



A Bit of Sex Stabilizes Host–Parasite Dynamics

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To date, only a few studies have focused on the effects of sex on population dynamics. Previous models have typically found that sexual reproduction dampens population fluctuations. Although asexual and sexual reproduction are just the two endpoints along a continuum of varying rates of sex, previous work has ignored the effects of intermediate degrees of sex on population dynamics. Here we study the effects of partial sexual reproduction (i.e. sex occurs only every few generations or with small probability in each generation) on the coupled population dynamics of a Nicholson–Bailey host–parasite model. We show that complex dynamics are simplified for high host population growth rates if the frequency of sex is sufficiently high in both host and parasite: sex decreases fluctuations in population density, and leads to non-chaotic dynamics for population growth rates that would result in chaotic dynamics in the absence of sexual reproduction. However, the simplification does not increase gradually with an increasing frequency of sex but appears abruptly at low-to-intermediate frequencies of sex. For some parameter settings, intermediate frequencies of sexual reproduction can simplify the dynamics more than lower or higher frequencies. Thus, in agreement with earlier results, sexual reproduction typically stabilizes complex population dynamics in our models. Additionally, our results suggest that low-to-intermediate frequencies of sex may often be as (or even more) stabilizing as high frequencies.

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Introduction

While traditional ecological modelling deals with asexual organisms, only a few studies have focused on the effects of sexual reproduction on population dynamics, i.e. changes of the number of individuals or population densities over time (e.g. Doebeli & Koella, 1994; Castillo-Chavez & Huang, 1995; Doebeli, 1995, 1996, 1997; Ruxton, 1995; Lindström & Kokko, 1998; Doebeli & De Jong, 1999; Ranta *et al.*, 1999). Previous

models show that sexual reproduction with segregation at one locus can drastically simplify population dynamics through coupling among genotypes, thereby reducing the propensity of the system to exhibit chaotic dynamics (Doebeli & Koella, 1994; Doebeli, 1995; Ruxton, 1995; Doebeli & De Jong, 1999). This simplification is enhanced if phenotypic variation is given by quantitative characters which are determined additively by many haploid or diploid loci, assuming that phenotypes differ in their dynamic behaviour (Doebeli, 1996, 1997). However, other authors found that sex does not necessarily affect population dynamics (Castillo-Chavez & Huang, 1995) or that it leads to destabilization, particularly when sexual dimorphism or complicated

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mating systems are considered (Lindström & Kokko, 1998; Ranta *et al.*, 1999).

Previous work has investigated the influence of sex on population dynamics by examining the competition between sexual and asexual populations (Hamilton, 1980, 1982; May & Anderson, 1983; Koella, 1988; Hamilton *et al.*, 1990; Doebeli, 1995), by comparing the dynamics of sexual and asexual systems (Doebeli & Koella, 1994; Ruxton, 1995; Doebeli, 1997), or by allowing sexual reproduction to occur through varying fractions of assortative vs. random mating (Ruxton, 1995). These studies suggest an increasing simplification of the dynamics from asexuality to sexuality but ignore the effects of intermediate degrees of sexual reproduction. However, asexuality and full sexuality are the two endpoints along a continuum of varying degrees of sexual reproduction. For example, bacteria vary from being panmictic to clonal, many angiosperm plants have varying levels of self-fertilization, and many fungi, eukaryotic microorganisms and invertebrates alternate long periods of asexual reproduction with periods of sex (Hebert, 1987; Hurst & Peck, 1996; Birky, 1999; Seger, 1999).

