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The twofold cost of sex unfolded

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ABSTRACT

Question: Considering ecological factors and life history, how easy is it for sexual reproduction (as a strategy) to invade and persist in a population where all individuals are reproducing asexually?

Mathematical method: We use a population growth equation that despite its simplicity captures several relevant ecological parameters: age-specific survival, differential birth rates, as well as both within-strategy and between-strategy competition. We perform invasion analysis to reach conclusions about the stability of the two evolutionary strategies.

Key assumptions: Sexual and asexual reproduction can be thought of as a strategy game. Instead of focusing on the genetic advantages of sexual reproduction, we explore the ecological and demographic conditions under which the two main reproductive strategies are maintained.

Conclusions: From an ecological point of view, sexual reproduction remains enigmatic only if the sexual strategy implies monogamy, there are no ecological interactions between the alternative reproductive strategies, and the life histories of both asexual and sexual strategies are limited to semelparity. Relaxation of those very restrictive ecological conditions allows for the co-existence of sexual and asexual reproduction as well as mutual invasion of the two strategies.

Keywords: co-existence, evolution of sex, invasion, life history, population dynamics.

INTRODUCTION

A recurrent issue in evolutionary biology is the widespread occurrence of sex despite its basic twofold cost in relation to asexual reproduction (Maynard Smith, 1978; Bell, 1982; Roughgarden, 1991; Hurst and Peck, 1996). There is convincing evidence that genetic recombination and diversification through sexual reproduction often suffice to overcome the apparent fitness disadvantage of producing two sexes of which one (males) in other respects would be redundant (Hurst and Peck, 1996; Otto and Nuismer, 2004). Recently, it has also been shown empirically that sexual reproduction can increase the rate of adaptation to harsh environments (Goddard *et al.*, 2005). In addition, the ecological costs and benefits of sex have also been shown to provide

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at least partial answers to the question of why sex prevails (Doncaster *et al.*, 2000; Pound *et al.*, 2002, 2004; Scheu and Drossel, 2007). Here we use a very generic and basic population model in which at least three critical aspects of ecological interactions and life history are included: differential density-dependent fitness, competition for common resources, and differential survival (reflecting longevity). We show that the disadvantage of sexual reproduction only emerges under very restrictive ecological circumstances. Of course, this does not preclude or diminish the genetic advantages underlying the evolution of sexual reproduction, but our analysis underscores the importance of the ecological context in which sexual reproduction may evolve or be selected against. Introducing more flexible and ecologically richer stages for the evolutionary play also allows for more fruitful discussion of both the ecology and evolution of various reproductive modes.

MODEL

We will assume that both sexual and asexual reproduction can potentially exist within the population. Individuals of both reproductive strategies compete for common resources. The strength of this competition may or may not differ between strategies or between the sexes. We will further assume that it is only reproduction, irrespective of strategy, and not survival, that is density dependent. This simplification is immaterial for our analysis. Let the population dynamics of both sexual and asexual strategies be governed by the same basic renewal equation,

$$N(t+1) = sN(t) + B(t), \tag{1}$$

where N is population density, s is adult survival, and B is a birth function. If we now allow reproduction to be density dependent, a rather straightforward birth function for the asexual females (hereafter indexed p) can be written (ignoring time index):

$$B_p = N_p k_p \frac{1}{1 + \mu_{pp} N_p + \alpha_{pm} N_m + \alpha_{pf} N_f}. \tag{2}$$

The first factor in the expression ($N_p k_p$, where N_p is the number or density of asexual females and k_p is their per capita clutch size) gives the gross reproduction (number of offspring) per time step. The second factor specifies the density dependence within a strategy (μ) and among strategies (α). The parameter μ_{pp} specifies the strength of density dependence among individuals of the asexual strategy, and the parameter α_{pi} (i is either males, m, or females, f) specifies the strength of density dependence from males and females on the asexual strategy. The birth function for the sexual population can be written somewhat differently. We follow Caswell (2001) and let the sexual birth function be written as $B_s = N_m f_m + N_f f_f$, where N_m and N_f are the number of sexual males and females, and f_m and f_f represent male and female fecundity, respectively. We assume that males and females contribute equally ($f_m = f_f$) to the zygotes (i.e. it takes one female and one male to form a zygote) and therefore B_s can be simplified to $f_f(N_f + N_m)$. Assuming that males and females are equally abundant in the population, B_s is equal to $2N_f f_f$. This means that the per capita fecundity is f_f (and since it is only females that give birth to offspring, their clutch size (k) will be $2f_f$).

