VARIATION IN THE STRENGTH OF MALE MATE CHOICE ALLOWS LONG-TERM COEXISTENCE OF SPERM-DEPENDENT ASEXUALS AND THEIR SEXUAL HOSTS

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In several asexual taxa, reproduction requires mating with related sexual species to stimulate egg development, even though genetic material is not incorporated from the sexuals (gynogenesis). In cases in which gynogens do not invest in male function, they can potentially have a twofold competitive advantage over sexuals because the asexuals avoid the cost of producing males. If unmitigated, however, the competitive success of the asexuals would ultimately lead to their own demise, following the extinction of the sexual species that stimulate egg development. We have studied a model of mate choice among sexual individuals and asexual gynogens, where males of the sexual species preferentially mate with sexual females over gynogenetic females, to determine if such mating preferences can stably maintain both gynogenetic and sexual individuals within a community. Our model shows that stable coexistence of gynogens and their sexual hosts can occur when there is variation among males in the degree of preference for mating with sexual females and when pickier males pay a higher cost of preference.

Among asexual vertebrates, a variety of different reproductive modes exist, lying along a continuum from fully asexual to nearly sexual reproduction (Hellriegel and Reyer 2000). Bisexual hybridogenic frogs (*Rana esculenta*) fall closest to the sexual end of the continuum (Hellriegel and Reyer 2000). Both male and female hybridogenic frogs premeiotically exclude one parental genome, clonally pass the other genome on to gametes, and then reconstitute a "hemiclonal" diploid hybrid genome by mating with a parental species (Schultz 1969; Graf and Pelaz 1989). Certain hybridogenic fish (e.g., *Poeciliopsis* spp.), which also produce hemiclonal offspring, fall farther from the sexual end of the continuum because they avoid the production of males (Vrijenhoek et al. 1977). Further still along the continuum are gynogenetic hybrid salamanders and fish (e.g., *Ambystoma* spp., *Phoxinus* spp., *Poecilia* spp.), which, like the unisexual hybridogens, are all female and require sperm from a parental species for reproduction. Unlike the hybridogens, however, gynogens produce fully clonal diploid offspring and require sperm only to stimulate egg development (Goddard et al. 1989, 1998). Certain hybrid lizards (e.g., *Lacerta unisexualis*) are parthenogenic and, therefore, represent the extreme asexual end of the continuum, requiring no parental input for reproduction (Darevsky et al. 1989; Echelle et al. 1989), although reproduction in some parthenogenic lizards is facilitated by behavioral cues resembling sexual reproduction (Crews et al. 1986).

Of the approximately 50 species of asexually reproducing vertebrates, nearly all are known to be of hybrid origin (Dawley and Bogart 1989). Hybrid asexual vertebrates share several interesting characteristics. The hybrids are typically ecologically similar to their parental species (they generally have overlapping

ecological niches and likely compete), they must (with the exception of the parthenogens) coexist with a parental species, and in systems with all-female hybrids they inherently have twice the reproductive output relative to a bisexual parental species. How, then, do the hybrids not outcompete the parentals given the potential benefits of hybrid vigor and the avoidance of producing costly males (Agrawal 2006)?

Asexual hybrids with sperm dependence present additional challenges to coexistence. All else being equal, if sexual males do not limit the sperm available to asexual hybrids by discriminating between asexual and sexual females when choosing a mate, the competitive success of the asexuals will ultimately lead to the extinction of both forms. Because males gain no fitness from mating with sperm-dependent asexual hybrids (Schlupp et al. 1994; Goddard et al. 1998), one should expect males to evolve a preference for conspecific sexual females. Preference for conspecific mates has been detected in a number of sperm-dependent asexual systems (Moore and McKay 1971; Abt and Reyer 1993; Schlupp et al. 1998; Engeler and Reyer 2001; Dries 2003), although it is not universal (Balsano et al. 1981; Balsano et al. 1985; Woodhead and Armstrong 1985; Schlupp et al. 1991). This preference, where it exists, is also not absolute. Of course, if absolute preferences had evolved, sperm-dependent asexuals would not persist and so would not be observed. Presumably, costs of preference and/or insufficient time have prevented the evolution of absolute preferences in those systems in which asexuals and sexuals persist together. Explaining the coexistence of sperm-dependent asexuals with sexually-reproducing sperm donors is a considerable challenge for evolutionary biologists.

Two types of hypotheses explaining coexistence in systems with sperm-dependent asexuals have been proposed (Schlupp 2005). First, niche separation hypotheses suggest that, although sperm dependence necessitates habitat overlap between asexuals and sexual species, there may be enough niche separation to reduce competition to a degree that facilitates coexistence (Vrijenhoek 1979; Schley et al. 2004). When the asexuals are of hybrid origin, their ecological niche may be intermediate between or on the margins of the parental niches. Occasionally, asexuals might hit upon an ecologically successful phenotype that breeds true in the absence of sex, which Vrijenhoek (1979) called the "frozen niche variation" hypothesis for the occasional success of asexual clones.

The second type of hypothesis suggests that the effect of preference by sexual males for sexual females may become more intense as asexuals become more common. The resulting frequency-dependent selection against asexuals can limit the growth of asexual populations and allow coexistence. For example, Moore (1976) has shown that coexistence can be maintained if it is assumed that males become more picky as asexuals become more common.

Moore (1976) modeled coexistence in a system with unisexual hybridogenic fish in the genus *Poeciliopsis*. Males in this system have been shown to prefer to mate with conspecific females, but subordinate males show reduced mate discrimination and will mate with hybridogenic females (Moore and McKay 1971). As a result, when the abundance of hybridogens relative to sexual fish in a given location is low, there are many subordinate males, and the hybridogen population can increase in numbers rapidly. This increase is held in check by reduced numbers of subordinate males as sexuals become rarer (males become, on average, pickier when rare). Stable coexistence in Moore's (1976) model is dependent on a simple assumption that male preferences select more strongly against asexuals as asexuals rise in frequency, resulting in the fecundity of hybridogens exhibiting negative frequency dependence, which stabilizes coexistence.

A model by Heubel et al. (2009) of coexistence in a system with the gynogenetic fish *Poecilia formosa* has shown that, similar to the model by Moore (1976), coexistence can be maintained if the gynogens become more sperm limited as they become more common. Their finite population model considers both the effect of the strength of male mate preference and male fertilization efficiency. When males are highly efficient, a single male can fertilize many females. The model by Heubel et al. (2009) shows that stable coexistence is possible only when sperm is limiting and when male mate preference is sufficiently strong for this limitation to affect gynogenetic females much more than sexual females. Unlike the model by Moore (1976) described in the preceding paragraph, there is no assumption in the model by Heubel et al. (2009) that males become pickier as gynogens become more common. Stable coexistence in the model by Heubel et al. (2009) depends on gynogens being more sperm limited than sexual females when gynogens become common. Heubel et al. (2009) noted that, in their model, the range of values for the preference and male efficiency parameters that leads to stable coexistence is very small and the parameter values in this range are possibly unrealistic. Also, the frequency of sexuals at the coexistence equilibrium was very low, so that coexistence is unlikely to be stable on an evolutionary time scale due to stochastic perturbations in population size. Long-term coexistence would therefore depend on metapopulation dynamics (Kokko et al. 2008); indeed, other authors have suggested that dispersal between patches can play an important role in allowing coexistence, especially if asexuals "follow" sexual species from patch to patch (Hellriegel and Reyer 2000).

In this article, we present a model motivated by a desire to understand the coexistence of gynogenetic hybrids and sexually reproducing parental fish in the genus *Phoxinus*. In our model, like the model by Heubel et al. (2009), males are not assumed to become pickier as asexuals become more common, and the asexuals' ecological niche does not differ from that of

the sexuals. A novel hypothesis emerges from our model to explain the coexistence of sperm-dependent asexuals and sexually reproducing species: variation among males in the degree of preference for conspecific females can lead to stable coexistence as long as pickier males pay a higher cost of preference. In essence, a coevolutionary rock–paper–scissors dynamic arises, with asexuals spreading in populations with unpicky males, followed by the spread of more choosy males and the decline of the asexuals, followed by the decline in frequency of males bearing costly preferences, leading the cycle to begin again. Moreover, in the model considered, this dynamic approaches a stable equilibrium with all three types present (asexuals, picky sexuals, and less-picky sexuals).

