

# ON LUCK AND SEX

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Sex has many costs with respect to asexual reproduction, so its ubiquity is a puzzle. There has been a continuing effort to identify general circumstances in which aspects of sex generate an evolutionary advantage over asexual reproduction. Here we focus on the generality that individuals can experience good and bad “luck” at various stages of their life history regardless of genotype, and on the interindividual nature of sex. Sexual outcrossing combines genetic information from individuals with potentially different experiences, so it is conceivable that sex might reduce the contribution of individual luck to noise in inheritance. In a simple way, we derive expressions for noise in inheritance in terms of some sources of within-generation ecological noise. We demonstrate that interindividual reproduction can indeed dampen the effects of ecological noise better than lone-individual modes, but there are conditions under which it does not. Empirical and theoretical work on plants, modeled here, suggest noise dampening conditions. Ecological noise dampening operates alongside other features of sex such as recombination and segregation and, because noise in inheritance weakens the role of selection in genetic change, we speculate that noise dampening may offer a benefit to be deducted from the costs of sex. We also suggest that the amount of selfing relative to outcrossing observed in natural populations may be influenced by the amount of individual-level ecological noise in a given habitat.

**KEY WORDS:** Cost of sex, ecological noise, genetic drift, outcrossing, reproductive strategies, self-fertilization.

Sexual reproduction incurs risks and costs including the making and fusing of gametes, the production of males, difficulty of finding a mate, risk of infection, risks of breaking up good gene combinations, and nonoptimal consequences of sexual selection (Crow 1999). Although particular features of sex such as having two parents or having differentiation among the sexes are clearly beneficial under specific ecological circumstances, it has proven difficult to identify advantages that hold over a wide enough range of circumstances to justify the ubiquity of sexual reproduction. The quest for general explanations is a matter of identifying a widespread circumstance paired with means by which known aspects of sex can generate an advantage relative to asexual reproduction. The advantage is usually sought in terms of how sexual reproduction might facilitate the maintenance and/or construction of genotypes that are enough better-adapted to pay for the costs of sex. This enduring puzzle has even forced consideration of the possibility that maintenance of sex may be a consequence of different mechanisms under different circumstances, acting independently and/or in synergy (West et al. 1999).

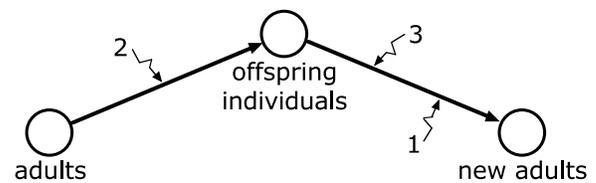
Nature’s variety can make definition of categories difficult. In his review Kondrashov (1993) chose amphimixis versus apomixis because they are clearer categories than sexual versus asexual reproduction. His choice reflects, and has reinforced, the tendency of evolutionary theorists to view sexual reproduction as reproduction-with-recombination. As Kondrashov pointed out, some amphimictic species have neither sexes of individual nor sexes of gamete. We note that in most species with sexes, the gametes being fused are from different individuals. And most of the costs of “sexual reproduction” listed above have to do with its interindividual nature. Here we focus on “interindividualness” rather than recombination, and examine the former for implications with respect to the evolution or maintenance of sexual reproduction.

Because different individuals necessarily occupy different locations in space and time, they can have differing experiences of the same habitat simply due to small-scale spatial heterogeneity in landscape and events. For example, in acquiring resources or incurring injury, individuals of both better- and worse-adapted

genotypes can have both good and bad “luck.” This individual-level ecological noise is certainly widespread, and by contributing to noise in the transmission of alleles from one generation to the next it weakens the role of selection in genetic change. We wondered whether combining genes from individuals with separate experiences of ecological noise can “average out” luck and thereby reduce noise in inheritance. To our knowledge the relative degree to which reproductive modes compound within-generation individual-level noise has not been addressed before. What is needed for the comparison is expressions of noise in inheritance in terms of parameters describing the effects of ecological noise on the individuals of a population, under different reproductive schemes.

