

# The cost of males in non-equilibrium populations

Curtis M. Lively

*Department of Biology, Indiana University, Bloomington, Indiana, USA*

---

## ABSTRACT

**Question:** What is the cost of producing males in non-equilibrium sexual species?

**Background:** Asexual reproduction is generally associated with non-equilibrium (*r*-selected) species, while sexual reproduction is generally associated with equilibrium (*K*-selected) species.

**Mathematical methods:** The cost of males per reproductive time step was calculated as the ratio of the per-capita growth rate of an asexual population relative to the per-capita growth rate of a sexual population.

**Key assumptions:** Sexual and asexual individuals are ecologically similar. Sexual females produce males, which do not contribute to the per-capita birth rate, whereas asexual females produce only female offspring. All else is equal.

**Conclusion:** The cost of males per reproductive time step approaches two-fold in non-equilibrium populations where the birth rate is much greater than the death rate. In contrast, the cost of males per time step can be much less than two-fold in iteroparous populations at equilibrium. These results are consistent with the distribution of parthenogenesis in natural populations.

*Keywords:* cost of males, *K*-selection, maintenance of sex, non-equilibrium populations, *r*-selection.

## INTRODUCTION

The existence of obligate sexual reproduction in most plants and animals has been difficult to explain. The reason is that obligate parthenogens can have very large reproductive advantages. The disadvantage to sexual reproduction stems directly from the production of males, which do not contribute directly to offspring production in the sexual population. This reduction in the per-capita growth rate has been called the ‘cost of males’ (Maynard Smith, 1971, 1978). Assuming all else is equal, the cost of males is expected to give a two-fold reproductive advantage to the asexual sub-population. Explaining the persistence of obligate sex, given such a large cost, has rendered sex an anomaly on evolutionary theory (Williams, 1975; Maynard Smith, 1978; Bell, 1982).

One important clue to the possible reasons for the persistence of sexual reproduction comes from the distribution of parthenogenesis. In general, parthenogenetic reproduction is

---

Correspondence: C.M. Lively, Department of Biology, Indiana University, Bloomington, IN 47405, USA.  
e-mail: [clively@indiana.edu](mailto:clively@indiana.edu)

Consult the copyright statement on the inside front cover for non-commercial copying policies.

---

more common in  $r$ -selected, non-equilibrium species, than in  $K$ -selected, equilibrium species. For example, in an early study by Jaenike and Selander (1979), the authors stated that, ‘The evidence indicates that parthenogenetic earthworms commonly occur in ephemeral or unstable habitats, in which  $r$ -selection may be expected, whereas sexual species tend to inhabit more stable environmental situations, where  $K$ -selection may be more important’. This same conclusion was reached by Bell (1982) from his extensive survey of the distribution of parthenogenesis across a broad swath of plants and animals. The pattern, therefore, seems to be general.

The biogeographic distribution of asexual reproduction led Bell (1982) to conclude that sex was likely to be favoured by either: (1) intraspecific competition in spatially heterogeneous, stable environments, or (2) by host–parasite co-evolution in similarly stable environments. Empirical studies have tended to favour the co-evolution model (also known as the Red Queen hypothesis). For example, a long-term field study of a mixed (sexual and asexual) population of freshwater snails showed that common clones became disproportionately infected over time by digenetic trematodes, and that the common clones decreased in frequency, while the sexual population remained relatively constant (Jokela *et al.*, 2009). Frequency-dependent selection by these same trematodes against common snail clones was also found in a controlled laboratory experiment (Koskella and Lively, 2009). Comparative studies have also favoured the host–parasite co-evolution model (e.g. Burt and Bell, 1987; Lively, 1987; Busch *et al.*, 2004).