Female fecundity will be a function of her maximal fecundity ($f_{\max}$) and the proportion of males in the population. Differences and consequences of different f_f will be discussed later, but first we start with a linear relationship; $f_f = af_{\max}$, where a is the proportion of males in the sexual population (i.e. $a = N_m/(N_m + N_f)$) and $f_{\max} = k_{\max}/2$ (half of the maximum clutch size the female can give birth to) is maximal fecundity. Hence, $f_f = f_{\max}N_m/(N_m + N_f)$. Using the expression for the birth function (B_s) above, the total birth function for the sexual strategy, including a factor for density dependence, is

$$B_s = \frac{2N_mN_f}{N_m + N_f} f_{\max} \frac{1}{1 + \mu_{ss}N_m + \mu_{ss}N_f + \alpha_{sp}N_p}. \tag{3}$$

The first factor in equation (3), $\frac{2N_mN_f}{N_m + N_f} f_{\max}$, captures a simplified but critical frequency-dependent feedback on net sexual reproduction (Lindström and Kokko, 1998). It shows that offspring production is dependent on the current frequency of males and females. The exact form of the birth function in two-sex systems has been much debated but there is some consensus that the above expression is the most robust one (Caswell, 2001). However, as can be seen by the dotted line (a) in Fig. 1, using this equation underestimates female fecundity. Each female and male will in this case only produce half of their maximum fecundity. It is more likely that all or nearly all females get mated in a population consisting of equal numbers of males and females. Therefore, we have sketched two alternative curves, the dashed line (b) and the solid line (c), both of which have a higher fecundity at $a = 0.5$.

Using a birth function that incorporates both the number (or frequency) of females and males is a core issue when comparing asexual and sexual strategies from an ecological point of view. The density dependence factor includes μ (strength of within-strategy density dependence) and α (strength of among-strategy density dependence, with index ij indicating the effect of strategy or sex j on strategy or sex i). This latter parameter α_{ij} is a measure of interaction strengths and therefore implicitly maps to niche overlap; if α_{ij} is negligible, then

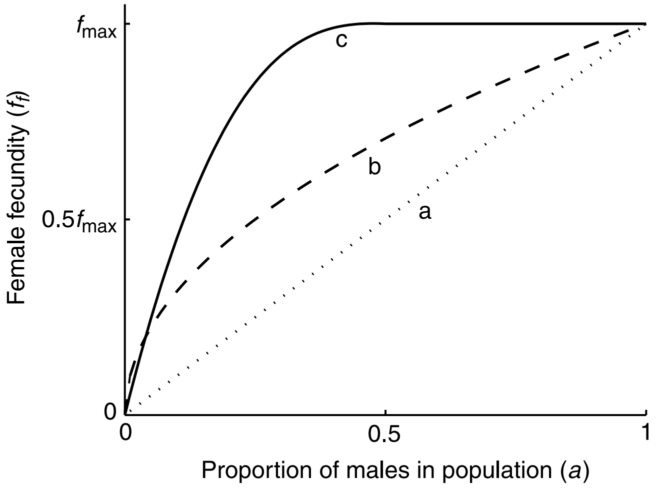

Fig. 1. Female fecundity as a function of the proportion of males in the population. The dotted line (a) describes a linear relationship between the frequency of males (a) and fecundity (f_f or f_m); the dashed (b) and solid (c) lines both describe non-linear relations between the two parameters. In our model, we assume an equal sex ratio and the point of interest is therefore $a = 0.5$.

the presence of the respective strategy has no influence on the other – that is, cannot be using the same resources. If α_{ij} is large, relative to μ_{ij}, then interspecific competition for common resources is strong and the two strategies are presumably using very similar parts of the environment (i.e. their niche overlap is large). We have chosen a rational expression for the density dependency but the exact form of that factor is not critical here. The last factor in equation (3) corresponds to the density dependence in equation (2).