Other contributors to noise in inheritance include genetic drift and Hill–Robertson interference, both of which have been well studied. Genetic drift (Wright 1945; Kimura and Maruyama 1963) is caused by the fact that, in a finite population, the new adult generation contains only a sample of all of the offspring producible by the previous adult generation. This sampling may over-represent inferior genotypes and under-represent superior genotypes, slowing selection or even causing maladaptive changes in gene frequencies. Selection acting in different directions at correlated loci is another source of noise in inheritance with respect to any of the loci (Hill and Robertson 1966; Felsenstein 1974). The reduction of this Hill–Robertson interference by recombination can facilitate adaptation (Barton 1995; Keightley and Otto 2006). Segregation reduces similar interference among whole chromosomes (Kirkpatrick and Jenkins 1989). We expect that any dampening of ecological noise would also facilitate adaptation.

To derive expressions for noise in inheritance in terms of individual luck, we modeled a population of annual hermaphroditic plants, which has a constant number of adults ( $N$ ). Because plants are sessile, genotype-independent individual-level noise is easily visualized as a consequence of spatial heterogeneity in landscape and events at the scale of individual plants. (But we note that motile organisms also experience ecological noise.) We consider three different reproductive modes: interindividual fertilization (Crosser), self-fertilization (Selfer, amphimixis that is not interindividual), and apomixis (Cloner, in which seeds are made by mitosis). A generic life history is diagrammed in Figure 1. In classical studies of drift, the  $N$  individuals of the new adult generation are each made from a pair of gametes drawn from an infinite gamete pool. This accomplishes two things: construction of offspring genotypes, and population regulation at constant size. Here we separate these steps, and model an explicit, finite, offspring pool (Fig. 1) produced from the limited reproductive resources of all individuals. We then choose  $N$  offspring at random from the pool to form the new adult generation, effectively creating a mortality rate proportional to the size of the offspring pool. We refer to this step as “simple density-dependence” (Fig. 1, source 1). It



**Figure 1.** A generic life history. The sources of noise in inheritance we consider are: (1) simple density dependence, (2) individual success in gathering reproductive resources, (3) spatial noise in offspring survival.

creates the sampling noise typically associated with genetic drift. The results using this structure are the same as the classical results when the pool of offspring individuals is very (infinitely) large, and into this generic structure it is easy to place additional sources of individual-level noise. Such noise can arise from many different processes operating at various life stages. We lump these into luck in fecundity of parents (Fig. 1, source 2), and luck in survival of offspring (Fig. 1, source 3). As examples, one plant might have its stem and/or leaves damaged by a cow, impairing the acquisition of reproductive resources, whereas another plant might be well-fertilized by the cow. And for no fault of genotype, plants might be located next to inhospitable habitat such as barren ground or a lake, or not, thus creating noise in the survival rate of individual plants’ dispersed seeds. (Similar assumptions could be made for many other organisms.) Luck in fecundity was assumed to result from luck in the acquisition of reproductive resources and was modeled as variance in the number of ova produced by an individual. Luck in the survival of progeny was modeled as a probability that all of a plant’s seeds survived to (or died before) the simple density dependence stage. The density dependence is then a subsetting of the surviving offspring to yield the constant adult population size.

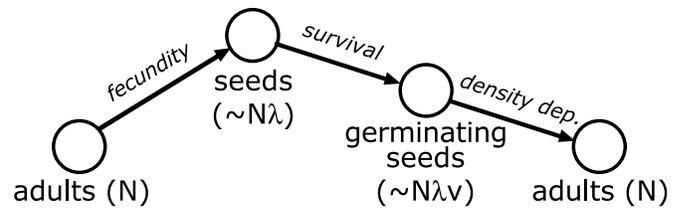
Plants are able to alter the portion of acquired resources they allocate to ova and pollen—when they have more resources they usually allocate relatively more to female function (Sarkissian et al. 2001). We characterized the Crosser strategy as having variable allocation such that pollen production is the same for all plants, and the amount of reproductive resources each plant manages to acquire is reflected only in the number of ova each produces. Later we consider a strategy in which ova and pollen are produced in a fixed ratio. Selfers do not need to produce as much pollen as outcrossers, and the Cloners would not need any pollen. So, compared with outcrossers, one would expect optimally adapted asexual strategies to allocate proportionally more reproductive resources to ova. In this article we examine only one factor, interindividualness, and do not simultaneously account for reallocation of resources among strategies. Another way to think of this work is that we are implicitly considering the problem of maintenance of sex and a possible benefit of sex compared to