The Model

MATE CHOICE IN PHOXINUS

Hybrid *Phoxinus* are the product of hybridization between *P. eos* Cope, 1861, and *P. neogaeus* Cope, 1867 (New 1962). The hybrids have been shown to reproduce gynogenetically, requiring sperm from a male of either parental species to stimulate egg development but not for its genetic constitution (Goddard et al. 1998). This mating system is summarized in Figure 1. Recent work investigating the origin of *Phoxinus* hybrids suggested that they have coexisted with their parental species for the last 50,000 years (Angers and Schlosser 2007), which corresponds to about 50,000 generations (Das and Nelson 1990; Powles et al. 1992). The hybrids and their parental species are widely distributed in lakes across most of Canada and northern USA. Both hybrids and parentals are abundant throughout their distribution, although hybrids typically coexist with only one parental species. Fertilization in *Phoxinus* is external, takes place among floating vegetation, and, although some degree of parental care is not impossible, there is no evidence that either parent tends the eggs after fertilization. Citing a presentation by Cooper at the first North American Wildlife Conference in 1936, Scott and Crossman (1979) report that males, attracted to a ripe female by her darting among vegetation, will dart into a mass of vegetation to join the female and, as a pair or group, struggle against the vegetation to complete the act of spawning. There is, therefore, opportunity for both males and females to choose whether to mate with a particular partner. The bright ventral coloration of males during breeding season suggests the existence of female mate choice (or male–male competition), but female mate choice is not relevant to the issue of coexistence in this case, as there are no male asexuals. There are no data on the tendency of males to prefer particular females. It is possible that slight differences in the pattern of horizontal stripes and in body size between female parental and hybrid *Phoxinus* might serve as cues for male mate choice.
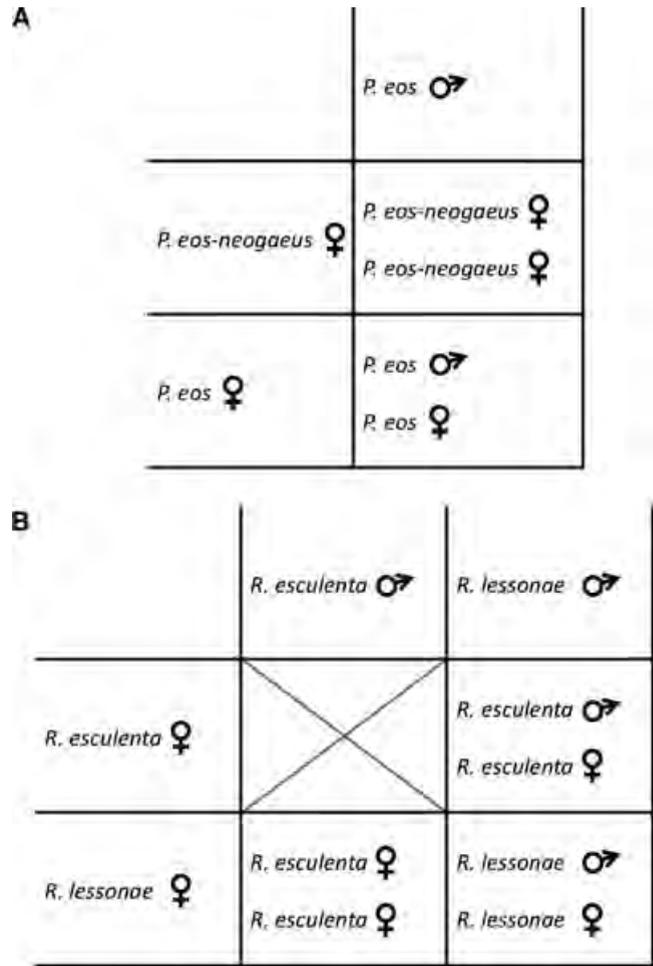
Figure 1. Summary of type and proportion of offspring produced from mating between sperm-dependent hybrids and sexually reproducing parental species. (A) Mating between gynogenetic *P. eos-neogaeus* and sexually reproducing *P. eos*. Note the 2:1 ratio of hybrid to parental daughters, assuming all females produce the same number of offspring. (B) Mating between hybridogenic *R. esculenta* and sexually reproducing *R. lessonae*, adapted from Engeler and Reyer (2001). Note the 3:1 ratio of *R. esculenta* to *R. lessonae* daughters, assuming all females produce the same number of offspring.

MODEL OF GYNOGEN-SEXUAL COEXISTENCE

The model borrows from the framework established by Kirkpatrick (1982) to explore the evolution of mate choice. There are three haploid genotypes: one gynogenetic (G, all female) and two sexual (E_1 and E_2, present in both males and females). Note that the two sexual genotypes represent a polymorphism within a single species, not two different sexual species (in our case, we arbitrarily envisioned *P. eos* as the polymorphic sexual species, hence the designation E_i). Males of genotype E_i prefer to mate with sexual females by a factor of a_i, according to the fixed relative-preference scheme of Kirkpatrick (1982). Thus, E_i males will mate with sexual females a_i times more frequently than with

asexual females, if presented with equal numbers of each. It seems reasonable to assume that these preferences are manifested as a lower rate of mating with asexuals, rather than a higher rate of mating with sexuals, but the mathematical equations are the same in either case. We arbitrarily assume that the E_2 males have a stronger preference for sexuals than E_1 males ($a_2 > a_1$). If the two types of males have equal preferences ($a_2 = a_1$), the results are equivalent to those observed with only a single sexual genotype. The effects of the E_1/E_2 polymorphism are assumed to be sex limited, affecting male mating preferences but having no effect on females.

Because we assume that females exert no mating preferences, the two types of males have equal mating success (i.e., the fraction of offspring sired by E_1 males is given by the frequency of E_1 among males, and the same holds for E_2 males, see Table 1). Similarly, there is no difference in mating success between E_1 and E_2 females, which are phenotypically equivalent. By contrast,

Table 1. Frequencies of mating among sexual genotypes, E_1 and E_2 (with frequencies x_1 and x_2, respectively), and the gynogenetic genotype, G (with frequency x_3). The degree of preference for sexual females by males of type E_i depends on the parameter a_i ($a_1 < a_2$). The frequencies of male and female genotypes prior to mating are shown as m_i and f_i, respectively. The T_m and T_f terms are normalizing factors for males and females, respectively, following the cost of preference (c), viability selection (s), and the twofold cost of sex. The term $\bar{a}_i$ represents the average mating preference of E_i males across the current population of females.

Mating pair		Mating frequency	Frequency of offspring type		
Male	Female		E_1	E_2	G
E_1	E_1	$\dfrac{m_1 f_1 a_1}{\bar{a}_1}$	1	0	0
E_1	E_2	$\dfrac{m_1 f_2 a_1}{\bar{a}_1}$	$1/2$	$1/2$	0
E_1	G	$\dfrac{m_1 f_3}{\bar{a}_1}$	0	0	1
E_2	E_1	$\dfrac{m_2 f_1 a_2}{\bar{a}_2}$	$1/2$	$1/2$	0
E_2	E_2	$\dfrac{m_2 f_2 a_2}{\bar{a}_2}$	0	1	0
E_2	G	$\dfrac{m_2 f_3}{\bar{a}_2}$	0	0	1

$$f_1 = x_1/T_f$$
$$f_2 = x_2/T_f$$
$$f_3 = 2x_3(1-s)/T_f$$
$$T_f = x_1 + x_2 + 2x_3(1-s)$$

$$m_1 = x_1/T_m$$
$$m_2 = x_2(1-c)/T_m$$
$$T_m = x_1 + x_2(1-c)$$

$$\bar{a}_i = a_i(f_1 + f_2) + f_3$$

because of male mating preferences, the fraction of offspring born to sexual females is higher than the proportion of sexual females by a factor:

$$X = freq(E_1 \text{ among males}) \times \frac{a_1}{\bar{a}_1} + freq(E_2 \text{ among males}) \times \frac{a_2}{\bar{a}_2}, \tag{1}$$

where $\bar{a}_i$ represents the average mating preference of E_i males across the current population of females:

$$\bar{a}_i = freq(\text{sexual females}) \times a_i + freq(\text{asexual females}) \times 1.$$

The fertility advantage of sexual females, X, depends on the frequency of E_1 and E_2 males and the strength of male mating preferences in the current population ($a_i/\bar{a}_i$).