THE UNFOLDING

We first assume that the asexual population is resident and at equilibrium and our task is now to determine whether a sexual strategy can invade a resident population of asexuals (the reverse problem and the issue of co-existence will be dealt with in the Appendix and below). Under this scenario, the asexual population will be at dynamic equilibrium, N_p^*, and the sexual mutant so rare that intraspecific density dependence is negligible. Invasion of the rare sexual mutant is possible if its growth rate $N(t+1)/N(t) > 1$. Using equations (1) and (3) and assuming an equal number of males and females at invasion, that growth rate condition is fulfilled when $s_s + \frac{1}{2} f_{\max} \dfrac{1}{1 + \alpha_{sp} N_p^*} > 1$. Now N_p^* can be calculated independently from equations (1) and (2) (and letting the density of the sexual strategy be approximated to zero in comparison to the resident asexual population; see also the Appendix), and when substituted into the invasion criterion and solving for $f_{\max}$ we have the critical fecundity, $\hat{f}_{\max}$,

$$\hat{f}_{\max} > 2(1 - s_s)\left(\frac{\alpha_{sp}}{\mu_{pp}} \frac{k_p - (1 - s_p)}{(1 - s_p)} + 1\right). \tag{4}$$

This is the fecundity the sexual population has to have per generation to invade a resident population of asexuals. Figures 2A and B show the invasion criteria for different adult survival rates for the sexual and asexual populations. Clearly, invasion of the asexual population is possible for a wide range of parameter values, especially if the third fecundity function from Fig. 1 is used (line c). Conversely, we can now ask whether a sexually reproducing resident population is resistant to invasion of an asexual strategy, and the recipe, albeit somewhat more cumbersome, is identical to the one outlined above (see Appendix). The criteria for invasion of a sexual population by asexuals are shown in Figs. 2C and D. Again, we see that asexuals have a competitive edge if adult survival in sexuals is low and the birth function of the sexual population used is the one described in equation (3).

Returning to equation (4), we see no apparent sign of the twofold cost of sex. This is because we yet have to make far more restrictive assumptions than this more general condition. Allowing adult survival rates, s_i, to be greater than zero implies that the populations are in effect iteroparous. We see that the larger s_s is, the more relaxed the invasion criterion becomes. Now let the sexual strategy have zero adult survival and hence be a semelaparous (annual) organism. The invasion criterion then reduces to

$$\hat{f}_{\max} > 2\left(\frac{\alpha_{sp}}{\mu_{pp}} \frac{(k_p - (1 - s_p))}{1 - s_p} + 1\right). \tag{5}$$