In spite of the empirical support for some kind of ecological explanation for sex, it is difficult to understand how selection to produce genetically diverse offspring could be sufficiently strong, in general, to favour sexual reproduction over all daughter-producing clones (May and Anderson, 1983; Howard and Lively, 1994; Otto and Nuismer, 2004). One possibility, however, is that the cost of males is sometimes much less than two-fold. For example, an ecological model of competition between sexual and asexual sub-populations has suggested that the two-fold cost of males is, in fact, not expected to be observed in most natural populations (Doncaster *et al.*, 2000). In particular, the model first showed that the carrying capacity of an asexual population ( $K_{\text{asex}}$ ) could be greater than that of a sexual population ( $K_{\text{sex}}$ ) when resources are limiting. Doncaster and colleagues (2000) then showed that the difference between  $K_{\text{asex}}$  and  $K_{\text{sex}}$  decreases with increasing birth rates and/or declining death rates, leading them to the conclusion that the cost of males is lower in high-fecundity organisms: ‘Males are less costly to species with high growth capacities’.

In a previous study, I also found that asexual populations can have higher carrying capacities than sexual populations when food resources limit population growth (Lively, 2009), which is consistent with the model of Doncaster *et al.* (2000). More recently, I directly calculated the cost of males (in a discrete-time model) as the ratio of the per-capita growth rates in co-existing sexual and asexual populations (Lively, 2010). The results showed that the cost of males per reproductive time step was two-fold for annual populations, but could be much less for iteroparous species. More specifically, the cost of males per reproductive time step was derived as one plus the probability of dying. This result suggested that sex would be easier to explain if the mechanism favouring outcrossing operated on a per-time-step basis (rather than a per-generation basis), and that asexual reproduction should be more common in short-lived organisms.

In the construction of this previous model, I assumed that the sexual population was at equilibrium upon introduction of the asexual mutant. Here I relax this assumption to consider the cost of males in non-equilibrium populations. The results suggest that the cost

of sex per reproductive time step is generally higher in non-equilibrium populations. This result might help to explain the well-known association between parthenogenesis and unstable environments. It might also help to explain why many facultatively parthenogenetic organisms switch to sexual reproduction as the population becomes resource limited.

### MODELS

The cost of males has usually been assumed to be the inverse of the female frequency in the sexual population, which gives a two-fold cost for a 1:1 sex ratio. An alternative formulation gives the cost of males ( $C_{\text{sex}}$ ) as the ratio of the per-capita growth rate of asexuals ( $A_{t+1}$ ) divided by the per-capita growth rate of sexuals ( $S_{t+1}$ ):

$$C_{\text{males}} = \frac{A_{t+1}}{S_{t+1}} = \frac{1 - D + B}{1 - D + (1 - s)B}, \quad (1)$$

where  $B$  is the mean number of offspring produced by each female,  $D$  is probability of dying ( $0 < D \leq 1$ ), and  $s$  is the frequency of males in the sexual population (Lively, 2010). The formulation assumes that all else is equal, except for the occurrence of males in the sexual population. Clearly, if all else is not equal, the cost of males can be lower (Olofsson and Lundberg, 2007; Scheu and Drossel, 2007).

At carrying capacity for the sexual population, the death rate ( $D$ ) is equal to the per-capita birth rate  $[(1 - s)B]$ ; hence:  $B = D/(1 - s)$ . Substituting for  $B$  in equation (1), the cost of sex per time step for a sexual population at carrying capacity,  $K_{\text{sex}}$ , assuming a 1:1 sex ratio (i.e.  $s = 1/2$ ) is, as shown elsewhere (Lively, 2010):

$$C_{\text{males}} \Big|_{K_{\text{sex}}} = \frac{A_{t+1}}{S_{t+1}} = 1 + D. \quad (2)$$

But what if the sexual population is not at carrying capacity? To visualize how the cost of males depends on variation in  $D$  and  $B$ , a contour plot is given in Fig. 1, as derived from equation (1). As is immediately apparent, the cost of males per time step in long-lived species at equilibrium is low compared with the cost of males in  $r$ -selected species. In general,  $K$ -selected species having low death rates in density-regulated populations would exist in the lower left-hand region of the figure, while  $r$ -selected species that are not regulated by density would exist in the upper right-hand side of the figure. The solid line gives the equilibrium situation, where the per-capita birth rate of sexuals is equal to the death rate, as given in equation (2). Along this line, the cost of males increases linearly with the death rate, reaching two-fold in annuals. In the parameter space above the line, the cost of males increases with the birth rate, except for cases where the death rate is high. Thus, all else equal,  $K$ -selected species would be expected to pay a lower cost of sex per time step than  $r$ -selected species.