Importantly, an assumption of our model is that the fertility advantage of sexual females, X, does not depend on the sex ratio and is the same whether males are rare or plentiful (assuming a given array of females so that $\bar{a}_i$ remains constant). This assumption was made to avoid introducing negative frequency-dependence directly into the structure of the model. That is, in our model, asexuals are not more or less likely to be fertilized relative to a sexual female as asexuals become common (and males become rare), either in the presence of E_1 males only or E_2 males only. Rather, our results are driven by the dynamical interaction between the three different genotypes (E_1, E_2, and G). In the next section, we discuss simulations that relax this assumption and allow the sex ratio to influence the relative fertilization success of asexual and sexual females.

Within our model, a generation begins with sexual genotypes E_1 and E_2 and gynogenetic genotype G at frequencies x_1, x_2, and x_3, respectively. These represent the overall offspring frequencies, but the frequencies among daughters and among sons differ because of the fact that gynogens produce only daughters. Assuming an equal sex ratio among sexuals and assuming that all gynogens are female, the frequency of E_1, E_2, and G among female offspring at the start of each generation is x_1/F, x_2/F, and $2x_3/F$, where $F = x_1 + x_2 + 2x_3$, whereas the frequency of E_1 and E_2 among male offspring is x_1/M and x_2/M, where $M = x_1 + x_2$. These assumptions give gynogens an automatic twofold competitive advantage for not producing males.

The fitness of gynogens and sexuals differ in two additional ways. First, due to viability selection, gynogens are $1 - s$ times as likely as sexuals to survive to the age of reproduction (where $-\infty < s < 1$). Depending on the value of s, viability selection can either augment or mitigate the twofold advantage of asexual reproduction. Second, due to the cost of preference, E_2 males are $1 - c$ times as likely as E_1 males to survive to reproduce (where $0 \leq c < 1$). After viability selection and selection against costly mate preferences, the frequencies of males, females, and all possible mating pairs are given in Table 1.

The frequencies of the sexual genotypes and the gynogen in each subsequent generation can be determined by iterating the following recursion equations:

$$x_{1,t+1} = \frac{a_1}{\bar{a}_1} \frac{x_{1,t}}{T_m} \left(\frac{x_{1,t}}{T_f} + \frac{1}{2} \frac{x_{2,t}}{T_f} \right) + \frac{a_2}{\bar{a}_2} \frac{1}{2} \frac{x_{2,t}(1-c)}{T_m} \frac{x_{1,t}}{T_f} \quad (2a)$$

$$x_{2,t+1} = \frac{a_1}{\bar{a}_1} \frac{1}{2} \frac{x_{1,t}}{T_m} \frac{x_{2,t}}{T_f} + \frac{a_2}{\bar{a}_2} \frac{x_{2,t}(1-c)}{T_m} \left(\frac{1}{2} \frac{x_{1,t}}{T_f} + \frac{x_{2,t}}{T_f} \right) \quad (2b)$$

$$x_{3,t+1} = \frac{1}{\bar{a}_1} \frac{x_{1,t}}{T_m} \frac{2x_{3,t}(1-s)}{T_f} + \frac{1}{\bar{a}_2} \frac{x_{2,t}(1-c)}{T_m} \frac{2x_{3,t}(1-s)}{T_f}, \quad (2c)$$

where T_m and T_f are normalizing factors for males and females, respectively, following the cost of preference, viability selection, and the twofold cost of sex (see Table 1). Setting $x_{i,t+1} = x_{i,t}$ and solving for x_i yields the following equilibrium frequencies:

$$\{x_1 = 1, x_2 = 0, x_3 = 0\} \quad (3a)$$

$$\{x_1 = 0, x_2 = 1, x_3 = 0\} \quad (3b)$$

$$\left\{ \begin{aligned} x_1 &= \frac{a_1 (a_1 - a_2 (1-c)) (a_2 - 2(1-s))}{(a_1 - a_2)(2a_2 (1-c)(1-s) - a_1 (2 - a_2 c - 2s))}, \\ x_2 &= \frac{a_2 (a_1 - a_2 (1-c))(2(1-s) - a_1)}{(a_1 - a_2)(2a_2 (1-c)(1-s) - a_1 (2 - a_2 c - 2s))}, \\ x_3 &= \frac{a_1 a_2 c}{2a_2 (1-c)(1-s) - a_1 (2 - a_2 c - 2s)} \end{aligned} \right\}. \quad (3c)$$

None of the above equilibria involve the coexistence of gynogens and parentals without the presence of both parental genotypes (both E_1 and E_2). Hence, our first result is that variation among males in the degree of preference for parental females is essential for coexistence in this model; there is no equilibrium that involves only one type of sexual (either E_1 or E_2) and asexuals.

The stability conditions for the three equilibria were determined by setting $x_1 = 1 - x_2 - x_3$ and evaluating the eigenvalues of the characteristic polynomial of the Jacobian matrix derived from equations (2b) and (2c). The stability conditions for the two equilibria lacking gynogens (3a and 3b) are straightforward and intuitive. When there are no gynogens and only E_1 sexuals present (3a), the E_2 genotype cannot invade because it is more costly, but the gynogens can invade as long as $2(1-s) > a_1$, that is, as long as the twofold advantage of not producing males times the fitness of the hybrids $(1-s)$ exceeds the mating bias that E_1 males have against asexuals. When no gynogens and only E_2 sexuals are present (3b), the E_1 genotype can invade as long as $c > 0$, and the gynogen can invade as long as $2(1-s) > a_2$. If $a_i = 2(1-s)$ exactly, the gynogens and only one of the sexual genotypes (E_1 or E_2) co-exist neutrally.

For the coexistence equilibrium (3c), the range of values for each parameter that yield positive frequencies for each genotype is limited to $a_1 < 2(1-s) < a_2$ and $0 < c < \frac{a_2 - a_1}{a_2}$. Under these conditions, not only is the coexistence equilibrium valid, it is also stable. Thus, stable coexistence between gynogens and sexuals requires not only variation in preference, but pickier males must suffer a cost relative to less-picky males. Although the equilibrium is stable when it exists, the eigenvalues are always complex, resulting in damped oscillations in the frequencies of sexual and gynogenetic genotypes. These dynamics can be visualized for a given set of parameter values as shown in Figure 2; they exhibit rock–paper–scissors behavior, with the asexual genotype G spreading in populations dominated by the less-picky E_1 genotype, the E_1 genotype spreading in populations dominated by the pickier (and more costly) E_2 genotype, and the picky E_2 genotype spreading in populations dominated by asexuals. Similar dynamics are observed, with a stable equilibrium reached via damped oscillations, in a diploid version of this model, regardless of whether the male preference gene is sex linked or autosomal (simulation data not shown).

The range of parameter values that allow stable coexistence between gynogenetic and sexual species is summarized in Figure 3. A notable result of this model, clearly evident in Figure 3, is that, to achieve and maintain coexistence, mate choice must not be too weak for a given strength of viability selection favoring gynogens (also, viability selection favoring gynogens must not be too strong for a given degree of pickiness among males). Note that stable coexistence is possible whether viability selection enhances ($s < 0$) or lessens ($s > 0$) the twofold advantage gained by gynogens for not producing males. If gynogens have relatively high viability (e.g., if they benefit from hybrid vigor), then E_2 males must be even pickier in their preference for conspecific females. If gynogens have relatively low viability (e.g., if they lack hybrid vigor, suffer from hybrid incompatibilities, or are is advantaged by low population-level genetic diversity) then coexistence is facilitated, in that males need not exhibit such a high degree of preference. In addition, if the cost of preference in E_2 males is high, E_2 males must be pickier to support the coexistence of sexuals and asexuals. A higher cost of preference also increases the equilibrium frequency of gynogens. Although E_1 males must be present to support coexistence between gynogens and parentals, having less-picky E_1 males increases the parameter space (in terms of both s and c) where coexistence is possible.