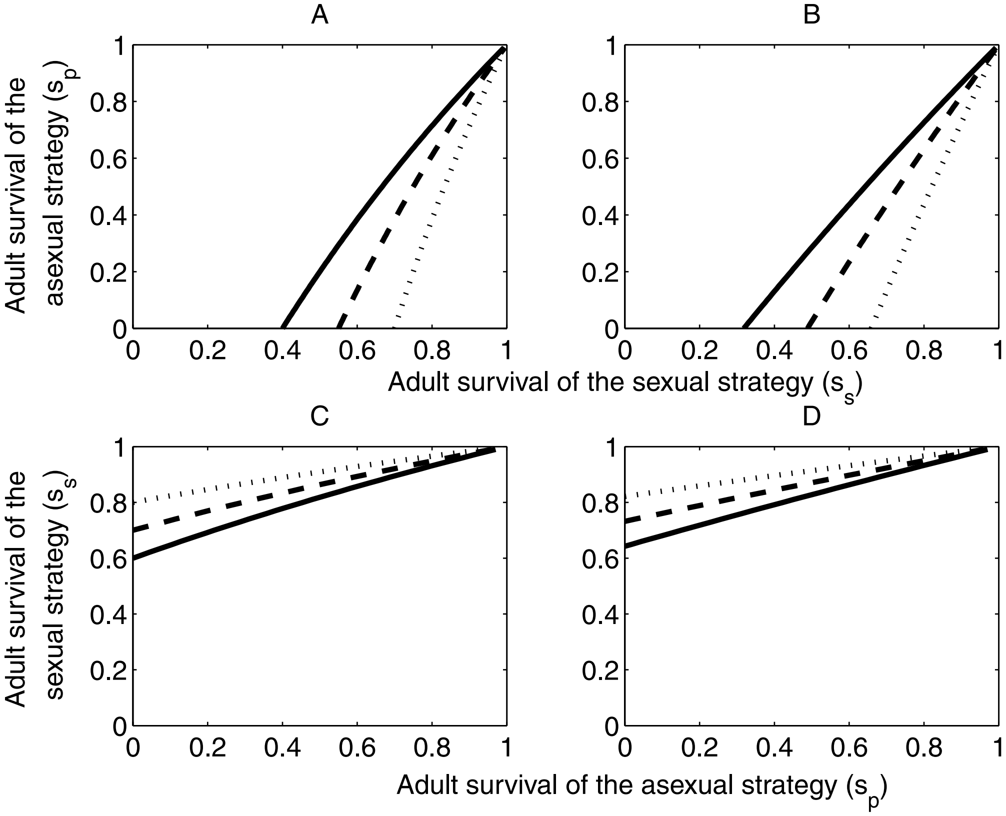

Fig. 2. (A, B) Invasion of a sexual strategy into a resident asexual strategy is possible under the lines. (C, D) Invasion of an asexual strategy into a resident sexual strategy is possible under the lines. The three lines use different fecundity functions (see Fig. 1), which give the sexual female different clutch sizes: $k_s = 2f_f = 2\beta f_{\max}$, where β is 0.5 for the dotted line, 0.75 for the dashed line, and 1 for the solid line. $f_{\max}$ is equal to 5 in (A) and 10 in (B); the clutch size for the asexual females (k_p) is 10 in (A) and 20 in (B).

Three parameters, apart from asexual fecundity, still determine invasion success – adult survival rate of the asexual strategy (s_p), within-strategy density dependence in the resident asexual population (μ_{pp}), and among-strategy interaction strength (and a measure of niche overlap, α_{sp}). As shown in Fig. 2, invasion of the asexual population is more difficult (for a given fecundity function) if the sexual strategy is semelparous and the asexual one is not. Making also the asexual resident semelparous reduces equation (5) to

$$\hat{f}_{\max} > 2\left(\frac{\alpha_{sp}}{\mu_{pp}}(k_p - 1) + 1\right). \tag{6}$$

The next step is to make the critical assumption that within-strategy density dependence among asexuals (μ_{pp}) and the density dependence that sexuals suffer from asexuals (α_{sp}) are identical. Doncaster *et al.* (2000) and Pound *et al.* (2002) discuss the importance of the relationship between intra- and interspecific density dependence for the maintenance of sexual reproduction, but most models of the problem implicitly omit this relationship.

Letting $\alpha_{sp} = \mu_{pp}$, which means that the per capita influence of asexuals on themselves and on sexuals is identical, indicating that the resources used also are identical, results in

$$\hat{f}_{\max} > 2k_p \, . \tag{7}$$

The fecundity of the invading sexual strategy now has to exceed the asexual clutch size by a factor of 2. Because $f_{\max}$ is only half the maximal clutch size $k_{\max}$, we therefore get a cost four times as high:

$$\hat{k}_{\max} > 4k_p \, . \tag{8}$$

So far, we have chosen a linear f_f-function ($f_f = af_{\max}$, where a equals the proportion of males in the population; line a in Fig. 1), which means that at $a = 0.5$ (the sex ratio of the sexual population when they invade the asexual population) f_f is $f_{\max}/2$. However, it is quite likely that f_f can be much closer to $f_{\max}$ also when the proportion of males in the population is around or above 0.5 because the probability of being fertilized by a male is already high and not very sensitive to a unless it is very small (see Fig. 1 for an illustration).