Here we study the effects of the whole range of partial sexual reproduction on population dynamics, from asexuality to sexuality. For this purpose we introduce population genetics into a well-known host–parasite model, the Nicholson–Bailey model, and examine how different combinations of frequencies of sex in the host and in the parasite affect the dynamics of the system. We have chosen the Nicholson–Bailey model for two reasons. First, we do not attempt to model a specific biological system with partial sexual reproduction but rather investigate the effects of partial sexual reproduction on the dynamics of this quite general two-species model, having well-known dynamical properties (e.g. Beddington *et al.*, 1975). The Nicholson–Bailey model can be applied quite generally to discrete-time host–parasitoid, host–parasite and predator–prey systems. Second, we are interested in the role of sexual reproduction in host–parasite systems. It has been suggested that sex has evolved and is being maintained because of the co-evolutionary dynamics in host–parasite systems. For instance, recombination may benefit a host through the production of genetically variable offspring,

thereby hindering the evolution of the parasite into an optimal level of virulence (Red Queen hypothesis; e.g. Ebert & Hamilton, 1996). However, recombination may not be the only reason why sexual reproduction is evolutionarily advantageous in host–parasite systems. First, if sex dampens population fluctuations, group selection may favour its evolution because systems with smaller fluctuations are less threatened by extinction due to chance events than systems with large fluctuations (e.g. Berryman & Millstein, 1989). Second, a smaller variance in fitness implies a higher geometric mean fitness (Gillespie, 1977), and decreased fluctuations can, in principle, lead to an evolutionary advantage of sexual reproduction based on individual selection. For instance, Hamilton (1980, 1982; see also Hamilton *et al.*, 1990) studied the effect of sex on the dynamics of gene frequencies in host–parasite models and observed that sex reduces the fitness variance in frequency-dependent host–parasite systems, leading to a higher mean population growth rate. Thus, understanding how sexual reproduction influences the population dynamics of host–parasite systems is an important issue in evolutionary ecology.

Here we show that the frequency of sex considerably influences the dynamics of the Nicholson–Bailey host–parasite system. Particularly, we demonstrate that “a bit of sex”, i.e. low-to-intermediate frequencies of sex, can be as (or even more) stabilizing for population dynamics as “a lot”, where we use the term “stabilization” in its intuitive meaning of a reduction in the magnitude and complexity of population fluctuations. Thus, low-to-intermediate frequencies of sex can, for example, stabilize the system by reducing its dynamic complexity from chaos to stable limit cycles.

The Model

Our starting point is the Nicholson–Bailey host–parasite model with self-regulation in the host (Beddington *et al.*, 1975). The model is set in discrete time and has the following form. Let H_t and P_t be the host and parasite densities at time t . Then,

$$\begin{aligned} H_{t+1} &= H_t \exp[\ln(\lambda) (1 - H_t/K) - aP_t], \\ P_{t+1} &= c H_t [1 - \exp(-aP_t)]. \end{aligned} \quad (1)$$

The growth of these populations is governed by λ , the host population growth rate, and by c , the conversion rate of attacked hosts into parasites, i.e. the parasite's fecundity in terms of the mean number of parasites emerging from a successfully attacked host. The growth of the host population is assumed to be density dependent, and K represents the host's carrying capacity. Note that we are working with population densities (i.e. real numbers), not numbers of individuals (i.e. integers). Thus, we are assuming—like most genetic and ecological models—infinately large populations. This assumption is realistic in the limit of large population size. The parameter a is a measure of the parasite's searching efficiency, and the term $\exp(-a P_t)$ is the probability that a host individual escapes parasitism. This exponential term corresponds to assuming a Poisson distribution describing the number of encounters of a host facing a population of P_t parasites with searching efficiency a (Edelstein-Keshet, 1987). Thus, a particular host individual is parasitized and converted with probability $[1 - \exp(-aP_t)]$ into c parasite individuals. The dynamics of the system range from stable equilibria to limit cycles or chaos, depending on parameter values. The dynamics are mainly determined by the host population growth rate λ and by a , the parasite's searching efficiency. If the parasite is extremely efficient (large a), it is able to hold hosts below their carrying capacity, K , and the dynamics are determined more strongly by the unstable host-parasite interaction. If the parasite is inefficient (small a), the dynamics are determined largely by the density-dependent feedback in the host. In the absence of the parasite, K is an equilibrium of the host dynamics which may be stable or unstable depending on the value of λ . In isolation, the host dynamics undergoes a series of period-doubling bifurcations as λ increases, and the dynamics can be chaotic if λ is large enough.