strategies that are less interindividual. (Reversion to at least partial selfing is a frequent evolutionary occurrence in plants [Harder and Barrett 2006].) We discount the possibility that a single mutation could simultaneously produce both reversion to selfing (or cloning) and optimal resource reallocation, and assume that the sex-to-asex mutation comes first, and that evolution of reallocation of reproductive resources comes later. Thus the strategies would have initially identical resource allocation schemes. For these reasons, we model luck in fecundity as variance in the number of ova produced by a plant, for all reproductive strategies.

An allele frequency ( $p$ ) drifts because of variance in the change in  $p$  from one generation to the next. But instead of comparing variance in gene frequency, it is customary to compare the “variance effective population size,”  $N_e$ , for which  $p(1-p)/(2N_e)$  equals the observed variance of the allele frequency  $p$ . There is an extensive population genetics literature on  $N_e$  (Wright 1938; Kimura and Crow 1963; Crow and Kimura 1970; Ewens 1982; Crow and Denniston 1988). We note emphatically that in the  $N_e$  literature variance in “reproductive success,” “family size,” “offspring number,” and “successful offspring,” all refer to the variance of the distribution of “new adults” sensu Figure 1. This is not the same as the within-generation “luck in fecundity” or “variance in number of ova produced” with which we deal. Variance in “family size,” or in number of gametes that end up in new adults, already incorporates the consequences of all ecological noise-generating processes. This lumped result is a basic element of many  $N_e$  derivations. For example, it is well known that Crow and Kimura (1970) compiled expressions for variance effective population size for different modes of reproduction (p. 362). But in their “retrospective approach of defining the effective number” (p. 353) they start from the distribution of gametes contributed to the new adult generation—which as our results will show might already differ in variance among reproductive modes for individuals that are otherwise identical and under similar ecological circumstances. More recent work on  $N_e$  (Caballero 1994; Whitlock and Barton 1997; Wang and Caballero, 1999; Laporte and Charlesworth 2002) continues to skip within-generation noise as it deals with complexities such as population subdivision, sex and age classes, class-specific rates, and autosomal versus sex chromosome inheritance. To address our question about dampening of ecological noise we need expressions containing parameters describing sources of within-generation individual-level noise.

## Method

The particular life history we modeled is shown in Figure 2, along with approximate numbers of individuals at each stage. The negative binomial distribution was used to describe ova production because, unlike the Poisson distribution, its variance is not constrained to be the same as its mean. The negative binomial has two



**Figure 2.** The specific life history used, showing the numbers at each stage.  $N$  is population size,  $\lambda$  is mean fecundity,  $v$  is the probability of survival to germination. The fecundity, survival, and density-dependent processes all produce noise.

parameters: mean  $\lambda$ , and a parameter  $\omega$  that influences variance. When  $\omega$  is very large, the negative binomial is identical to the Poisson and has a variance of  $\lambda$ . As  $\omega$  decreases, the variance of the negative binomial increases, allowing representation of greater noise caused by individual luck in fecundity. A greater or lesser proportion of a plant’s seeds may survive only by accident of the plant’s location. An extreme form of such luck was modeled by introducing a parameter  $v$  describing the probability that all seeds survive from time of production until germination, after which the density dependence is considered to act. With probability  $(1-v)$  all seeds from a plant are lost before germination.