Assuming that f_f indeed is approximately equal to $f_{\max}$ at $a = 0.5$, and recalling that $k = 2f_{\max}$, then equation (8) changes to

$$\hat{k}_{\max} > 2k_p \, . \tag{9}$$

This is the twofold cost of sexual reproduction; the sexual clutch size has to be at least twice the asexual one. This is true only after having made more and more restrictive assumptions about the ecology and life history of both the sexual and asexual populations. The twofold cost hence emerges only as a special and – under most ecological and evolutionary scenarios – a rather uninteresting case. Our results extend previous analyses of the ecological conditions for the existence of sexual reproduction (Doncaster *et al.*, 2000; Pound *et al.*, 2002) and underscore that the ecological context is crucial when evaluating the relative success of sexual and asexual reproduction. Our model and invasion analysis includes a far wider suite of ecological and life-history situations. As shown in Fig. 2 there is not, however, a perfect symmetry in the mutual invasability. An asexual strategy is generally resistant to invasion for a wider range of parameter values, and there are situations when a semelparous asexual mutant is capable of invading a sexual resident but not vice versa. A recurrent pattern is that the asymmetry in invasibility emerges as a result of the difference in the number of female offspring that the asexual and sexual females can produce. A closer look at the growth rates (λ) for the two different populations at the time of invasion shows that

$$\begin{aligned} \lambda_p &= s_p + \frac{k_p}{1 + \alpha_{pm}N_m^* + \alpha_{pf}N_f^*} \\ \lambda_f &= s_f + \frac{k_s/2}{1 + \alpha_{fp}N_p^*} \\ \lambda_m &= s_m + \frac{k_s/2}{1 + \alpha_{mp}N_p^*} \, , \end{aligned} \tag{10}$$

where $k_s = 2\beta f_{\max}$, and β is the 'fecundity index'. Following line a in Fig. 1, β would be 0.5 and line c gives us the maximum index value of 1. If we don't take any ecology or life history into account, the only difference between the two equations is the number of female offspring produced (k vs. $k/2$) and it is very easy to see 'the twofold cost of sex'; this is also