To study how different frequencies of sex affect population dynamics, we extend model (1) by incorporating population genetics. Let the genetics of both host and parasite be governed by one locus with two alleles. We assume that the three host genotypes produce three different phenotypes and that each of these phenotypes is susceptible to a specialized parasite. For this

purpose, we use a diploid matching-alleles model: the host genotypes AA , Aa and aa are susceptible to the parasite genotypes BB , Bb and bb , respectively. In all other pairings the parasite is assumed to be ineffective. This very simple matching-alleles model rests on the commonly made assumption that parasite genotypes cannot be optimally adapted to different host genotypes (Parker, 1994; Frank, 1996). Other models of host-parasite susceptibility (e.g. gene for gene interactions) are likely to change the effects of partial sexual reproduction on population dynamics, but this is beyond the focus of the present paper. Let $H_{AA,t}$, $H_{Aa,t}$, $H_{aa,t}$, and $P_{BB,t}$, $P_{Bb,t}$, $P_{bb,t}$, be the densities of the host and parasite genotypes at time t . At the beginning of each generation, three pairs of demographic recursion equations of type (1) determine the interaction between hosts and parasites. Each pair consists of the equations for the population dynamics of the respective parasite genotype IJ ($I = B, b$; $J = B, b$) and its susceptible host genotype ij ($i = A, a$; $j = A, a$):

$$H'_{ij} = H_{ij} \lambda \exp(-H \ln \lambda/K) \exp(-aP_{IJ}),$$

$$P'_{IJ} = c H_{ij} [1 - \exp(-aP_{IJ})]. \quad (2)$$

where $H = H_{AA} + H_{Aa} + H_{aa}$ is the total host density before selection. For simplicity, we have omitted the subscript t in these equations, and the superscript ' denotes densities after selection, i.e. after the host-parasite interaction. Here we have assumed that the different host and parasite genotypes only differ in their compatibility to each other, but not in their demographic parameters. After selection resulting from the host-parasite interaction, reproduction occurs in both host and parasite. Note that we do not allow for mutation, i.e. allele frequencies change due to selection only.

For simplicity, we assume that only females contribute to and limit the rate of population growth (demographic dominance of females; Charlesworth, 1994). Thus, we are assuming that the population dynamics are determined by the female sex independent of the relative abundance of males. This implies that there are no demographic sex differences, a 50:50 sex ratio, and that males (not being explicitly modelled) are always

abundant enough to fertilize all females (Caswell, 1989).

To study the effects of the frequency of sex on population dynamics we introduce the control parameter \mathcal{G} that determines the amount of sexual reproduction in the system. We define \mathcal{G} as the frequency of sex, ranging from complete asexuality ($\mathcal{G} = 0$) to complete sexuality ($\mathcal{G} = 1$). If $\mathcal{G} > 0$, sexual reproduction is assumed to occur through random mating. For instance, if $\mathcal{G} = 0.2$, 20% of the population is involved in random mating in a given generation whereas 80% of the population reproduces asexually. The frequencies of sex of host and parasite are denoted by \mathcal{G}_H and \mathcal{G}_P , respectively. In the host, the frequency of allele A after selection, p' , is given by

$$p' = \frac{H'_{AA} + \left(\frac{H'_{Aa}}{2}\right)}{H'} \quad (3)$$

where H'_{AA} and H'_{Aa} are given by eqns (2), and where $H' = H'_{AA} + H'_{Aa} + H'_{aa}$ is the total host density after selection. With Mendelian segregation, the new densities of the host genotypes AA , Aa and aa at time $t + 1$ after random mating are given by

$$\begin{aligned} H_{AA,t+1} &= (1 - \mathcal{G}_H) H'_{AA} + \mathcal{G}_H p'^2 H' \\ H_{Aa,t+1} &= (1 - \mathcal{G}_H) H'_{Aa} + \mathcal{G}_H 2p'(1 - p') H' \\ H_{aa,t+1} &= (1 - \mathcal{G}_H) H'_{aa} + \mathcal{G}_H (1 - p')^2 H'. \end{aligned} \quad (4)$$