The results suggest that the cost of males declines as the sexual population gets closer to its equilibrium population size, at least for death rates less than 1. But the shape of the relationship is unclear. To see the relationship, let  $B$  and  $D$  be potentially density dependent, such that  $B = b - aN$ , and  $D = d + cN$ , where  $b$  is the maximum fecundity,  $d$  is the density-independent mortality rate,  $a$  is a constant that scales the effect of density on the total birth rate ( $B$ ), and  $c$  is a constant that scales the effect of density on the death rate (see Pielou, 1969; Gotelli, 1995). The carrying capacity in the sexual population,  $K_{\text{sex}}$ , can be shown to be

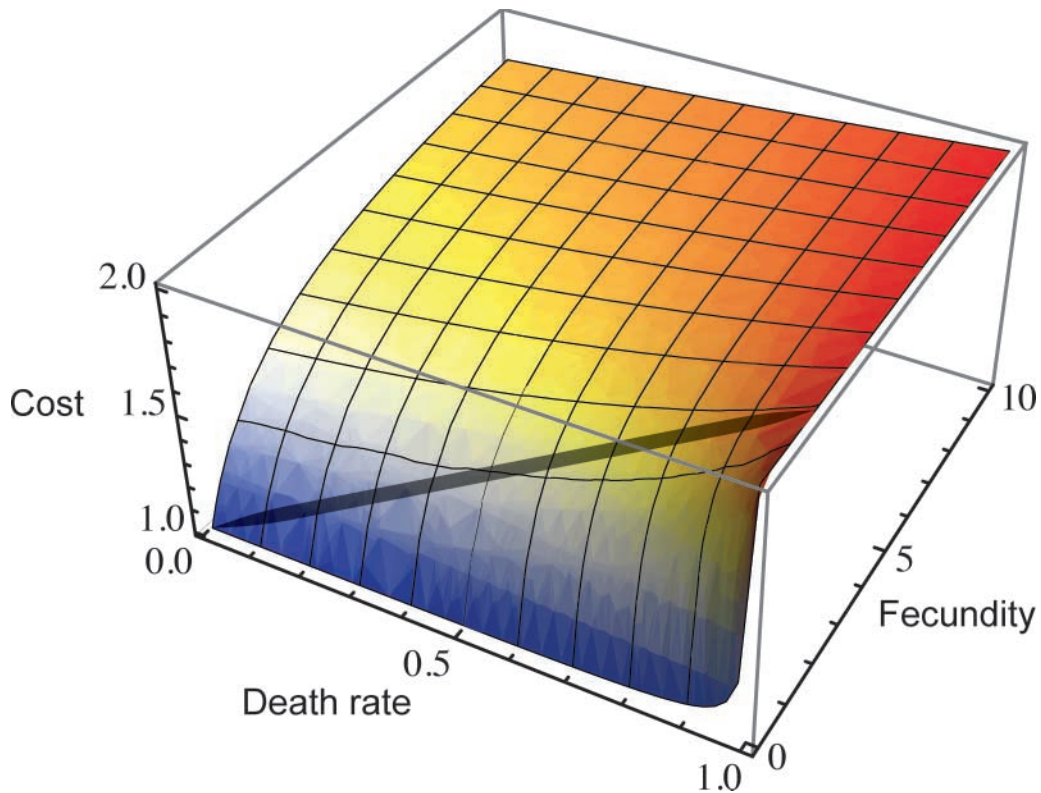
$$K_{\text{sex}} = \frac{(1-s)b-d}{(1-s)a+c}, \quad (3)$$