We denote as  $\sigma^2$  the variance in the number of copies of a focal allele from a given adult that make it into the next generation. That is a direct measure of noise in inheritance. We used moment generating functions (MGFs) to derive expressions for  $\sigma^2$  in terms of the parameters of the fecundity distribution ( $\lambda$  and  $\omega$ ) and probability of survival ( $v$ ) for each of the three breeding strategies: Crosser, Selfer, and Cloner. MGFs are a way to uniquely specify a probability distribution. There are established rules for producing the MGF of some compound distributions by transforming and combining the MGFs of their component distributions. And it is straightforward to derive the variance of a distribution from its MGF. The method is to start with the MGF describing the number of ova produced by an individual, and then move step by step through the life history outlined in Figure 2 successively building the MGFs to describe: the number of gametes of an individual that makes it into the offspring pool (seeds), the number of focal alleles in the offspring pool, the number of focal alleles that are in offspring that survive to germination and, finally, the number of focal alleles that survive the density-dependent mortality to make it into the new adult generation. From this final MGF the variance  $\sigma^2$  was then computed. The derivations assumed global pollination and that  $N$  is not very small. The analytical work was done using Mathematica (Wolfram Research Inc. 2001), and the results were checked with numerical simulations using R (R Development Core Team 2006). See the Appendix for a brief example of the procedure. A Mathematica notebook fully describing the methods for all results, and the R script, are in the Supporting Information.

**Table 1.** Variance in number of copies of a focal allele transmitted into the new adult generation ( $\sigma^2$ ) given only simple density dependence.

Crosser:	$1 - \frac{1}{\lambda} + \frac{3}{4\lambda}(1 - \frac{1}{3N})$
Selfer:	$1 - \frac{1}{\lambda} + \frac{1}{2}$
Cloner:	$1 - \frac{1}{\lambda}$

$N$  is the census size of the population,  $\lambda$  is mean fecundity. There is no variance in fecundity.

## Results

Our results are in the form of expressions for  $\sigma^2$ , and our figures compare the relative size of  $\sigma^2$  for one reproductive strategy versus another. As a conceptual baseline we first derived  $\sigma^2$  for no variance in fecundity (all individuals produce exactly  $\lambda$  offspring), and no individual variance in seed survival. Table 1 shows the results for simple density dependence only. The expressions reflect the reality that the gamete/offspring pool produced by a finite population is finite—there is a dependence on mean fecundity. Note that  $\sigma^2$  increases with mean fecundity because the greater the size of the finite offspring pool, the deeper the subsetting of that pool via density dependence to create the new adults. Cloner has the least noise in inheritance, which is approached by Crosser at large mean fecundity. Segregation contributes to the  $\sigma^2$  of both Crosser and Selfer, but for  $\lambda > 1$  (integer values, because each parent produces exactly  $\lambda$  offspring in this case), Selfer has the higher  $\sigma^2$  due to the greater variance in number of copies of focal alleles in Selfer offspring (many offspring have two copies or none).

Because we are modeling a population at constant size, the expected number of copies of a neutral focal allele in the new adult generation is 1. So variation of Poisson magnitude would mean a  $\sigma^2$  that is also 1. For  $\lambda > 2$  the Selfer variation cannot be that low, even in this (unrealistic) case without noise in either fecundity or survival.

**Table 2.** Variance in number of copies of a focal allele transmitted into the new adult generation ( $\sigma^2$ ) given simple density dependence, variance in fecundity, and noise in survival.

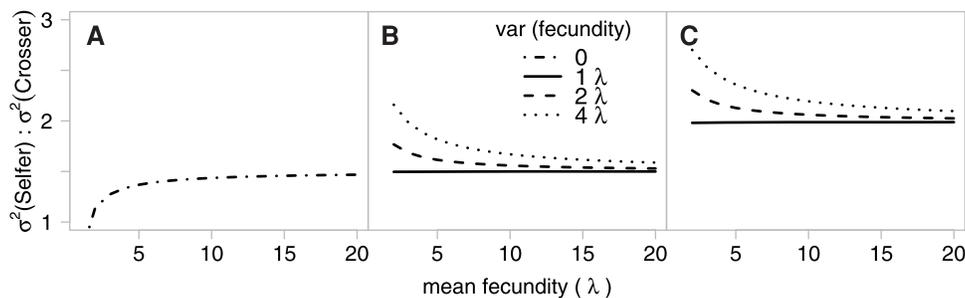
Crosser:	$\frac{1}{v}(1 + \frac{1}{\omega}) + \frac{1}{2}$
Selfer:	$-\frac{1}{4} - \frac{3}{4N})(\frac{1}{v} - 1) - \frac{1}{v}(\frac{3}{4\omega}(1 - \frac{1}{N}) + \frac{1}{2}(1 - \frac{1}{N\lambda}))$
Cloner:	$\frac{1}{v}(1 + \frac{1}{\omega}) + \frac{1}{2}$