The total density at time $t + 1$ is simply $H_{t+1} = H' = H_{AA,t+1} + H_{Aa,t+1} + H_{aa,t+1}$. Similarly for the parasite, let

$$q' = \frac{P'_{BB} + \left(\frac{P'_{Bb}}{2}\right)}{P'} \quad (5)$$

be the frequency of allele B after selection and $P' = P'_{BB} + P'_{Bb} + P'_{bb}$ the total density of the parasite. Then,

$$\begin{aligned} P_{BB,t+1} &= (1 - \mathcal{G}_P) P'_{BB} + \mathcal{G}_P q'^2 P', \\ P_{Bb,t+1} &= (1 - \mathcal{G}_P) P'_{Bb} + \mathcal{G}_P 2q'(1 - q') P', \\ P_{bb,t+1} &= (1 - \mathcal{G}_P) P'_{bb} + \mathcal{G}_P (1 - q')^2 P'. \end{aligned} \quad (6)$$

give the densities of the parasite genotypes at time $t + 1$. Note that

$$P_{t+1} = P' = P_{BB,t+1} + P_{Bb,t+1} + P_{bb,t+1}.$$

We studied the effects of the frequency of sex on population dynamics by examining a wide range of combinations of the parameters \mathcal{G}_H , \mathcal{G}_P , and λ , using computer simulations. For a given parameter combination, we let the system run for 100 000 generations to remove transient effects of the initial conditions and then displayed the parasite (or host) population density for the next 40 generations in bifurcation diagrams, using either λ or \mathcal{G}_P (or \mathcal{G}_H) as the bifurcation parameters. We used such a long warm-up time to increase the likelihood of observing asymptotic, i.e. equilibrium, dynamics. Furthermore, using long warm-up times allows us to avoid “long transient” dynamics which may be present in complex ecological models (Hastings & Higgins, 1994). Populations were assumed to be extinct if their density dropped below a certain threshold. This threshold was set to 10^{-14} , representing the lowest viable population density. That is, whenever densities fell below this threshold, then the corresponding simulation was stopped. Initial allele frequencies for host and parasite were randomized to avoid starting the system at an unstable fixed point (e.g. $p = 0.5$).

Results

Our extensive numerical simulations suggest that the examples shown in Figs 1–3 are representative of the effects of sexual reproduction on population dynamics in our system over a wide range of parameter settings. We studied the dynamics of the system both in dependence of λ (for different combinations of \mathcal{G}_P and \mathcal{G}_H) and \mathcal{G} (for different values of λ and \mathcal{G} in the other species).

First, we used λ as the bifurcation parameter and compared the dynamics for different values of \mathcal{G}_P while keeping \mathcal{G}_H constant. For example, we compared how different frequencies of sex of the parasite ($\mathcal{G}_P = 0, 0.5, 1$) affect the dynamics if the host is assumed to be fully sexual ($\mathcal{G}_H = 1$). Figure 1 shows a typical example of the dynamics in dependence on the host growth rate λ .