ALLOWING SEX RATIO TO IMPACT RELATIVE FERTILIZATION SUCCESS

Sex ratio is likely to be a critical determinant of fertilization rates in sexuals and asexuals. At one extreme, when males are plentiful, all females might be successfully fertilized, even though males prefer sexuals in each mating attempt. Thus, only when
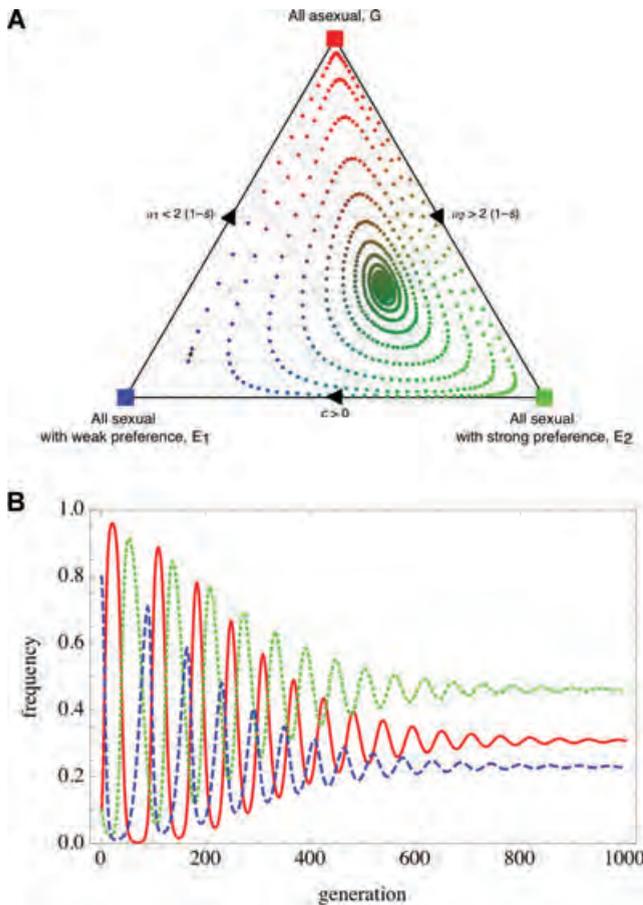
Figure 2. Illustrations of the behavior a system approaching stable equilibrium with coexistence of a gynogen, a sexual genotype with less- picky males, and a sexual genotype with picky males. (A) A de Finetti diagram (produced with Mathematica code available at http://mathgis.blogspot.com/2008/12/how-to-make-tenary-plot.html) in which closer proximity to a point of the triangle indicates higher frequency of the genotype at that point. Cycles are illustrated in a clockwise direction, with peak genotype frequencies occurring in a particular order (E_1, G, then E_2). The black arrows on the sides of the triangle indicate the behavior of the system when only two genotypes are present and when the adjacent inequalities are satisfied. (B) An example of damped oscillations approaching stability over 1000 generations. The curves illustrate the frequencies of the low preference sexual genotype E_1 (blue, thick-dashed curve), the high preference sexual genotype E_2 (green, fine-dashed curve), and the gynogen G (red, solid curve). The parameter values for the examples in both A and B are $a_1 = 1$, $a_2 = 2$, $s = 0.25$, and $c = 0.2$ (see text for explanation of parameters). These parameter values, as well as the equilibrium genotype frequencies shown in this figure, are equivalent to those used to parameterize and initiate the simulations (with $a_{max} = 6$) presented in this article.

males are rare might an asexual female fail to be fertilized. We used individual-based simulations to explore whether our results were robust to including the potential influence of fluctuations in sex ratio, with asexuals remaining unfertilized more often when males are rare (as in Heubel et al. 2009). In these simulations (Supporting information), each male was allowed to have a fixed number of mating attempts. In each attempt, the male preferred sexual females over asexual females, but as long as a female had received at least one mating attempt she was considered fertilized. Consequently, when males were common, all females were likely to mate, but as males became rare, it became more likely that no male had ever attempted to mate with a given asexual female (inducing negative frequency-dependent selection on the asexuals). These simulations showed that the rock–paper–scissors dynamic is displayed over a wide variety of parameter combinations. Furthermore, stable coexistence is possible for a broader range of parameter values when mating preferences varied than when they were fixed. We thus conclude that variation in male mating preferences is likely to be an important mechanism allowing the stable coexistence between gynogens and sexuals, even when negative frequency dependence might also be at play.

SIMULATION MODEL OF GYNOGEN-SEXUAL COEXISTENCE WITH MUTATION

We designed simulations to investigate what would happen to the coexistence of gynogens and sexuals if male preferences were allowed to evolve via mutation. The simulations mimic the analytical model, above, except that the preference genotype of each sexual individual (a_i) changes in increments of ± 0.05 due to mutations that occur at frequency μ in each generation. In addition, the cost of preference is scaled according to the strength of preference of a given male. Specifically, when a male prefers to mate with conspecifics (i.e., when $a_i > 1$), then his fitness is reduced by a factor $1 - (a_i - 1)/(a_{max} - 1)$, so that a_{max} is the maximum strength to which preference can evolve before fitness declines to zero. When a male prefers to mate with gynogens (i.e., when $0 < a_i < 1$), then his fitness is reduced by a factor a_i. The cost of mating preferences can be adjusted in our simulations by altering the value of a_{max} (lower values of a_{max} correspond to preferences for conspecifics being more costly and vice versa). Each simulation began with 4000 gynogens and 6000 sexuals, with the population size ($N = 10,000$) held constant over time. The sexual population began with only two preference genotypes: two-thirds of sexual individuals had $a = 2$, whereas the remainder had $a = 1$. As in the analytical model, the viability of gynogens is $1 - s$ relative to sexuals; in the simulations reported, we set $s = 0.25$, reducing the twofold advantage of asexual reproduction.

In our simulations, we investigated the effects of varying the mutation rate and, separately, the cost of preference. We ran 10 replicate simulations of five different parameter combinations for 20,000 generations (summarized in Table 2). For the parameter values explored, our analytical model predicts stable coexistence of asexuals and sexuals for the initial population with two initial preference genotypes.
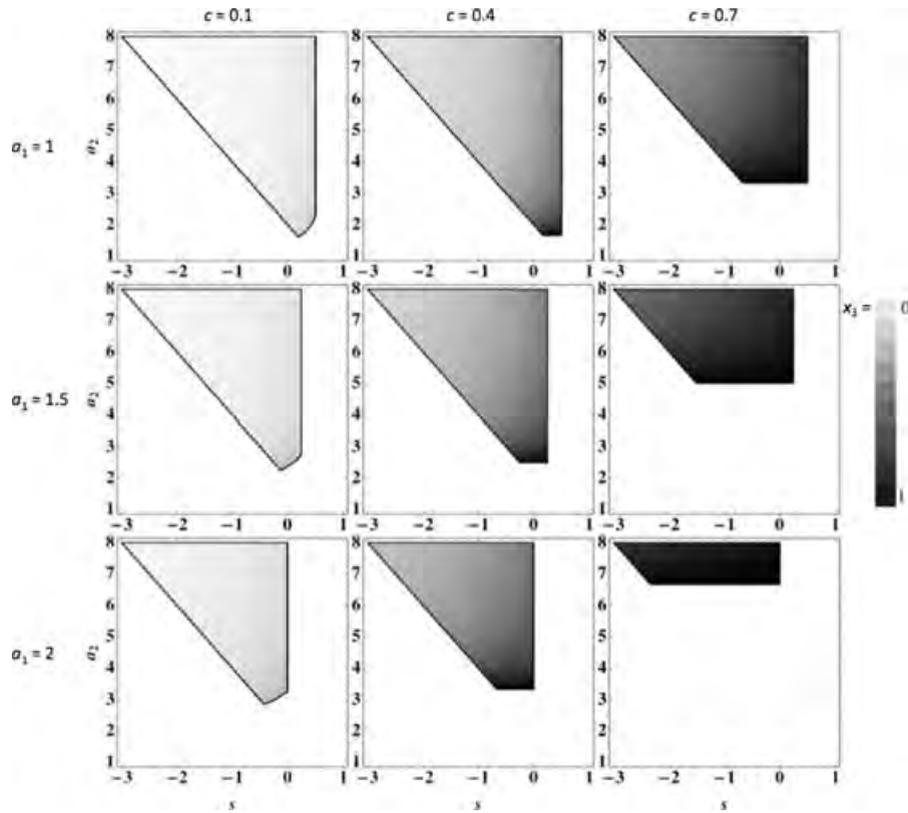
Figure 3. Parameter space allowing stable coexistence of gynogenetic and sexual individuals. Parameter combinations within the frame outside the black boundary do not allow a polymorphism to exist. In this region of the figures (pure white background), either gynogens dominate (i.e., $x_3 \rightarrow 1$) and the community goes extinct, or sexuals dominate (with the less costly male preference allele spreading to fixation, $x_1 \rightarrow 1$). The darker shading represents a higher equilibrium frequency of gynogens.