(see Lively, 2009), while the carrying capacity in the asexual population,  $K_{\text{asex}}$ , is (Pielou, 1969; Gotelli, 1995):

$$K_{\text{asex}} = \frac{b-d}{a+c}. \quad (4)$$

The cost of males per time step can now be rewritten in a more explicitly density-dependent form as:

$$C_{\text{males}} = \frac{1 + (b-d)\left(1 - \frac{N}{K_{\text{asex}}}\right)}{1 + [(1-s)b-d]\left(1 - \frac{N}{K_{\text{sex}}}\right)}, \quad (5)$$



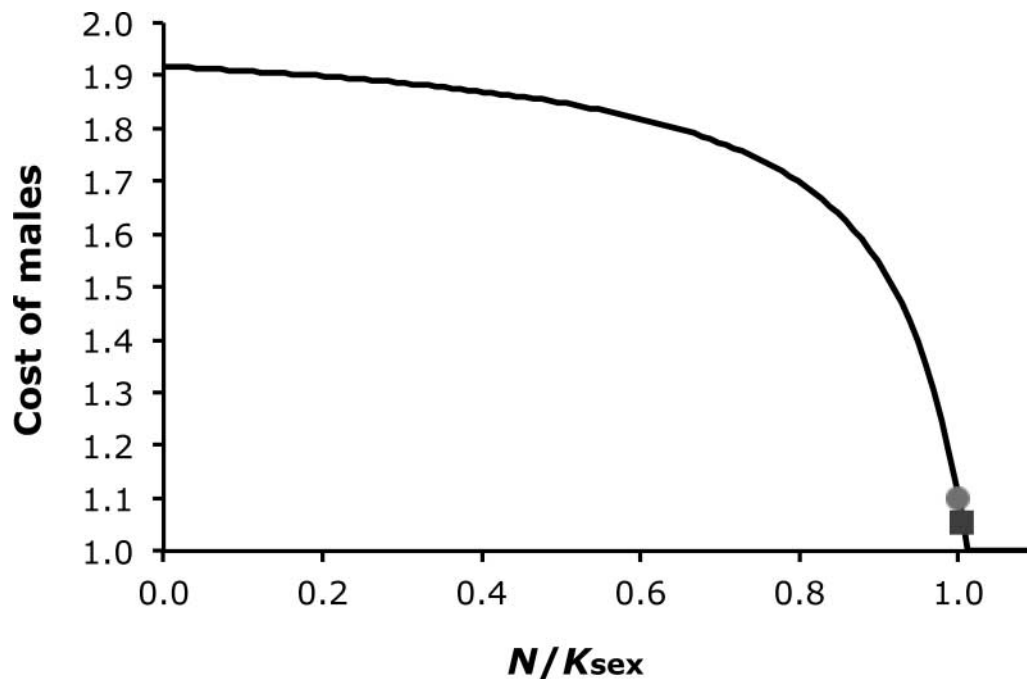
**Fig. 1.** The cost of males as a function of mortality and fecundity. Warmer colours indicate a higher cost, while colder colours indicate a lower cost. The thick solid line indicates equilibrium conditions in the sexual population upon introduction of an asexual mutant (i.e.  $B = 2D$ ). In general,  $K$ -selected species at equilibrium would be in the lower left-hand corner of the graph, while non-equilibrium  $r$ -selected species would be expected to be closer to the upper right-hand corner of the graph, where fecundity is high and the death rate is high.

where  $N$  is the total number of individuals in the population. The effects of density on the cost of sex can now be plotted for specific values of  $b$ ,  $d$ ,  $a$ , and  $c$ . The results suggest that, for species having low death rates (more  $K$ -selected), the cost of males per time step declines dramatically as the population density approaches  $K_{\text{sex}}$  (Fig. 2). These results suggest that the cost of males could be experimentally manipulated by perturbing populations to levels below carrying capacity.

