \leq 1$) as males become more common. Then it is fairly easy to see (from eq. [4]) that males will be maintained in the population as long as

$$\alpha_{w \sim 1} > \frac{2\beta(1 - \delta)}{(1 - \sigma)} .$$

In general, then, if males, when rare, are fairly fecund, they will be maintained in the population despite the twofold cost of producing males. Even if $\beta(1 - \delta)$ is equal to one (no cost of selfing) and males are less viable (say, half as viable as hermaphrodites), males may still be maintained if each rare male mates with four or more hermaphrodites. If the hermaphrodites were cross-fertile rather than selfing only, the rare males would have to compete with the hermaphrodites in order to copulate and would therefore be less likely to mate with several hermaphrodites ($\alpha_{w \sim 1}$ would be lower), which is less favorable for the maintenance of males. Experiments that aim to determine the relationship between the proportion of eggs that are fertilized by outcrossing and the frequency of males within a population would be extremely valuable. These empirical findings could then be used to fine-tune the model discussed above.

CONCLUSIONS

We have presented a model in which the unusual mating system of *Eulimnadia texana* is investigated. The system will equilibrate either at a polymorphism defined by equation (2) or at fixation on the SS mating type, depending on whether $\alpha(1 - \sigma) > 2\beta(1 - \delta)$ holds or is reversed, respectively. This condition compares the advantage of outcrossing to that of selfing. To illustrate, consider the S fixation state, where the population is composed solely of SS hermaphrodites that reproduce through selfing. Since such a population does not produce males, this population does not pay the cost of sex. This cost (Williams 1975; Maynard Smith 1978) refers to the fact that the reproductive unit is the couple under outcrossing, whereas it is the individual hermaphrodite under selfing. Assuming that both reproductive units produce the same number of offspring on the average, outcrossing will "cost" more (generally twice as much) since more resources will be required to produce a couple than an individual. A population of SS hermaphrodites will nevertheless pay some cost of sex if they produce both sperm and eggs (the cost of meiosis and differentiated sex organs relative to mitosis). However, the cost of producing both male and female gametes should be small relative to the cost of producing both male and female individuals (see also Bell 1982). We have discussed several factors that are able to compensate for this cost of outcrossing and lead to the maintenance of males within the population. These factors include high inbreeding depression (large δ), low self-fertility (small β), high male viability (small σ), or a high fecundity of males especially when rare (large α). If *E. texana* were a classic case of androdioecy in which the hermaphrodites were cross-fertile, then outcrossing would occur in the absence of males and males could not be maintained to avoid inbreeding depression. Furthermore, the fact that *E. texana* hermaphrodites are cross-sterile makes it plausible that rare males are highly fecund since they are the only individuals able to provide sperm. If rare males are highly fecund and fertilize more than two hermaphrodites on the average, then males can be maintained despite the twofold cost of sex and even in the absence of other advantages to outcrossing such as the avoidance of inbreeding. These considerations make the evolution of androdioecy from a hermaphroditic system more likely when the hermaphrodites are selfing only, as in the case of *E. texana,* than when they are cross-fertile.

ACKNOWLEDGMENTS

This material is based on work supported under a National Science Foundation Graduate Fellowship to S.P.O. and National Institutes of Health grant 28016 to M.W.F. We would like to thank J. Bull, D. Goldstein, H.-R. Gregorius, M. Nordborg, and P. Wiener for their helpful comments on this manuscript. We are extremely grateful to D. Charlesworth for her detailed suggestions, especially her recommendation that we include inbreeding depression within the model and relate our analysis to that of D. Lloyd (1977).

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Submitted July 1, 1991; Revised January 22, 1992; Accepted February 12, 1992

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Associate Editor: Deborah Charlesworth