THE MAINTENANCE OF SEX

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ABSTRACT: Asexual reproduction theoretically has a high [up to two fold] fitness advantage over sexual reproduction. Yet displacement of sexual populations by asexual clones that arise from them is rare. Previous explanations have given only limited consideration to the environmental changes caused by the growth of the asexual clone itself, with its significantly higher per capita birth rate of females. These changes may initially reduce the adaptedness of the clone and the sexual population. The sexual population has a greater potential than the clone to adapt to the changes, and improve its fitness relative to the clone. The strength of the selection favouring the maintenance of sex should be greater for specialised members of saturated stable communities. This is consistent with the ecology of sex. Significantly, these processes can account for the maintenance of sex in populations that do not continually encounter selective environmental variety. This contrasts with the main previous ecological explanations which require the perpetual operation of intense selection associated with spatial and/or temporal heterogeneity, even in apparently stable and predictable habitats.

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THE PROBLEM OF SEX

At least for the first half of this century, it was widely accepted that the existence of sexual reproduction is sufficiently explained by its function as a mechanism for adaptive evolutionary change. This advantage of sex was often expressed in group selectionist terms as benefiting the species as a whole.

More recently this has been overtaken by recognition of the need to further explain the maintenance of sex within a population between periods of significant evolutionary change, in the face of mutation to efficient parthenogenesis. This need was underlined by Maynard Smith's [1971] theoretical demonstration of a two fold advantage in fitness of asexual reproduction over sexual reproduction in general circumstances. The cost of sex arises where part of the reproductive effort goes into the production of males which don't themselves produce offspring, and which contribute only genetic material to the next generation.

The fundamental difficulty is to explain why it is not common for sexual reproduction to be ousted by mutation to efficient parthenogenesis during long periods of apparent stability and genetic equilibrium in populations. An 'optimal' genotype that also has the advantage of parthenogenesis should prevail in the absence of sufficiently strong countervailing selection.

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PREVIOUS EXPLANATIONS

Most theories devised to overcome this difficulty postulate the existence of spatial and/or temporal variation that impacts differentially on the fitness of genotypes. The variation operates so that no particular genotype, even with the advantage of parthenogenesis, will retain a sufficiently high relative fitness through time to displace a genotypically diverse sexual population. In these circumstances overall selective advantage can accrue to the individual that produces a variety of young through' sexual reproduction.

The main source of variation included in a number of these models is environmental heterogeneity which ensures that no particular genotype can be 'optimal' in all circumstances due to spatial variation or due to other heterogeneity which multiplies niche opportunities [Ghiselin 1974, Williams 1975, Maynard Smith 1978, Bell 1982, Case and Taper 1986, Koella 1988].

Another group of models rely primarily on temporal environmental variation such as fluctuations in abiotic factors, or, consistent with Van Valen's [1973] Red Queen's Hypothesis, continual changes and counter changes in co-evolving organisms such as parasites and their hosts [Williams 1975, Glesener and Tilman 1978, Jaenike 1978, Hamilton 1980, Hamilton et al. 1990, Roughgarden 1991]. Temporal variation which arises within the genetic system itself has also been proposed as preventing any particular genotype from retaining sufficient relative fitness in an asexual clone. Variation of this type includes harmful mutations which accumulate through the process known as Mulier's ratchet [Muller 1932], and damage to the genetic material [Bernstein 1977, Bernstein et al. 1984].

Continual operation of the source of variation is generally an essential feature of these theories. This is because a mutation to efficient parthenogenesis is postulated as being able to occur at any time, and none of the theories involve a mechanism that would 'switch on' the selective variation whenever an efficient clone arises. It is on this basis that occasional directional selection has not been considered sufficient to account for the maintenance of sex; although directional selection is generally accepted as being capable of conferring an overall advantage to sex while it operates with the necessary intensity, this does not explain the absence of successful parthenogenesis before or following the directional selection.

THE CONSEQUENCES OF AN EFFICIENT CLONE

This paper proposes that sex can be maintained through time in stable circumstances without the continual operation of some source of strong selective variation. In certain widely applicable circumstances discussed below, the emergence of a clone that is initially efficient is itself likely to set off changes that can culminate in the clone's demise. In essence, the growth of the clone causes the environmental variation which can provide a selective advantage to sex.