Alternatively, the cost of males could be calculated per generation, rather than per time step. The cost of males per generation can be estimated as  $C_{\text{males}}^{1/D}$ . In equilibrium populations (where  $B = 2D$ ), the cost of males goes to  $e$  as the death rate approaches zero (Lively, 2010), but in non-equilibrium populations (where  $B > 2D$ ) the cost of males per generation becomes infinitely large as the death rate approaches zero.

### DISCUSSION

The cost of males is at the conceptual root of the controversy regarding the long-term persistence of obligate sexual reproduction in natural populations. The intrinsic cost is normally thought to be two-fold, assuming that half the sexual individuals are males. Doncaster *et al.* (2000) questioned the generality of the two-fold cost using an ecological



**Fig. 2.** The cost of males as a function of population density, where density is given as the number of individuals divided by the carrying capacity ( $N/K_{\text{sex}}$ ). The circle gives the cost of males at  $K_{\text{sex}}$ , while the square gives the cost of males at  $K_{\text{asex}}$ . Variables were as follows:  $b = 20$ ,  $d = 0.10$ ,  $a = 0.001$ ,  $c = 0.00$ . Note that the cost of males per time step decreases sharply as  $N$  approaches  $K_{\text{sex}}$ . These results rely on the assumption that the death rate is very weakly related to density. As the death rate becomes strongly density dependent, the cost of males per time step is asymptotic on 2.0 as density increases.

(Lotka-Volterra) model of competition between sexual and asexual morphs. Although they did not directly solve for the cost of males, their analysis indicated that increasing  $R_0$  in sexual populations would reduce the impact of producing males, where  $R_0$  is given by the ratio of the birth rate to the death rate. More specifically, assuming that sexuals did not completely overlap with asexuals in terms of resource use, the frequency of sexuals at equilibrium increased asymptotically with the magnitude of  $R_0$ , suggesting that the cost of males declined.

In a previous study, I directly calculated the cost of males as the ratio of the per-capita growth rates of asexuals relative to sexuals. I assumed that the sexual population was at carrying capacity ( $K_{\text{sex}}$ ) upon introduction of an asexual mutant, and that all else was equal. The results suggested that the cost of males per reproductive time step declined with the death rate such that the cost was two-fold in annuals, decreasing linearly to near unity (meaning no cost) as the death rate decreased (Lively, 2010). Hence the results were similar to those reported by Doncaster *et al.* (2000) in that decreasing the death rate decreased the cost of males (per time step) in my model, and it increased the frequency of sexuals at the joint equilibrium in the model of Doncaster *et al.* (2000).

The present paper extends my previous result by considering non-equilibrium populations. The results suggest that  $K$ -selected species [which have low death rates, and exist near carrying capacity ( $K_{\text{sex}}$ )], would pay a lower cost of males per time step than  $r$ -selected species, which exist below carrying capacity (Fig. 1). Thus the results suggest that, all else equal, asexual reproduction should be more common in unstable environments, which tend to select for higher birth rates. As such, the model is consistent with the well-known correlates of asexual reproduction (Bell, 1982).

The model was formulated in terms of the cost of males per reproductive time step. Hence the conclusions are restricted to mechanisms for sex that operate on that time scale. As parasite generation times can be much faster than host generation times, host-parasite co-evolution stands as a possible mechanism to favour host sex, especially in  $K$ -selected species. However, the model is not inherently restricted to any particular mechanism, as long as the mechanism operates on the order of reproductive time steps rather than generations for the target species.