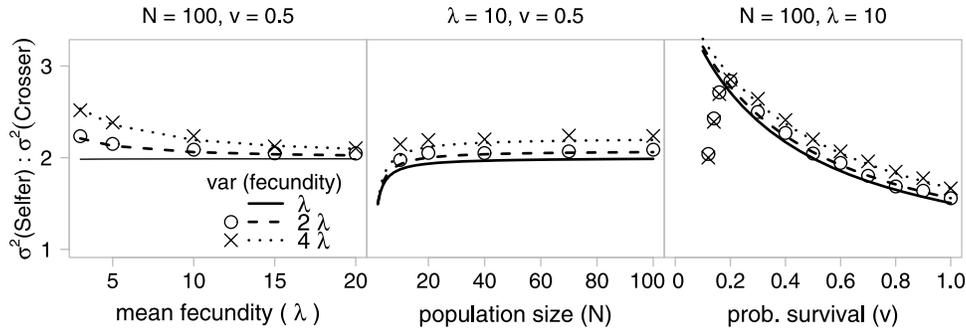
$N$  is the census size of the population,  $\lambda$  and  $\omega$  are the parameters of the individual fecundity distribution,  $v$  is probability that a plant's seeds are not all lost.

Table 2 lists the results when all three sources of noise (Fig. 1) are incorporated. It should be noted that increased individual-level noise (smaller  $v$  or  $\omega$ ) always increases noise in inheritance. Also, the two uniparental means of reproduction differ only in a very simple way, due to the effects of segregation in Selfer. The  $\sigma^2$  for Crosser can be lower than that of either other strategy. Lower noise in inheritance (smaller  $\sigma^2$ ) means a greater role of selection in changing the frequencies of alleles within a population, which is advantageous to the extent that natural selection builds a better match of genotype to the local environment. (Obviously  $\sigma^2$  and response to selection are population-level attributes.)

Figure 3 illustrates that, as more sources of noise are taken into account, the  $\sigma^2$  of Selfer increases relative to that of Crosser. The dip in relative advantage for Crosser at low mean fecundity (Fig. 3A) is eliminated or reversed when variance in fecundity is included (Fig. 3B). The greater the variance in fecundity (smaller  $\omega$  in Table 2) the smaller the relative size of  $\sigma^2$  for the sexual strategy, especially at low fecundities. In addition, greater noise in survival boosts that relative advantage of outcrossing across all mean fecundities (Fig. 3C).

Figure 4 shows analytical and simulation results across ranges of mean fecundity, population size, and probability of offspring survival. It can be noted that the advantage of Crosser relative to Selfer does not decline with increasing population size.

**Figure 3.** Relative noise in inheritance for selfing versus outcrossing given (A) simple density dependence only, no variance in fecundity, (B) simple density dependence plus variance in fecundity, and (C) all three variance sources: simple density dependence, fecundity, and survival ( $v = 0.5$ ).



**Figure 4.**  $\sigma^2$  of Selfer relative to  $\sigma^2$  of Crosser across each of the parameters  $\lambda$ ,  $N$ , and  $v$ . All three sources of noise are included. The lines are analytical results for one, two, and four times Poisson variance in fecundity. The points are from variances of 50,000 simulation runs. For clarity the simulation results for Poisson variation are omitted.

The relative advantage climbs as it becomes more likely that all of a given plant’s offspring be lost. But for small values of  $v$  the Crossers run out of other-ova spatial refuges for their gametes, their variances become more similar to that of a Selfer, and the relative advantage decreases. The analytical results are not accurate for small numbers of surviving individuals, as expected from the assumptions made in the derivation of  $\sigma^2$ .