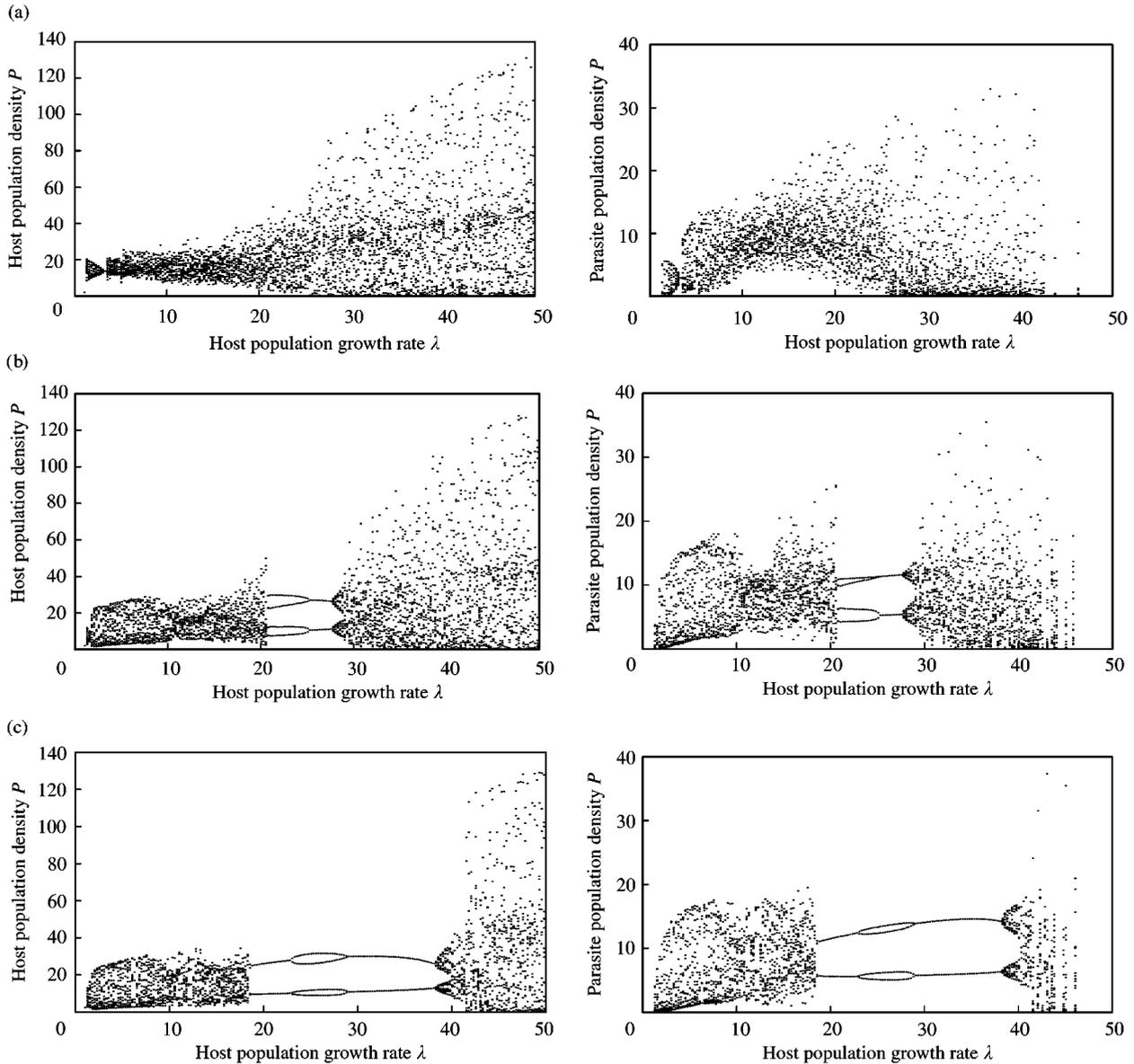


FIG. 1. Bifurcation diagrams for different frequencies of sex of the parasite \mathcal{G}_p with the host population growth rate λ as the bifurcation parameter. The host is assumed to be sexual ($\mathcal{G}_H = 1$). (a) Asexual parasite ($\mathcal{G}_p = 0$), (b) parasite with an intermediate frequency of sex ($\mathcal{G}_p = 0.5$), (c) sexual parasite ($\mathcal{G}_p = 1$). Increasing \mathcal{G}_p simplifies the dynamics by dampening fluctuations in population density and by moving the system onto stable limit cycles for a wide range of λ . Note the similarities in the dynamics of host and parasite. Parameter combinations used in the simulations were $H_0 = 10$, $P_0 = 1$, $K = 10$, $p = 0.55$, $q = 0.48$, $c = 1$, $a = 0.45$.