It is of particular interest to note that mechanisms that favour the production of genetically variable progeny might also affect the cost of males. For example, if parasites increase the death rate of infected individuals, then they could increase the initial cost of males (as calculated upon invasion by an asexual mutant). On the other hand, parasites that increase the death rates of infected individuals would have higher virulence, which would increase the strength of parasite-mediated selection against infected individuals. Moreover, if parasites evolve to disproportionately infect common clonal individuals (as expected under the Red Queen hypothesis), the mean mortality rate in the sexual population would decrease, thereby decreasing the cost of males. Thus, in general, the cost of males per reproductive time step is not a fixed parameter.

In summary, the results of the present model suggest that parthenogenesis should be more likely to be found in species that are held below their resource-mediated carrying capacities by forces unrelated to intraspecific competition. Such forces might include disturbance or predation. The model also suggests that facultatively sexual species would be more likely to switch to sexual reproduction as resources become limiting and the cost of males declines (Fig. 2). Both of these expectations are consistent with Bell's (1982) review on the ecology of sex.

## ACKNOWLEDGEMENTS

I thank Lynda Delph, Patrick Doncaster, and Levi Morran for helpful suggestions. This study was supported by the US National Science Foundation (DEB-0919015, DEB-0640639).

## REFERENCES

- Bell, G. 1982. *The Masterpiece of Nature: The Evolution and Genetics of Sexuality*. Berkeley, CA: University of California Press.
- Burt, A. and Bell, G. 1987. Mammalian chiasma frequencies as a test of two theories of recombination. *Nature*, **326**: 803–805.
- Busch, J.W., Neiman, M. and Koslow, J.M. 2004. Evidence for the maintenance of sex by pathogens in plants. *Evolution*, **58**: 2584–2590.
- Doncaster, C.P., Pound, G.E. and Cox, S.J. 2000. The ecological cost of sex. *Nature*, **404**: 281–285.
- Gotelli, N.J. 1995. *A Primer of Ecology*. Sunderland, MA: Sinauer Associates.
- Howard, R.S. and Lively, C.M. 1994. Parasitism, mutation accumulation and the maintenance of sex. *Nature*, **367**: 554–557.
- Jaenike, J. and Selander, R.K. 1979. Evolution and ecology of parthenogenesis in earthworms. *Am. Zool.*, **19**: 729–737.
- Jokela, J., Dybdahl, M. and Lively, C.M. 2009. The maintenance of sex, clonal dynamics, and host–parasite coevolution in a mixed population of sexual and asexual snails. *Am. Nat.*, **174**: S43–S53.
- Koskella, B. and Lively, C.M. 2009. Evidence for negative frequency-dependent selection during experimental coevolution of a freshwater snail and a sterilizing trematode. *Evolution*, **63**: 2213–2221.
- Lively, C.M. 1987. Evidence from a New Zealand snail for the maintenance of sex by parasitism. *Nature*, **328**: 519–521.
- Lively, C.M. 2009. The maintenance of sex: host–parasite coevolution with density-dependent virulence. *J. Evol. Biol.*, **22**: 2086–2093.
- Lively, C.M. 2010. Parasite virulence, host life history, and the costs and benefits of sex. *Ecology*, **91**: 3–6.
- May, R.M. and Anderson, R.M. 1983. Epidemiology and genetics in the coevolution of parasites and hosts. *Proc. R. Soc. Lond. B*, **219**: 281–313.
- Maynard Smith, J. 1971. What use is sex? *J. Theor. Biol.*, **30**: 319–335.
- Maynard Smith, J. 1978. *The Evolution of Sex*. Cambridge: Cambridge University Press.
- Olofsson, H. and Lundberg, P. 2007. The twofold cost of sex unfolded. *Evol. Ecol. Res.*, **9**: 1119–1129.
- Otto, S.P. and Nuismer, S.L. 2004. Species interactions and the evolution of sex. *Science*, **304**: 1018–1020.
- Pielou, E.C. 1969. *An Introduction to Mathematical Ecology*. New York: Wiley.
- 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.
- Williams, G.C. 1975. *Sex and Evolution*. Princeton, NJ: Princeton University Press.