We note that the allocation scheme used in Crosser is commonly both empirically observed (Sarkissian et al. 2001; Méndez and Traveset 2003; Andrieu et al. 2007) and theoretically predicted for other reasons (Brunet 1992; Greeff et al. 2001; Zhang and Jiang 2002; Sato 2004). But as a contrast with the plastic Crosser strategy, we also examined an extreme in which the ratio of ova to pollen produced is fixed, and termed this strategy *Crosser<sub>ALT</sub>*, and found this expression for  $v = 1$

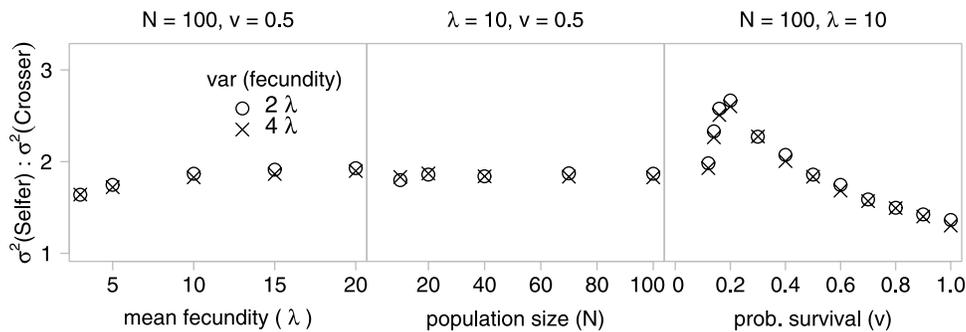
$$\sigma^2 \text{ of } Crosser_{ALT} = 1 + \frac{1}{\omega} + \frac{1}{2} \left( \frac{3}{2\lambda} \right) \left( 1 - \frac{1}{3N} \right).$$

We were unable to derive an expression for *Crosser<sub>ALT</sub>* that includes the probability of progeny survival, so we used numerical simulations. Figure 5 illustrates the performance of *Crosser<sub>ALT</sub>* across mean fecundity, population size, and offspring survival,

relative to the Selfer strategy toward which a plant could revert. It is notable that *Crosser<sub>ALT</sub>*, unlike Crosser, does not dampen noise in fecundity. This is because a *Crosser<sub>ALT</sub>* plant that produces more than the average number of ova, can also fertilize more than the average proportion of all ova in the population. At the offspring stage, there is always more variance for a *Crosser<sub>ALT</sub>* than for a Selfer. The final  $\sigma^2$  is always lower for *Crosser<sub>ALT</sub>* only because simple density dependence adds more variance in the Selfer strategy due to the greater variance in number of copies of the focal allele in the offspring, mentioned above. *Crosser<sub>ALT</sub>* does, however, generate the same relative advantages as Crosser at lower probabilities of progeny survival.

### Discussion

For both interindividual and lone-individual means of reproduction, we have built forward through a life cycle to produce expressions for noise in inheritance that include parameters describing two sources of individual-level ecological noise. Our results (Table 2, Fig. 4) show that the interindividual Crosser strategy can dampen the effects of noise in fecundity and in progeny survival relative to the lone-individual Selfer and Cloner strategies. This means that under similar ecological conditions, otherwise



**Figure 5.**  $\sigma^2$  of Selfer relative to  $\sigma^2$  of *Crosser<sub>ALT</sub>* across each of the parameters  $\lambda$ ,  $N$ , and  $v$ . All three sources of noise are included. The points are from variances of 50,000 simulation runs.

identical individuals can generate different distributions of recruits (“successful offspring,” “family size”) or of “successful gametes,” depending on mode of reproduction. This is of importance to calculations of variance effective population size, which often use the variance of the latter distributions.