Our simulations showed that coexistence is maintained over many generations even in the face of evolving preferences. The replicates that ended in either extinction (fixation of gynogens) or loss of coexistence (fixation of sexuals) did so due to stochastic fluctuations in population numbers at the peaks or troughs of oscillations in genotype frequencies. There was no deterministic loss of coexistence with the addition of mutation. Replicate simulations with the lowest cost of preference had the lowest equilibrium frequency of gynogens, as predicted by our analytical model, and were therefore most prone to loss of asexuality (see Table 2).

Table 2. Summary of simulation parameters and results. Each set of parameters (i.e., each column) was used in 10 replicate simulations, each of which was run for 20,000 generations, or until the coexistence was lost or the populations went extinct. Parameter values common to all simulations and replicates: $s=0.25$, $N=10,000$, $a_{init.}=\{1, 2\}$ (see text for more details on parameters).

Simulation parameters					
Mutation rate (μ)	0.0001	0.001	0.001	0.001	0.01
a_{max}	6	11	6	5	6
Cost of preference[1]	moderate	low	moderate	High	moderate
Simulation results					
Maximum generations to extinction or loss of coexistence	>20,000	12,121	>20,000	>20,000	>20,000
Mean generations to extinction or loss of coexistence	16,773	7230	12,881	12,498	19,680
Minimum generations to extinction or loss of coexistence	11,709	4618	7369	4603	16,795
Num. reps. with loss of coexistence	4	10	6	4	1
Num. reps. with extinction	2	0	3	3	0

[1]Cost of preference depends on the strength of preference of a given male, and on the maximum possible strength of preference (a_{max}).
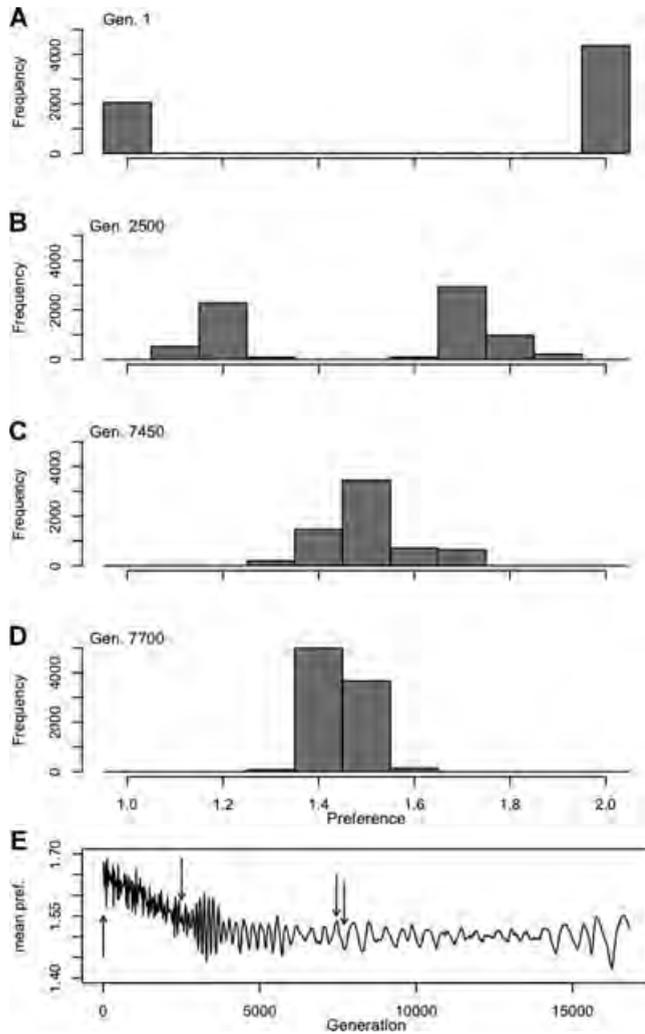
Figure 4. An example of the simulated evolution of mate preference. In this example, $a_{max} = 6$ and $\mu = 0.001$. Panels A through D illustrate the course of evolution from the start of the simulation until mutation–selection balance is reached. Panels C and D represent the distribution of strengths of preference at the peak and trough, respectively, of a cycle in mean strength of preference after mutation–selection balance has been reached. Panel E shows the change in mean strength of preference over generations, with the generations represented in panels A through D indicated with arrows.

In all simulations, the preference genotypes evolved toward $a = 1.5$, and when mutation–selection balance was reached the preferences oscillated within approximately ± 0.25 of $a = 1.5$ (see panel E in Fig. 4). At $a = 1.5$, the fitness of sexuals and asexuals exactly balance in the analytic model, so that the sexuals and asexuals coexist neutrally. Selection drives the preference values toward $a = 2(1 - s)$ because this strength of preference is high enough to give the sexuals a sufficient fertility advantage to balance the twofold cost of sexual reproduction (mitigated in our simulations by viability selection) and any stronger preference

would be more costly. The standard deviation in preference over the last 1000 generations was constant at about 0.06 when $\mu = 0.001$, but increased to 0.1 when $\mu = 0.01$. As such, the oscillations in mean preference around $a = 2(1 - s)$ (Fig. 4) are likely driven by the continual appearance of new mutations.

To elucidate the role of mutation in the above results, we ran an additional set of 10 replicate simulations without mutations ($\mu = 0$) but with initial variation in mating preferences (starting with equal proportions of preference genotypes $a = 1.45$, $a = 1.5$, and $a = 1.55$ in the sexual population and $a_{max} = 6$) (Fig. 5). When either the minimum or maximum preference genotype (i.e., either $a = 1.45$ or $a = 1.55$) was lost (in 7 of 10 replicates), the other extreme genotype (i.e., either $a = 1.55$ or $a = 1.45$, respectively) was lost in short order, leaving a monomorphic population with $a = 1.5$. Once preference variation was lost, the frequency of gynogens drifted neutrally, leading eventually to extinction of the system or loss of the asexuals. In one replicate (indicated in bold in Fig. 5), the intermediate ("optimal") genotype was lost first, which resulted in sustained oscillations in mean preference and gynogen frequency. These simulations thus confirm that variation in male mating preferences is key to maintaining the coexistence of sexuals and asexuals in this model and that mutation (and potentially migration) is a critical source of preference variation.

Discussion

Our model of mate choice among gynogenetic hybrids and a sexual parental species (as in the *Phoxinus* system) proposes that coexistence of sperm-dependent asexuals with their sexually reproducing sperm donors can be explained by the presence of heritable variation among males in their degree of preference for sexual females. Heritable variation in the degree of mate preference certainly exists in nature, but empirical studies investigating its presence in species coexisting with sperm-dependent asexuals are lacking. The prediction of our model, that substantial variation in male preferences should exist in long-standing gynogenetic-sexual systems, thus remains to be tested.