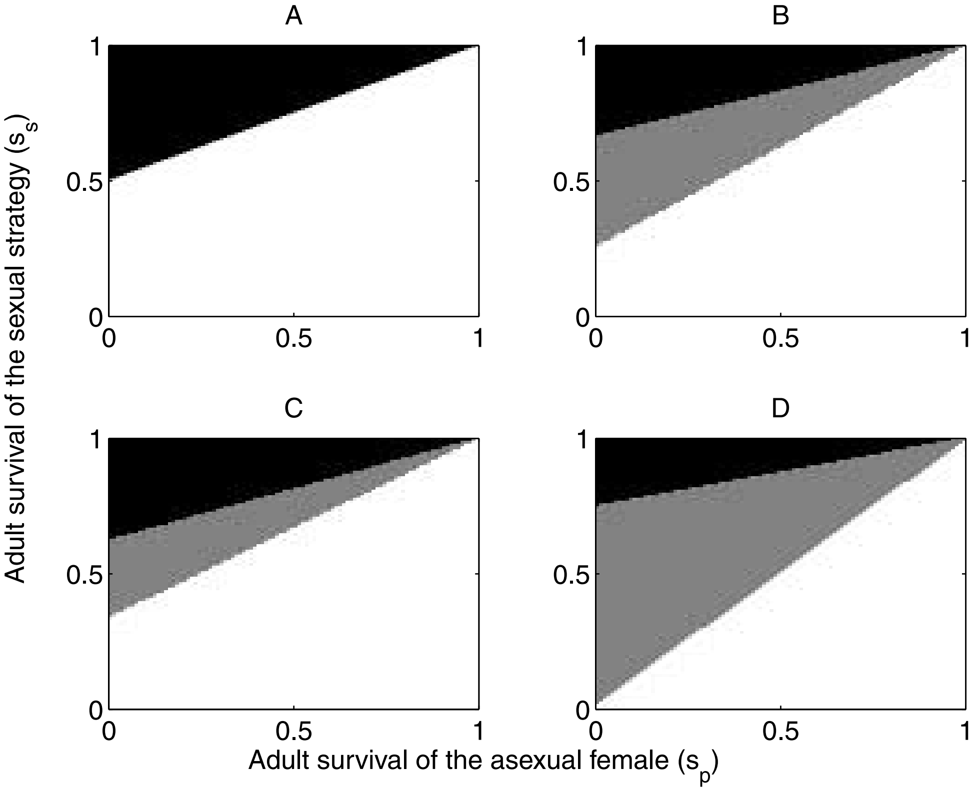

Fig. 3. The panels show which strategies are present in the equilibrium populations. Co-existence between sexual and asexual selection is possible in the grey areas; black areas correspond to the sexual strategy only and asexuals out-compete sexuals in the white areas. Female fecundity is equal to her maximum fecundity in all panels, i.e. the clutch size $k_s = 2f_f = 2f_{\max} = 10$. In (A), all $\mu = 0.3$, $\alpha = 0.3$, i.e. within-strategy competition and among-strategy competition are equal. In (B), $\mu = 0.3$, $\alpha = 0.2$, which corresponds to more competition within a strategy than between strategies. In (C), $\mu = 0.4$, $\alpha = 0.3$, similar to B, but harder competition overall. In (D), $\mu = 0.4$, $\alpha = 0.2$.

given that we do not use the birth function from earlier, but only assume that the sexual and asexual females have identical clutch sizes and that all sexual females are mated. However, by including possible ecological differences between strategies, the differential strength of competition between strategies might outweigh this cost.

What now remains is the possible co-existence of the two evolutionary strategies. In principle, the problem is simple, in that it suffices to calculate the joint equilibrium (N_s and N_p) from equations (1) to (3), but in this case it is quite an intractable exercise. In Fig. 3 we show the co-existence conditions from numerical solutions of the system. Decreasing the competition between the strategies increases the possibilities for co-existence and hence also the possibilities for the sexual strategy to exist at all (Figs. 3B, C, and D). Increasing the clutch size also increases the possibilities for co-existence (not shown here). The overall picture is nevertheless clear – a wide range of ecological and life-history conditions allow for mutual invasion and co-existence of sexually and asexually reproducing strategies.

DISCUSSION

Our model synthesizes a number of approaches taken to explain the putative evolutionary enigma of sexual reproduction. Although the genetic arguments are strong and possibly key for the prevalence of sexual reproduction (see, for example, Bell, 1982; Case and Taper, 1986; Hurst and Peck, 1996; Bürger, 1999), it is unquestionable that the ecological context must play an important and decisive role for the success of a mutant alternative reproductive strategy (Case and Taper, 1986; Doncaster *et al.*, 2000; Pound *et al.*, 2002; Scheu and Drossel, 2007). As shown by Pound *et al.* (2004), there is also an important interplay between the genetic and the ecological conditions (niche differentiation) that may determine the potential advantage of sexual reproduction. The apparent disadvantage of sexual reproduction is rather easily outweighed as soon as the very restrictive assumptions of adult longevity and niche overlap among strategies are relaxed. Those factors have received little attention in traditional analyses of the problem. The longevity of adults appears to play a crucial role. Although our model is sketchy as regards life-history alternatives, it nevertheless reveals that high adult survival is important for the sexual strategy, but less so for the asexual one. As also shown by Kerszberg (2000), long life (i.e. high adult survival) is a possible way of overcoming the disadvantage of slow per time unit reproduction.

The functions found in Lindström and Kokko (1998) and Caswell (2001) have the consequence that when males and females are equally common in the population, half of the females do not get mated. This arises from the belief that all females that are mated produce a maximal clutch size. So in Fig. 1, line a, at 50% males and females, on average female clutch size is half of her maximal capacity. This means that if all mated females produce a maximal clutch size, this would correspond to the fact that only half of the females are mated. This is highly unlikely and we therefore show the effect of two different alternative mating functions, which increases the proportion of females that are mated. By doing so, the possibilities for successful invasion as well as co-existence with the asexual strategy are increased. Co-existence of asexually and sexually reproducing strategies is rather infrequent, but widespread among animal taxa (Bell, 1982), including mites (Getz, 2001), snails (Dybdahl and Lively, 1995), and lizards (Case, 1990). Several species of the small invertebrate tardigrades show a complicated pattern of asexual, polygynous, and polyandrous breeding systems, possibly co-occurring within the same population (Altiero and Rebecchi, 2003; Rebecchi *et al.*, 2003). Whether any of the ecological and life-history conditions for co-existence defined above are in play here is unknown. Data on the ecological conditions under which asexual and sexual strategies co-exist in nature are largely missing.