The noise-dampening properties of the Crosser strategy can be understood in the following ways. First, under the reproductive resource allocation scheme assumed for Crosser only female gametes are influenced by noise in fecundity—each individual contributes equally to the pollen pool, so the only pollination noise is in the draw from that pool to fertilize each ovum produced in the population. In Selfer, noise in fecundity hits male and female gametes equally because they are matched one-to-one. Second, noise in progeny survival is relatively well-buffered by the sexual strategy because pollination is an additional means of dispersal for alleles, and dispersal is a well-known buffer against spatial heterogeneity.

The results show that, without proper attention to within-generation sources of noise, analytical and simulation models of evolution may overestimate the effectiveness of selection, and may hide differences among reproductive strategies. Simulations that construct the new adult generation by drawing gametes from parents, with probability of choosing a given parent being weighted by its relative fitness, produce Poisson-distributed successful gametes (unless the population is growing very quickly). This accounts for the effects of relative fitness and drift, but not of ecological noise. Our results show that, given ecological noise, variance in transmitted alleles cannot be as low as Poisson variance (Table 2). Only Crosser can approach the latter, when both fecundity and population size are very large.

We have confined this article to illustrating a difference between reproductive modes. Work remains in quantifying the relative importance of noise dampening, and to what extent it can influence the maintenance or invasion of sex at the within-population level of individual selection. The relative merits found for sexual versus asexual reproduction depend on many factors, including population size, the product of population size and mutation rate ( $N\mu$ ), the presence of epistasis, the existence of linkage disequilibrium, the distribution of sizes of selection coefficients, and the substitution model used (Kim and Orr 2005). But some qualitative statements follow.

The differential amplification of individual luck has consequences for adaptation. Casually phrased, adaptation is a matter of (1) producing the right variants, and (2) getting them to the right frequency. Gillespie (Gillespie 1994) has termed these “origination” and “fixation” processes, respectively. Noise in inheritance impacts both.

Variance effective population size varies inversely with  $\sigma^2$ , and in the case of Crosser, it is exactly  $N_e = N/\sigma^2$  (Gillespie 2004 p. 49). With regard to “fixation,” in results from existing

theory that combines the effects of selection and drift,  $N_e$  and  $s$  (the selection coefficient) usually appear multiplied together. The generation of homozygosity by selfing can have the effect of increasing the size of  $s$  (Lynch et al. 1995; Glémin 2003), facilitating selection. On the other hand, a larger  $N_e$  allows selection a role in changing the frequencies of alleles of smaller effects, both deleterious and beneficial. Work on the distribution of sizes of mutational effects finds that mutations become exponentially more frequent at smaller sizes of  $s$  (Lynch et al. 1999; Orr 2006). So it seems reasonable that conditions allowing selection a greater role in changing the frequencies of mutations of small effect could have significant consequences with respect to fitness. Indeed, the results of a previous theoretical study (Peck et al. 1997) of hermaphroditic plants that incorporated mutations of various effect sizes suggested that “even traits that have small effect on  $N_e$  may have large effects on fitness.” And differential amplification of ecological noise into  $\sigma^2$  affects  $N_e$ .

Concerning “origination,” note that selection is strongest on alleles at intermediate frequencies (near 0.5) and it is vanishingly weak on alleles at very low frequencies, such as just after they appear by mutation. Even highly beneficial alleles can be lost at this stage, simply through the noise of individual luck. If beneficial mutations are rare, then they may limit adaptation to a changing environment. Any dampening of the effects of individual-level noise would reduce the chance of throwing away any new allele just by accident, and let selection “see” farther into low allele frequencies, thus allowing a greater number of beneficial mutations to be recruited into a population.

If individual-level noise is ubiquitous, and if empirically observed sexual strategies dampen the effects of such individual luck and facilitate adaptation, then this noise-dampening is a general benefit that should be deducted from the costs of sex. The extent of this cost deduction awaits further study. We note that such noise-dampening is merely a consequence of the interindividualness of sex, and that the effects reported here happen in addition to other sexual processes, such as recombination and segregation.

Within the realm of plant reproduction, current theory about sex allocation in hermaphroditic plants (Klinkhamer et al. 1997; Cadet et al. 2004) takes into account the importance of plant size, the size of budget available for reproduction, and the frequencies of other strategies in the locale. Our results show that allocation schemes (e.g., Crosser and *Crosser<sub>ALT</sub>*) can differ with respect to noise-dampening, which suggests that this property should be considered when evaluating allocation strategies on an evolutionary time scale.