The following discussion focuses on the consequences of the emergence of a single efficient clone. In principle the same processes will apply for each efficient clone that arises, whether or not it is accompanied by other clones. However, mutation to efficient parthenogenesis is generally rare [Williams 1975], and a propensity to mutate to full parthenogenesis would be selected against within a sexual population.

Consider a sexually reproducing population which has coadapted morphological, physiological, behavioural, life history and other traits that, subject to genetic and other constraints, are optimal given specific biotic and abiotic features of the environment e.g. given particular characteristics of food resources, predators, parasites, conspecifics and other competitors. The biotic constituents of the environment in turn exhibit traits whose optimal values are influenced by the characteristics of the given population.

An efficient parthenogen that arises from the sexual population will in this sense be initially optimally adapted to the community, except that it will also produce up to twice as many reproducing progeny as its sexual counterpart, due to the advantage of parthenogenesis. It is important to recognise that any capacity of the clone to threaten the sexual population arises from the environmental impact of this higher per capita birth rate of females. For the clone to displace the sexual population, the impact has to be sufficient to ensure that the sexual population can no longer reproduce itself. The specific impacts of the growth of the clone on the environment will depend on the particular circumstances, but may include changes to the availability of food resources, the density of predators or parasites, the characteristics of competitive interactions with other species and con-specifics, and the nature of competition for non-food resources. Even if the overall density of the organism does not change due to density dependent regulation of the population, its ecological relationships are still likely to vary because the population's total production of offspring will increase as the proportion of asexuals grows.

In addition to these direct ecological consequences, members of the biotic community, including the original sexual population itself, may adapt genetically to the changed circumstances arising from the growth of the clone. All these changes may in turn set off further changes, and so on, propagating sequences of change in the community through time. Some of these changes may be greater than otherwise because the parthenogenetic population has very little capacity to adapt to them genetically.

In general, the extent of the impact of the growth of the clone will be frequency dependent, as will the selection which results from it.

The important consequence of these environmental changes is that characteristics of the environment which are critical in determining the fitness of the parthenogenic genotype may be significantly different from those to which the genotype was initially adapted. To the extent that this occurs, the parthenogenic population will no longer be optimally adapted to this changed environment, and the extent of this maladaptation may vary through time.

The sexual population has a far greater potential than the clone to adapt to any changed circumstances, and to thereby improve its fitness relative to the asexual clone. Any such adaptation would, of course, result from selection operating at the level of the individual.

The nature of these processes should not be significantly changed where the clone may be initially ecologically different to the parental sexual population e.g. where the clone arises by a hybridization event [Bierzychudek 1985]. The growth of such a clone is still likely to set off environmental changes which may reduce its fitness, and there does not appear to be any mechanism which would somehow ensure that the clone would turn out to be fitter in the changed circumstances than variants produced by the sexual population.

CONDITIONS THAT FAVOUR SEX

The fundamental issue is whether the sexual population will increase its fitness through adaptation sufficiently to overcome any fitness advantage accruing to the clone because of its initially higher per capita birth rate of females.

The potential for the relative fitness of the sexual population to improve will be significantly influenced by the extent to which environmental characteristics which are ecologically important to the clone are changed by its growth, and the effects of this on the adaptedness of the clone.

The critical determinants of this can be explored in broad terms using Hutchinson's [1957] representation of a population's fundamental ecological niche as the n-dimensional hypervolume defining the entire range of conditions in which the population can replace itself. Each axis represents a biological or physical environmental variable. The range along each axis within which the population displays a given level of performance can be characterised as more or less specialised relative to other species' populations. Populations can also differ in the number of environmental variables for which they are specialised. Specialisations to particular ranges of environmental variables will generally be reflected in correspondingly specialised complexes of behavioural, physiological, life history or other traits. Where an environmental variable takes on values outside the range which is optimal for the population, fitness will decline. Subsequent evolution of the relevant traits can, in principle, tend to improve fitness by optimising the traits to the new values, subject to genetic and other constraints. Where the values fluctuate, selection may favour reduced specialisation in some circumstances.