Our results show that ecological and life-history conditions can both constrain and enhance alternative reproductive modes, regardless of the genetic mechanisms involved. The evolution of adaptive traits must be understood at two levels: the response to selection (the genotype–phenotype mapping) and the opportunity for selection (the demography–mean fitness map). Here, we have shown that the opportunities for selection can be substantially relaxed if critical components of the ecological feedback environment are identified. Real density-dependent feedback is likely to be more complex than we represent by our indices of density dependence (α and μ). These indices nevertheless generate dynamics that conform to previous predictions of a potentially crucial role for competition and niche overlap. Our analysis, moreover, shows how skews in reproduction and survival can independently facilitate the persistence of sex. The frequency-dependent birth function for sexual reproduction is, of course, also overly simple. But it allows examinations of what would happen if male and female survival were different in the population, and the circumstances in which harems would form [the parameter *h* in Lindström and Kokko (1998)]. An extreme polygynous system could be the first step from asexual reproduction to sexual reproduction. Combining population genetics, demography (life history), and population dynamics into an adaptive dynamics framework to identify the relevant evolutionary feedback environment for the evolution of reproductive modes is an important challenge for the future. The ecological processes identified here must not be omitted unless we wish to cling to the notion that sexual reproduction is 'enigmatic', which our ecological unfolding has shown it is not.

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REFERENCES

Altiero, T. and Rebecchi, L. 2003. First evidence of achiasmatic male meiosis in the water bears *Richtersius coronifer* and *Macrobiotus richtersi* (Eutardigrada, Macrobiotidae). *Hereditas*, **139**: 116–120.

Bell, G. 1982. *The Masterpiece of Nature*. London: Croom Helm.

Bürger, R. 1999. Evolution of genetic variability and the advantage of sex and recombination in changing environments. *Genetics*, **153**: 1055–1069.

Case, T.J. 1990. Patterns of coexistence in sexual and asexual species of *Cnemidophorus* lizards. *Oecologia*, **83**: 220–227.

Case, T.J. and Taper, M.L. 1986. On the coexistence and evolution of asexual and sexual competitors. *Evolution*, **40**: 366–387.

Caswell, H. 2001. *Matrix Population Models*, 2nd edn. Sunderland, MA: Sinauer Associates.

Doncaster, C.P., Pound, G.E. and Cox, S.J. 2000. The ecological cost of sex. *Nature*, **404**: 281–285.

Dybdahl, M.F. and Lively, C.M. 1995. Diverse, endemic and polyphyletic clones in mixed population of a freshwater snail (*Potamopyrgus antipodarum*). *J. Evol. Biol.*, **8**: 385–398.

Getz, W.M. 2001. Competition, extinction, and the sexuality of species. *Ann. Zool. Fenn.*, **38**: 315–330.

Goddard, M.R., Godfray, H.C.J. and Burt, A. 2005. Sex increases the efficacy of natural selection in experimental yeast populations. *Nature*, **434**: 636–640.

Hurst, L.D. and Peck, J.R. 1996. Recent advances in understanding of the evolution and maintenance of sex. *Trends. Ecol. Evol.*, **11**: 46–52.

Kerszberg, M. 2000. The survival of slow reproducers. *J. Theor. Biol.*, **206**: 81–89.

Lindström, J. and Kokko, H. 1998. Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. *Proc R. Soc. Lond. B*, **265**: 483–488.

Maynard Smith, J. 1978. *The Evolution of Sex*. Cambridge: Cambridge University Press.

Otto, S.P. and Nuismer, S.L. 2004. Species interactions and the evolution of sex. *Science*, **304**: 1018–1020.