Generally, the dynamics of both host and parasite are similar because they are demographically coupled through the host–parasite interaction. Whereas sexual reproduction in the host results in the genetic coupling of the three host genotype subpopulations, the asexual parasite consists of three genetically uncoupled genotype subpopulations [Fig. 1(a)]. Despite the genetic coupling in

the host, the dynamics of the system are chaotic for a wide range of host growth rates. For increasing values of λ , fluctuations in population density rapidly reach high amplitudes [Fig. 1(a)]. In contrast, increasing the frequency of sex of the parasite to $\mathcal{G}_p = 0.5$ simplifies the dynamics of both host and parasite [Fig. 1(b)]. When compared to the asexual system [$\mathcal{G}_p = 0$; Fig. 1(a)],

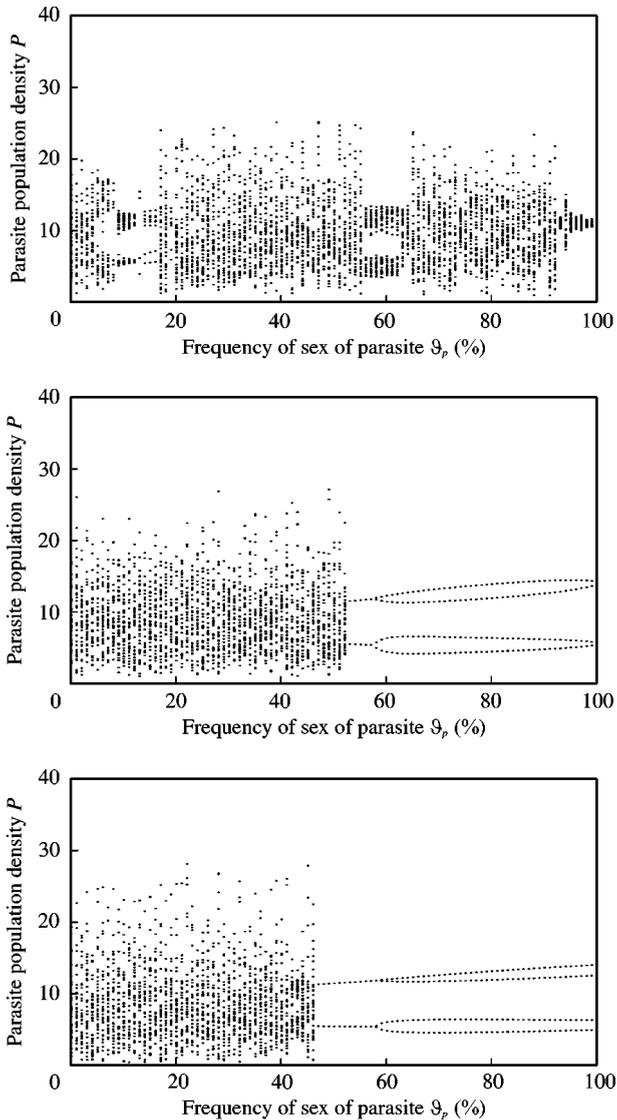


FIG. 2. Bifurcation diagrams for different frequencies of sex of the host g_H with the frequency of sex of the parasite g_p as the bifurcation parameter. In all cases, the dynamics of the host (not displayed) are qualitatively similar to the dynamics of the parasite. $\lambda = 26$ and $g_H = 0.1$ (top), $g_H = 0.7$ (centre), $g_H = 0.9$ (bottom). All other parameters were as in Fig. 1. Simple dynamics occur abruptly whenever g is sufficiently high in both host and parasite.

there is a window of λ values with simple dynamics [$20 \lesssim \lambda \lesssim 28$; Fig. 1(b)]. Full sexual reproduction in the parasite ($g_p = 1$) simplifies the dynamics even more [Fig. 1(c)]. Genetic coupling in the parasite has two consequences. First, it considerably dampens fluctuations in population density for most values of λ ($\lambda \lesssim 42$) in both host and parasite. Second, there is a large window of simple dynamics in both host and parasite,