It can be readily seen that the impact on fitness of a given environmental change is likely to be greater the more narrowly specialised a species. Consequently, the more narrowly specialised the members of an invariant clone, the greater the likely decline in their adaptedness as the environment changes, and the greater the likely potential for the remaining sexual population to overcome any fitness differential through adaptation to the new circumstances. Conversely, the adaptedness of a more versatile, robust generalist is likely to be less affected as the environment changes.

Adaptation by the sexual population to the changed circumstances is likely to occur more readily where this can proceed through '"re- optimising' existing traits, particularly where this involves quantitative rather than qualitative changes in traits, and where the traits have previously undergone optimising processes. Again, this is more likely for highly adapted and specialised species.

Ecological conditions which are said to promote specialisation [and which should therefore promote the processes I have described] include: relatively stable, predictable environments which allow finer specialisation and narrower niches [Pianka 1966] and which also allow the extensive coevolution of communities, resulting in increased biological accommodation and associated specialisation [Slobodkin and Sanders 1969]; and saturated environments with high levels of interspecific competition where specialists may be more efficient and therefore exclude generalists [MacArthur and Levins 1964]. Futuyma and Moreno [1988] provide a recent review.

The processes I have outlined are also likely to be further strengthened in highly coevolved communities where the growth of the clone is more likely to set off changes and counter-changes in other members of the community. These in turn may impact on the clone and its parental sexual population, and so on.

The relative importance to fitness of the clone's initially superior per capita birth rate of females will also vary with circumstances [MacArthur and Wilson 1967, Pianka 1978]. Consider a sexual population and an efficient clone arising from it that are initially ecologically equivalent except for the clone's higher per capita birth rate of females. As the sexual population adapts, the equivalence will end. If it were not for the clone's higher per capita birth rate of females, the sexual population would be fitter. This higher birth rate will contribute relatively more to fitness in species that compete largely on the basis of fecundities e.g. species in highly variable and unpredictable environments where density independent factors often cause mass mortality that has relatively little to do with the genotypes and phenotypes of the organisms involved. In contrast, the higher birth rate will contribute relatively less to fitness where efficient use of limiting scarce resources is more important than rapid population growth. At the theoretical extreme of full truncation selection, the higher birth rate will make no contribution to fitness at all e.g. in saturated habitats where only those individuals that rank sufficiently highly in coping with strong competition and high Gensities contribute to the next generation. The ability to produce greater numbers of genotypes will be irrelevant if the genotypes are otherwise inferior and don't rank sufficiently highly to breed. In these circumstances, any relative improvement in the fitness of the sexual population will tend to oust the clone. In theory, the sexual population would also prevail where the clone is inferior for any other reason e.g. if the clone is initially more specialised than the sexual population, it may suffer a greater decline in fitness as a result of the environmental changes. The potency of truncation selection in overcoming any advantage accruing from a clone's higher birth rate of females is illustrated by Hamilton et al's [1990] model of parasite and host coevolution.

In some circumstances, the sexual population may also adapt to the growth of a clone in ways which reduce competition with the asexual population e.g. by exploiting some resources not efficiently utilized by the clone. Case and Taper [1986] have considered resource competition between an asexual and a sexual species where the sexual species has a larger overall niche width than the asexual. Thus the sexual population exists partly in a "competitor-free space" where the asexual clone has almost no influence on the outcome of the interaction. Case and Taper's models predict that coexistence or displacement of the asexual can occur under certain conditions. Koella [1988] argues that when the dynamics of the competitive interaction are also considered, the rather narrow circumstances in which displacement of the asexual is predicted are widened. Koella provides a model in which the higher rate of increase of a clone contributes to the destabilisation of the dynamics of the two-population system.

However, neither of these approaches include the processes which are central to my hypothesis. The mechanism I have described can account for the success of a sexual population over a clone where they are in direct competition for the same resources i.e. where there is no differential niche width or similar feature that provides the sexual population with an area of reduced competition. My hypothesis relys on the parental sexual population producing variants that are able to directly outcompete the clone in the changed circumstances resulting from the growth of the clone. In contrast, neither Koella or Case and Taper include these processes, and both predict that the sexual population will be displaced where there is only direct competition for the same resources, and no mechanism such as differential niche width that reduces it.