Pound, G.E., Doncaster, C.P. and Cox, S.J. 2002. A Lotka-Volterra model of coexistence between a sexual population and multipole asexual clones. *J. Theor. Biol.*, **217**: 535–545.

Pound, G.E., Cox, S.J. and Doncaster, C.P. 2004. The accumulation of deleterious mutations within the frozen niche variation hypothesis. *J. Evol. Biol.*, **17**: 651–662.

Rebecchi, L., Rossi, V., Altiero, T., Bertolani, R. and Menozzi, P. 2003. Reproductive modes and genetic polymorphism in the tardigrade *Richtersius coronifer* (Eutardigrada, Macrobiotidae). *Invertebrate Biol.*, **122**: 19–27.

Roughgarden, J. 1991. The evolution of sex. *Am. Nat.*, **138**: 934–953.

Scheu, S. and Drossel, B. 2007. Sexual reproduction prevails in a world of structured resources in short supply. *Proc. R. Soc. Lond. B*, **274**: 1225–1231.

APPENDIX: EQUILIBRIUM POPULATION DENSITIES

Calculating the equilibrium density of the asexual population when alone (N_p^*) is straightforward from equations (1) and (2). The equilibrium of the sexual population (N_f^* and N_m^*) is not much more complicated. Let the density from the asexual population be zero, then the males and females grow according to

$$N_m(t+1) = s_m N_m(t) + \frac{B_s}{2} \tag{A1}$$

$$N_f(t+1) = s_f N_f(t) + \frac{B_s}{2} \tag{A2}$$

$$B_s = 2N_f f_f \frac{1}{1 + \mu_{ss} N_m + \mu_{ss} N_f}. \tag{A3}$$

B_s is the birth function of the sexual population. In our case, the function consists of two parts, one density-dependent feedback term and one giving the number of births in the population. f_f is female fecundity, here assumed to be linearly dependent of female maximal fecundity ($f_{\max}$) and the proportion of males in the population (a):

$$f_f = a f_{\max}. \tag{A4}$$

This turns the birth function into:

$$B_s = \frac{2N_f N_m}{N_m + N_f} f_{\max} \frac{1}{1 + \mu_{ss} N_m + \mu_{ss} N_f}. \tag{A5}$$

At equilibrium, $N_f(t+1) = N_f(t)$ and $N_m(t+1) = N_m(t)$, and solving for N_m and N_f results in

$$N_m^* = N_f^* = \frac{f_{\max} - 2(1 - s_s)}{4(1 - s_s)\mu_{ss}}. \tag{A6}$$

Our derivation from equations (4)–(9) (in the main text) can be done in the same way but from the perspective of asexual invasion. The expressions for N_m^* and $N_f{}^*$ are inserted into the invasion criterion:

$$s_p + \frac{k_p}{1 + \alpha_{pm} N_m^* + \alpha_{pf} N_f^*} > 1. \tag{A7}$$

Simplifying the expression by choosing s_p, s_m, and $s_f = 0$ and letting α_{pm}, α_{pf}, and α_{ps} be equal, equation (A7) reduces to

$$\frac{k_p}{1+\frac{\alpha_{px}}{\mu_{ss}}\frac{f_{\max}-2}{2}} > 1. \tag{A8}$$

Now, let $\alpha_{ps} = \mu_{ss}$ and solve for f_p, and we have

$$k_p > \frac{f_{\max}}{2}. \tag{A9}$$

Female maximal fecundity is equal to half the clutch size that she can give birth to ($f_{\max} = \frac{1}{2} k_{\max}$), so

$$k_p > \frac{k_{\max}}{4}. \tag{A10}$$

However, as we conclude in the main text (between equations 8 and 9), it is more likely that $f_{\max} = k_{\max}$. Equation (A10) then becomes

$$k_p > \frac{k_{\max}}{2}. \tag{A11}$$

That is, for the asexual female to successfully invade a sexually reproducing population, it is enough that she has a clutch size at least half as big as the clutch size of the sexually reproducing female. This is the same result as the twofold cost of males.