In addition to variation in male mate preference, our model requires that there be costs associated with increased mate preference, which is well documented in other systems (Gwynne 1989; Iwasa and Pomiankowski 1991; Magnhagen and Vestergaard 1991; Pomiankowski et al. 1991; Forsgren and Magnhagen 1993; Rowe 1994; Magnhagen 1995; Godin and Briggs 1996; Mappes et al. 1996; Booksmythe et al. 2008; Sakurai and Kasuya 2008). The strength of preference required to allow coexistence depends on the relative fitness of asexuals and sexuals. For example, the presence of hybrid vigor in asexuals augments the benefits from the twofold cost of sex and necessitates a higher degree of preference by males for conspecifics for coexistence to occur.
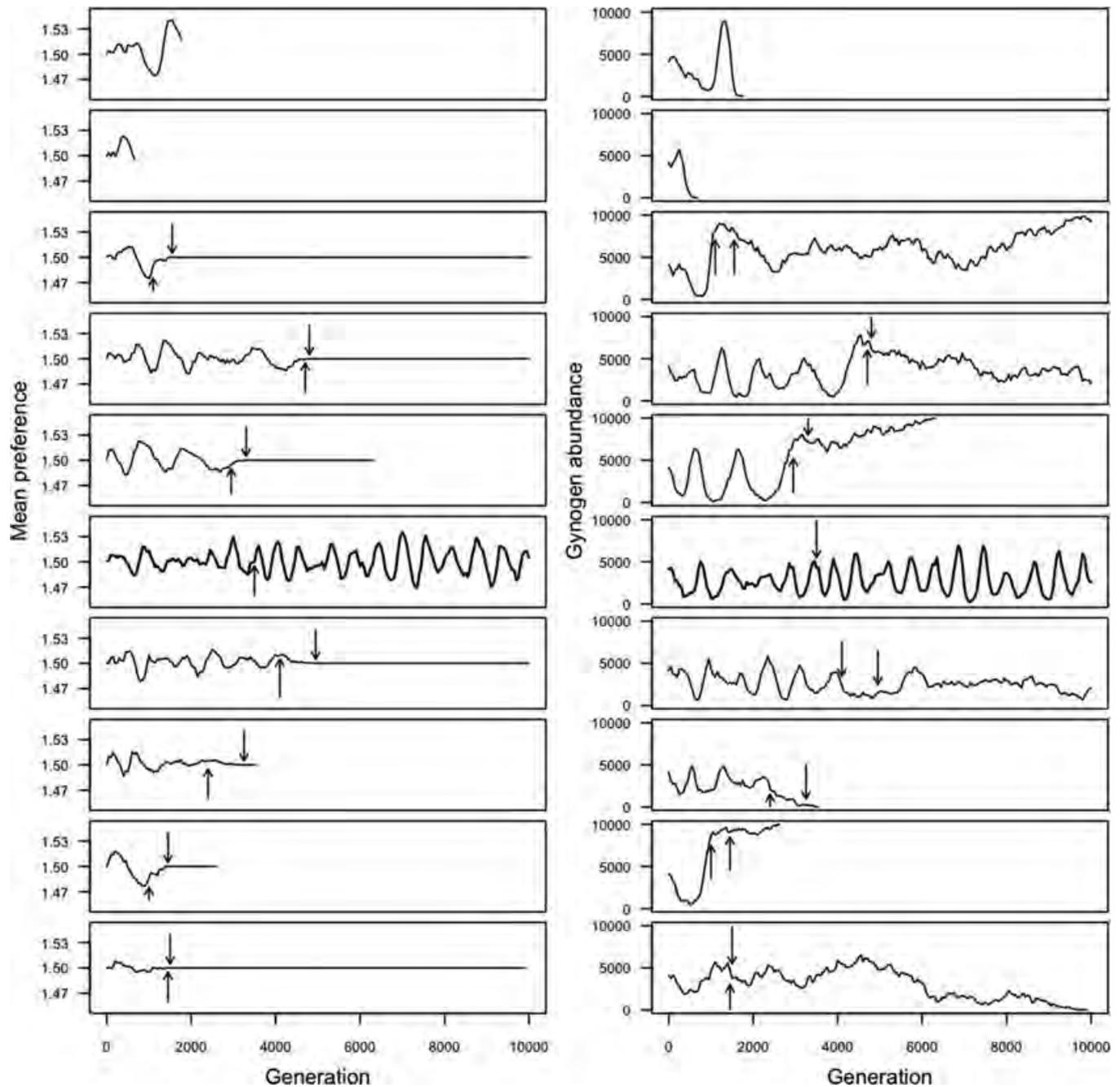
Figure 5. Replicate simulations of mate preference evolution with no mutation. Preference genotypes at the beginning of each replicate were *a* = 1.45, *a* = 1.5, and *a* = 1.55 in equal proportions in the sexual population. Each row shows the change in mean preference (left) and gynogen abundance (right) for a single replicate. Arrows indicate the generation in which one of the three preference genotypes was lost. The sixth replicate (shown in bold) is the only replicate where the *a* = 1.5 genotype was lost first.

Conversely, depressed fitness in asexuals mitigates the benefits from the twofold cost of sex and allows a low degree of preference by males for conspecifics to maintain coexistence. There is evidence in the *Phoxinus* gynogenetic system that gynogens do not differ from parentals in fecundity (i.e., they lack hybrid vigor) (Das and Nelson 1990) and that the hybrids experience a higher parasite load than parentals (i.e., there may be depressed hybrid

fitness) (Mee and Rowe 2006). Such depressed hybrid fitness, according to our model, facilitates coexistence.

Previous authors have also modeled the coexistence of sperm-dependent asexuals and their sexual hosts (Moore 1976; Hellriegel and Reyer 2000; Heubel et al. 2009). None of these authors have included variation in male preference, but all have shown situations in which stable coexistence is possible. In the

case of hybridogenic *Poecilliopsis* modeled by Moore (1976), the natural history of the system suggests that a heritable polymorphism in male mate preference (i.e., dominant and subordinate males) may contribute to the maintenance of coexistence. The model by Moore (1976) does not, however, explore this possibility.

In a model by Hellriegel and Reyer (2000) of hybridogenic water frogs (*R. esculenta*) and their sexual counterpart (*Rana lessonae*), coexistence is maintained by an interesting and potentially unique mechanism. Hybridogenic water frogs (*R. esculenta*) are not all female, and both male and female hybridogens require mating with a parental species (*R. lessonae*) for successful reproduction (Schultz 1969). This mating system is summarized in Figure 1. All females (both hybridogens and parentals) prefer to mate with *R. lessonae* males (Abt and Reyer 1993; Engeler and Reyer 2001). When *R. lessonae* are common, *R. esculenta* males mate mostly with *R. lessonae* females producing only female *R. esculenta* offspring and thereby causing the *R. esculenta* fraction of the population to increase. When *R. esculenta* are common, *R. esculenta* males mate mostly with *R. esculenta* females producing no offspring and thereby allowing the *R. lessonae* fraction of the population to increase. Consequently, when the preference of *R. lessonae* females is greater than the preference of *R. esculenta* females for *R. lessonae* males, the hybridogenic water frog mating system generates negative frequency-dependent selection against hybrids, which allows stable coexistence. A simplification of the model by Hellriegel and Reyer (2000) with nonoverlapping generations and infinite population size (see Supporting information) confirms that stable coexistence of hybridogens and sexuals in this model depends on the unique mating system of hybridogenic water frogs (Fig. 1) and not on any assumption of frequency-dependent preference or variation in male (or female) preference.

The model by Moore (1976) includes an explicit frequency-dependent mate preference function, where the preference by sexual males for sexual females becomes more intense as asexuals become more common. Similarly, in the model by Heubel et al. (2009) coexistence depends solely on gynogens becoming more sperm limited as they become common. In the model by Hellriegel and Reyer (2000) coexistence depends on the unusual and potentially unique mating system of hybridogenic water frogs.

Our model proposes an alternative mechanism for stable coexistence between sperm-dependent asexuals and sexually reproducing species. This mechanism involves nontransitive interactions arising from variation in preferences among males for sexual versus asexual mates. When gynogens are at high frequency in our model, males that strongly prefer to mate with sexuals, E_2, can spread despite the cost of being picky, because of a process akin to the Fisherian runaway process. Choosy E_2 males produce daughters carrying E_2 who are more attractive than the asexuals to the males in the population; if the preference is strong enough,

this attractiveness outweighs the advantages of asexuality and allows E_2 to spread. When the frequency of the gynogens becomes low, E_1 benefits from not paying a high cost of preference and increases in frequency. The decrease in gynogen frequency and the replacement of E_2 by E_1 reduces the relative attractiveness of sexual females and allows the gynogens to increase in numbers. Thus, this mechanism involves nontransitive interactions that generate a rock–paper–scissors game, which in our model ultimately reaches a stable equilibrium (see Fig. 2).

The rock–paper–scissors dynamics that we describe requires variation in preferences among males for sexual versus asexual mates. Although our model applies specifically to systems with sperm-dependent asexuals, similar rock–paper–scissors dynamics have been observed in several other systems, including male mating strategies among color morphs in side-blotched lizards (Sinervo and Lively 1996), host–parasite interactions in microbial systems (Kerr et al. 2006), and toxin-resistance interactions among bacteria (Kerr et al. 2002).

It is important to emphasize that our model allows high frequencies of both gynogens and sexuals at equilibrium over a wide range of parameter values. As such, the coexistence in our model is more likely to be stable over evolutionary time without the requirement for dispersal and metapopulation dynamics observed in previous models (Kokko et al. 2008; Heubel et al. 2009). Of course, the mechanisms maintaining gynogenetic-sexual systems need not be mutually exclusive; we have shown that combining variation in male mate preference with a mechanistic model of mating that causes the fertilization rate of asexual females to depend on the number of males in the population (akin to the model of Heubel et al. 2009) results in an expanded range of parameter values for which coexistence is possible (see Supporting information). We also expect that including a behavioral component such that males become more likely to mate with sexuals when they are rare (as in Moore 1976) would further promote coexistence in our model.