In summary, the effects I have described will be particularly strong for low fecundity, specialised members of saturated, apparently stable communities. The effects will be weaker for robust generalists. This broadly accords with the ecological evidence which indicates that climax or "k-selected" kinds of species are usually sexual, and that the ""r-selected", colonising life forms are more likely to be parthenogenetic [Hamilton et al. 1990]. The evidence is reviewed in detail by Bell (1982) for animals, and by Bierzychudek [1985] for higher plants.

CONCLUSION

There is no generally accepted, comprehensive solution to the problem of what maintains sex after adaptation has produced an optimal genotype which could apparently be perpetuated more efficiently by cloning: Hamilton et al. [1990] wrote that "Darwinian theory has yet to explain adequately the fact of sex", and Roughgarden [1991] wrote that "Sexual reproduction raises the major unsolved problem of biology today: why do almost all organisms reproduce sexually rather than asexually?"

As we have seen, the main previous ecological explanations attempt to dissolve the problem by proposing that genetic adaptation is never complete in the sense that a single optimal genotype is never achieved; due to perpetual heterogeneity in space and/or time, there is continual benefit to the individual in the production of genetically variant progeny in the chance that some will be sufficiently adapted to the environmental circumstances they encounter.

The search for plausible ecological circumstances that would provide the required endless variation in relative fitness has produced a diversity of models. However, it is not possible to directly assess with any precision the extent to which many of the assumptions and processes which underpin the models correspond to actual circumstances. For example, little is known of the pattern and frequency of abiotic and biotic environmental change experienced by actual populations, or the magnitude of any corresponding changes in fitness.

None of the models have been accompanied by a comprehensive metatheory which would explain, for example, why the required ecological circumstances would necessarily apply perpetually with the ubiquity of sex, and why evolution would not produce, at least in some circumstances, an optimal genetic arrangement that would effectively deal with environmental heterogeneity without continual genetic adaptation e.g. some form of phenotypic plasticity, or, at the other extreme, robustness.

On the contrary, Bateson [1963] and Slobodkin and Rapoport [1974] have begun the development of a theoretical framework which suggests that for many organisms, genetic changes will be more of a last resort response to environmental perturbations; genetic adaptation will occur only after the failure of faster acting phenotypic responses that commit less of the resources of the organism or population. Selection favouring the evolution of mechanisms of phenotypic adaptation will be stronger where genetic adaptation is slower acting and its cost is higher e.g. in low fecundity, long lived species with a relatively high investment of resources per individual. However, this theoretical framework is not inconsistent with genetic adaptation operating as the primary response to on-going environmental variation in high fecundity, short lived species [see the models of Williams 1975]. In these circumstances, repetitive, non-progressive genetic adaptation can be a fast acting, low cost response to perturbations that may be dealt with in other organisms by similarly repetitive, non-progressive, physiological adaptation.

The lack of general acceptance of the previous explanations of sex seems to arise because the conditions under which they succeed do not appear to be sufficiently universal, and there are neither strong empirical or theoretical grounds to suggest otherwise; it seems unlikely that the endless and intense selective variation required by the models would be proposed as being almost universal if there were no need to explain the ubiquity of sex.

The hypothesis I have outlined points to a mechanism which can maintain sex without the continual operation of selective variation; for sex to be maintained, there need be no advantage to sex except when a clone arises. The mechanism will be particularly effective in circumstances where previous ecological theories have most difficulty in plausibly accounting for the maintenance of sex i.e. for low fecundity specialists which are subject to stable biotic and abiotic conditions which do not give rise to continual selective variation.

In these circumstances a sexual population can outcompete an efficient clone that arises from it because the sexual population can better adapt to the environmental changes resulting from the clone's higher per capita birth rate of females. Although asexuality can reproduce a given genotype more efficiently than sex, a clone has a very limited capacity to coevolve with the changes that result from this superior efficiency.

It is ironic that this attempt to resolve the paradox of sex seems to raise another: the inability of asexual reproduction to oust sex in common circumstances arises in part from the consequences of its supposed advantage over sex; its higher per capita birth rate of females. However, this is paradoxical only from the same perspective that gave rise to the original paradox of sex.

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