In nature, individual plants may engage in a mix of both outcrossing and selfing strategies and, within a given species, local populations may differ in the levels of partial selfing that is observed. Explanations have been sought in terms of balances or trade-offs between the advantages of selfing, such as

reproductive assurance, and its disadvantages, such as inbreeding depression. The present work suggests that another disadvantage of uniparental reproduction is relative vulnerability to individual-level ecological noise, and predicts that in habitats where there is more such noise, selfing should be less predominant.

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## Appendix

As a brief example we find  $\sigma^2$  for a Selfer, with noise in fecundity only. We use four rules about moment generating functions (MGF):

- (1)  $MGF_{X+Y}(t) = MGF_X(t) \cdot MGF_Y(t)$  for independent  $X$  and  $Y$
- (2)  $MGF_{aX}(t) = MGF_X(at)$
- (3)  $MGF_{X+b}(t) = e^{bt} \cdot MGF_X(t)$ .

We use the following result from Bowers et al. (1986, ch. 11). Consider the random sum  $S = X_1 + \dots + X_N$ . If the  $X_i$

are identically distributed random variables with  $MGF_X(t)$ ,  $N$  is a random number described by  $MGF_N(t)$ , and  $N$  and all  $X_i$  are mutually independent, then the MGF of  $S$  is

$$(4) \quad MGF_S(t) = MGF_N(\log MGF_X(t)).$$

The mean of a distribution is the first derivative of its MGF evaluated at  $t = 0$ . The variance of a distribution is the second derivative of its central moment generating function (CMGF) evaluated at  $t = 0$ . Given  $\mu$  as the mean of the distribution,

$$CMGF_X(t) = MGF_{X-\mu}(t) = e^{-\mu t} \cdot MGF_X(t),$$

which is an implementation of rule (3). The MGFs for the negative binomial distribution and the Bernoulli distribution are

$$\begin{aligned} mgfNegBin &= \left( \frac{w}{w + \lambda - e^t \lambda} \right)^w \\ mgfBer &= (1 - p) + p e^t. \end{aligned}$$

Fecundity, the distribution of seeds a Selfer puts into the offspring pool, is described by a negative binomial distribution, so  $mgfOff = mgfNegBin$ . Simple density dependence means only  $1/\lambda$  seeds become a new adult, and the number of those survival trials is determined by  $mgfOff$ , so we use rule (4) to describe the distribution of seeds that make it to adulthood.

$$\begin{aligned} mgfDensDep &= mgfBer |_{p=1/\lambda} \\ mgfAdSeed &= mgfOff |_{t=\log(mgfDensDep)}. \end{aligned}$$

A Selfer seed can have 0, 1, or 2 focal alleles. The number of gametes that make it to adulthood is twice  $mgfAdSeed$ , and each of those gametes has either the focal allele or its homologue.

$$\begin{aligned} mgfAdGam &= mgfAdSeed |_{t=2t} \\ mgfAlleleDraw &= mgfBer |_{p=1/2} \\ mgfAdFocal &= mgfAdGam |_{t=\log(mgfAlleleDraw)}. \end{aligned}$$

$mgfAdFocal$  describes the distribution of focal alleles making it into the new adult generation. As a check, we make sure the mean is 1 (constant population size)

$$\left. \frac{d}{dt}(mgfAdFocal) \right|_{t=0}$$

It is. We now compute the variance, which is the  $\sigma^2$  we want. This is the value in Table 2, without noise in progeny survival (i.e.,  $v = 1$ ).

$$\sigma^2 = \left. \frac{d^2}{(dt)^2}(e^{-t} \cdot mgfAdFocal) \right|_{t=0}$$

The result is  $3/2 + 1/w$ . For the derivation of all results, see the Supporting Information.

## Supporting Information

The following supporting information is available for this article:

Detail of Methods

1. Annotated Mathematica notebook.
2. R script used for simulations.

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

(This link will take you to the article abstract).

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