Some additional general conclusions about coexistence in systems with sperm-dependent asexuals can be drawn from the models discussed above. First, in our model as well as those by Moore (1976), Hellriegel and Reyer (2000), and Heubel et al. (2009), coexistence between a sperm-dependent asexual and a sexually reproducing sperm donor species depends on the presence of mate choice. Sexual species must prefer to mate with conspecifics. Second, coexistence is facilitated by the lack of hybrid vigor. This conclusion is evident in our model of the gynogenetic *Phoxinus* system (Fig. 3), as well as in models of a bisexual hybridogenic system (Hellriegel and Reyer 2000) and a unisexual hybridogenic system (Moore 1976). Coexistence may therefore be more common in systems with sperm-dependent asexuals where hybrid disadvantage mitigates the inherent population growth rate advantage of asexuals.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Parameter space allowing stable coexistence of hybridogenic and sexual individuals.

Table S1. Results of simulations showing the effects of sex ratio and variation in male mate preference on the coexistence of sperm-dependent asexuals and their sexual hosts.

Table S2. Frequencies of mating among sexual *R. lessonae* and the hybridogenic *R. esculenta* genotypes.

Supporting Information may be found in the online version of this article.

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Effects of sex ratio and variation in male mate preference on the coexistence of sperm-dependent asexuals and their sexual hosts

An important assumption in our analytical model is that the fertility advantage of sexual females over gynogens does not depend on male abundance (see main text). We designed simulations to investigate the effect of relaxing this assumption. The simulations mimicked our analytical model except that each male attempted to mate with H females. While in the model described in the main text male "mate preference" was determined by the parameter a, in these simulations we replaced a with a mechanistically explicit parameter, v, that determines a male's "visitation preference". A given male was v times more likely to attempt to mate with a sexual female than a gynogen. Any female that was visited multiple times, either by the same male or multiple males, was fertilized with the male sire chosen randomly from among the males that had visited her. Note that when $H \leq 1$, v is roughly equivalent to a because female fertilization success is limited by male mating attempts. By contrast, when $H > 1$, male mate preference (measured as the relative rate of fertilization of sexual versus asexual females, i.e., a) is effectively a function of both H and v. Critically, when $H > 1$, the fertility advantage of sexual females over gynogens decreases with increasing male abundance.

Each simulation began with 4000 gynogens and 6000 sexuals, with the population size ($N = 10\ 000$) held constant over time. The sexual population began with either one or two visitation preference genotypes. For simulations with only one preference type (i.e., no polymorphism), all sexual individuals had $v = \{1, 1.5, 2, 3, 4, 8, \text{or } 16\}$. For simulations that began with two preference types (i.e., those with polymorphism), half of

the sexual individuals at the beginning had $v = \{1.5, 2, 3, 4, 8,$ or $16\}$, and the remainder

had $v = 1$ (i.e., no preference). The viability of gynogens was $1 - s$ relative to sexuals,

and the viability of any male with $v > 1$ was $1 - c$. In the simulations explored, we set $s =$

0.25, $c = 0.2$, and $H = 5$ or 10. We ran 10 replicate simulations of 26 different parameter

combinations for 1000 generations.

The results of the simulations are reported in table S1, and the conclusions can be

summarized as follows. Without polymorphism in male preference and with no male

visitation preference (i.e. $v = 1$), gynogens take over and the system goes extinct. A

relatively low visitation preference can prevent the gynogen from taking over, but, with

low v, the sexuals remain at very low frequency. In our simulations, when $v = 1.5$, the

sexuals were lost due to stochastic frequency fluctuations after being driven to very low

frequency. The frequency of gynogens decreased with increasing v. With a high enough

value of v, gynogens were lost due to stochastic frequency fluctuations. Thus, without

polymorphism in male preference, there was only a limited range of values for v that

allowed coexistence in the face of stochastic fluctuations ($1.5 < v < 4$ for $H = 5$ and $1.5 <$

$v < 8$ for $H = 10$). Even when the cost of preference was increased substantially with

high v (e.g., $c = 0.5$), the gynogens did not gain enough of an advantage to persist

(simulation data not shown). Note that the model by Heubel et al. (2009) also examines

the effect of both male mating efficiency and mate preference using parameters akin to

our H and v, respectively. The results of our simulations without polymorphism

(described above) mirror the results of Heubel et al. (2009).

By contrast, the existence of variation in male preferences increased the range of

preference values allowing stable coexistence. This effect was observed when one male

type was very picky and the other male type was not. In these cases, coexistence was permitted with parameter values for which coexistence was not seen in the absence of male preference variation (i.e., when $4 \leq v$ for $H = 5$ and when $8 \leq v$ for $H = 10$). On the other hand, when both male types had low preferences for sexual females, the system tended to lose one male preference type, as we would expect from our analytical model when both male preferences are weak (see Figure 3). The mechanism allowing the maintenance of coexistence with variation in male preferences appears to be the same as that described in the main text: cycles in the frequency of preference types and gynogens appear that prevent the fixation of any one type (see main text). No such cycling is evident in simulations where coexistence is maintained without polymorphism. We thus conclude that the presence of variation in preference increases the range of parameter values for which coexistence is possible.

Mechanism of coexistence in hybridogenic water frogs

Mate choice in hybridogenic water frogs

Hybridogenic water frogs (*R. esculenta*) require mating with a parental species (*R. lessonae*) for successful reproduction (Schultz 1969). This mating system is summarized in figure 1. All females (both hybridogens and parentals) prefer to mate with *R. lessonae* males (Abt & Reyer 1993; Engeler & Reyer 2001). The preference among *R. lessonae* females for mating with conspecific males has been postulated to be selectively motivated due to the exclusion of the *R. lessonae* genome when the hybridogenic frogs produce gametes (the motivation for the preference of *R. esculenta* females is obvious, as offspring of *R. esculenta* males and females do not survive beyond the larval stage). Interestingly, the males do not show a preference for mating with female *R. lessonae*, presumably due to the low cost of wasting sperm (relative to eggs) and to the disadvantage of mating with hybridogenic females being balanced by a general preference among male frogs for larger females (female hybridogens are larger and more fecund than sexual females) (Engeler & Reyer 2001).

Model of bisexual hybridogen-sexual coexistence

In order to compare the requirements for coexistence in a gynogen-sexual system (main text) to the requirements for coexistence in the bisexual hybridogen-sexual coexistence, we analyzed a simplified version of a model by Hellriegel & Reyer (2000) that is analogous to our model. Our analysis of Hellriegel & Reyer's (2000) model has non-overlapping generations and an infinite population size (hence, density effects on tadpole survival and differences in survival and recruitment between various life history

stages are not included in our simplified version). Four different types of individuals are considered in the model: *R. lessonae* males and females (L_m and L_f) and *R. esculenta* males and females (E_m and E_f). *Rana lessonae* males and females are assumed to occur in equal proportions so the frequency of both male and female *R. lessonae* is $L/2$. *Rana esculenta* males and females may be found at different frequencies (E_m and E_f, respectively). Female *R. lessonae* prefer to mate with *R. lessonae* males a_L times more than *R. esculenta* males ($a_L \geq 1$). *Rana esculenta* females prefer to mate with *R. lessonae* males a_E times more than *R. esculenta* males ($a_E \geq 1$). Because preference does not vary within either sexuals or hybridogens, costs of preference are not included in the model (such costs might contribute to the relative fitness of sexuals vs hybridogens, as measured by the parameter s). Genotype frequencies in each generation depend on the frequency of each type of mating, the proportion of each type of offspring produced from each type of mating, and the average clutch size of *R. esculenta* females relative to *R. lessonae* females, given by $1 - s$ (where $-\infty < s < 1$) (see figure 1, main text, and table S2). Because no offspring are produced from mating between *R. esculenta* males and females, the following recursion equations are normalized by the sum of the offspring produced from all productive matings (M_t):

$$L_{t+1} = \frac{a_L L_t^2}{4 z_{L,t} M_t} \tag{4a}$$

$$E_{f,t+1} = \frac{L_t E_{m,t}}{2 z_{L,t} M_t} + \frac{a_E E_{f,t} L_t (1-s)}{4 z_{E,t} M_t} \tag{4b}$$

$$E_{m,t+1} = \frac{a_E E_{f,t} L_t (1-s)}{4 z_{E,t} M_t} \tag{4c}$$

Setting $L_{t+1} = L_t$ and $E_{i,t+1} = E_{i,t}$ and solving gives the following possible equilibria:

$$\{L = 1,\ E_f = 0,\ E_m = 0\} \tag{5a}$$

$$\left\{ \begin{aligned} L &= \frac{-a_L^2 - 2a_E + a_L a_E - 2a_E s - a_L a_E s}{a_L(-a_L - a_E + 2a_E s + a_L a_E s)}, \\ E_f &= \frac{(2 + a_L)a_E(-2 + 2s + a_L s)}{2a_L(-a_L - a_E + 2a_E s + a_L a_E s)}, \\ E_m &= \frac{a_E(-2 + 2s + a_L s)}{2(-a_L - a_E + 2a_E s + a_L a_E s)} \end{aligned} \right\} \tag{5b}$$

The stability of each equilibrium was determined by setting $L = 1 - (E_f + E_m)$ and evaluating the eigenvalues of the characteristic polynomial of the Jacobian matrix given by equations (4b) and (4c). The non-coexistence equilibrium (5a) is stable when $a_L > \frac{2(1-s)}{s}$, which is satisfied for any strength of conspecific mate preference when $s > \frac{2}{3}$. The coexistence equilibrium (5b) is valid and stable only when $a_L > a_E$ and the following conditions are satisfied:

$$a_L < \frac{2(1-s)}{s}$$

$$a_E < \frac{a_L^2}{(2 + a_L)(1-s)}$$

The range of parameter values that allow coexistence between bisexual hybridogens and a sexual parental species is summarized in figure S1. Persistent coexistence, in this case, requires that hybridogen fecundity (governed by the s parameter) is neither too high nor too low for a given degree of preference among *R. lessonae* females (the a_L parameter). Unlike the gynogenetic system, stable coexistence between hybrids and parentals in the bisexual hybridogenic system does not require variation among sexual males in their degree of preference, which is not included in equations (4). Stability in the bisexual hybridogenic system arises due to the unique mating system of hybridogenic water frogs (see figure 1, main text). When *R. lessonae* is common, *R. esculenta* males mate mostly with *R. lessonae* females, producing only female *R. esculenta* offspring and thereby causing the *R. esculenta* fraction of the population to increase. When *R. esculenta* is common, *R. esculenta* males mate mostly with *R. esculenta* females producing no offspring and thereby allowing the *R. lessonae* fraction of the population to increase. Consequently, when the preference of *R. lessonae* females is greater than the preference of *R. esculenta* females for *R. lessonae* males (i.e., $a_L > a_E$), the hybridogenic water frog mating system generates negative frequency-dependent selection against hybrids.

Table S1. Results of simulations showing the effects of sex ratio and variation in male mate preference on the coexistence of sperm-dependent asexuals and their sexual hosts. In these simulations, picky males were v times more likely to pair with (i.e., visit) a sexual rather than a gynogenetic female, and each male attempted H pairings ($H = 5$ in panel A, $H = 10$ in panel B). In the simulations with polymorphism in male mate preference, the least picky males had $v = 1$ (i.e., no visitation preference). All simulations ran for 1000 generations or until either the males or gynogens were lost (i.e., until extinction of loss of coexistence, respectively). The mean frequency of gynogens over the last 200 generations was averaged across replicates for each case where coexistence was maintained for > 1000 generations. Light shading indicates cases where coexistence was maintained for > 1000 generations without polymorphism. Dark shading indicates cases where coexistence was maintained for > 1000 generations with polymorphism in at least one replicate. Other parameter values were as follows: $N = 10000$, $c = 0.2$, $s = 0.25$ (see main text and SOI for further explanation of parameters and simulation conditions).

A ($H = 5$)

Visitation preference of pickiest males (v)		1	1.5	2	3	4	8	16
Mean generations to extinction or loss of coexistence	no poly.	11.1	60.6	> 1000	> 1000	122.9	14.9	7.3
	poly.		13.4	14.6	28.6	> 1000	> 1000	> 1000
Mean frequency of gynogens at equilibrium [1]	no poly.	0 (0)	0 (0)	0.68 (10)	0.36 (10)	0 (0)	0 (0)	0 (0)
	poly.		0 (0)	0 (0)	0 (0)	0.19 (10)	0.16 (10)	0.14 (10)

B ($H = 10$)

Visitation preference of pickiest males (v)		1	1.5	2	3	4	8	16
Mean generations to extinction or loss of coexistence	no poly.	12.1	55.7	> 1000	> 1000	> 1000	100.4	15.4
	poly.		14.4	17.8	see [2]	see [2]	see [3]	> 1000
Mean frequency of gynogens at equilibrium [1]	no poly.	0 (0)	0 (0)	0.84 (10)	0.73 (10)	0.66 (10)	0 (0)	0 (0)
	poly.		0 (0)	0 (0)	0.73 (10) [2]	0.66 (10) [2]	0.11 (4) [3]	0.13 (10)

[1] Numbers in brackets indicate the number of replicates in which coexistence persisted for > 1000 generations.
[2] In all replicates the low preference allele was lost and the frequency of gynogens equilibrated to the value found without polymorphism (coexistence maintained for >1000 generations).
[3] In 6 out of the 10 replicates the low preference allele was lost and the sexuals fixed, resulting in loss of coexistence (at 368 generations, on average). In 4 replicates, polymorphism was maintained and coexistence lasted for > 1000 generations.

Table S2. Frequencies of mating among sexual *R. lessonae* and the hybridogenic *R. esculenta* genotypes. The degree of preference for *R. lessonae* males by *R. lessonae* and *R. esculenta* females depends on the parameters a_L and a_E, respectively.

Mating pair		Mating	Relative numbers of offspring types			
Female	Male	frequency	L_f	L_m	E_f	E_m
L_f	L_m	$\dfrac{a_L}{z_L}\left(\dfrac{L}{2}\right)^2$	½	½	0	0
L_f	E_m	$\dfrac{1}{z_L}\dfrac{L}{2}E_m$	0	0	1	0
E_f	L_m	$\dfrac{a_E}{z_E}E_f\dfrac{L}{2}$	0	0	½$(1-s)$	½$(1-s)$
E_f	E_m	$\dfrac{1}{z_E}E_f E_m$	0	0	0	0

$$z_i = \left(E_m + a_i\frac{L}{2}\right)\left(E_f + \frac{L}{2}\right)$$
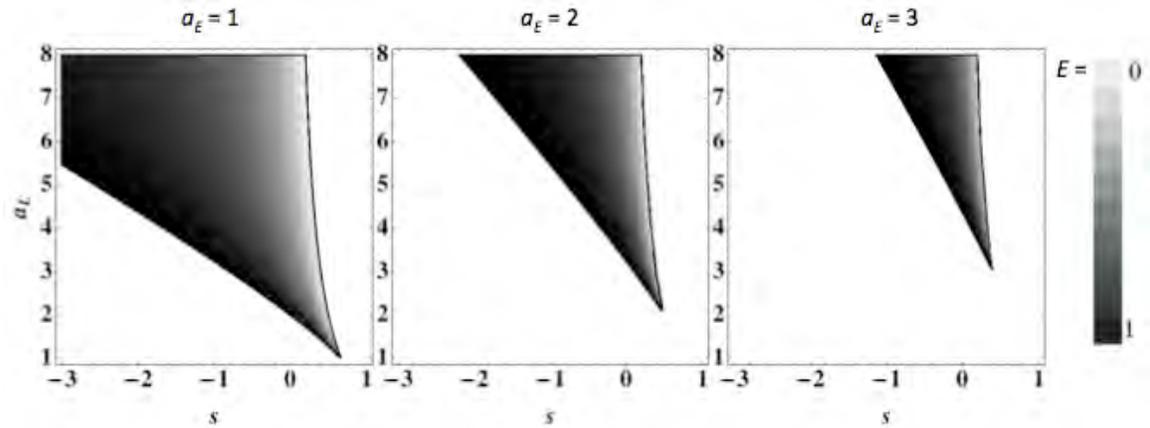
Figure S1. Parameter space allowing stable coexistence of hybridogenic and sexual individuals. Parameter combinations within the frame outside the black boundary do not allow a polymorphism to exist. In this region of the figures (pure white background), either hybridogens dominate (i.e., $E \rightarrow 1$) and the community crashes, or sexuals dominate (i.e., $L \rightarrow 1$) and the hybridogens cannot invade. The darker shading represents a higher equilibrium frequency of hybridogens.

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