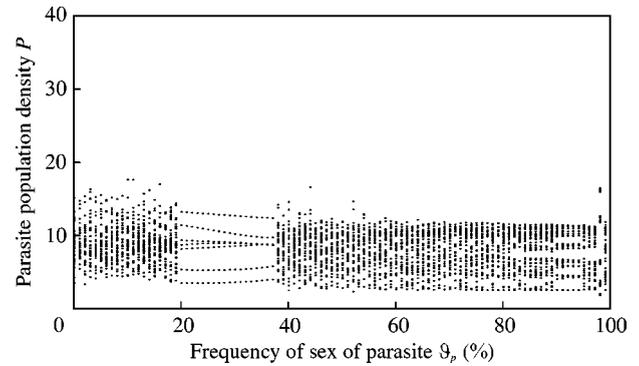


FIG. 3. Bifurcation diagram with the frequency of sex of the parasite g_p as the bifurcation parameter. The host is assumed to be sexual ($g_H = 1$). Note that the dynamics of the host are analogous to the dynamics of the parasite but that host population density is not displayed for reasons of clarity. $\lambda = 12$; all other parameters were as in Fig. 1. Intermediate frequencies of sex can simplify the dynamics more than lower or higher frequencies of sex.

leading to stable cycles of periods 2 and 4 for a wide range of λ ($18 \lesssim \lambda \lesssim 38$).

Second, we used g_p as the bifurcation parameter and compared the dynamics for different combinations of λ and g_H . Three observations are notable. First, whether a given combination of g_p and g_H leads to a simplification of the dynamics depends on λ . For high values of λ (e.g. $20 \lesssim \lambda \lesssim 36$) simple dynamics are observed whenever the frequency of sex is sufficiently high in both host and parasite (Fig. 2, top to bottom). In contrast, typically no simplification was observed for low values of λ (e.g. $\lambda = 5$), irrespective of the combination of values of g_p and g_H (not shown). Second, if λ is high enough, low-to-intermediate frequencies of sex are typically sufficient for a simplification of the dynamics, suggesting that “a bit of sex” is often enough to stabilize population dynamics, i.e. to reduce fluctuations in population densities and lead to non-chaotic dynamics (Fig. 2, centre and bottom). For instance, the changes in the dynamics are much larger if g_p is changed from a low to an intermediate value than if it is increased further to higher values. This simplifying effect does not gradually increase with an increasing value of g_p but appears abruptly, as a sudden transition from a region with complex dynamics to one with simpler dynamics. Note that λ can be interpreted as the maximal reproductive output under ideal conditions; it can therefore reach very high values.

Density dependence will lead to a geometric mean of the realized population growth rates equal to 1, even if λ is very high. High values of λ (e.g. $\lambda = 50$) are not necessarily biologically unrealistic (see e.g. Hassell *et al.*, 1976; Bellows, 1990). Generally, a simplification occurs whenever both \mathcal{G}_P and \mathcal{G}_H exceed a threshold value, \mathcal{G}_{Pcrit} and \mathcal{G}_{Hcrit} , respectively (typically $0.3 \lesssim \mathcal{G}_{Pcrit} \lesssim 0.6$ and $0.1 \lesssim \mathcal{G}_{Hcrit} \lesssim 0.3$, depending on parameter settings). Because the range of \mathcal{G}_{Pcrit} values is larger than that of \mathcal{G}_{Hcrit} values, simplification is usually stronger if \mathcal{G} is changed in the parasite than in the host, suggesting that there is an asymmetry between host and parasite. Third, irrespective of the value of λ and for a given value of \mathcal{G}_H , there are cases in which complex dynamics are interrupted by small or large windows of simple dynamics (e.g. $0.2 \lesssim \mathcal{G}_P \lesssim 0.4$), suggesting that too low or too high frequencies of sex may lead to more complex population dynamics than intermediate frequencies (Fig. 3).

Discussion

We have shown that sexual reproduction can “stabilize” the population dynamics of the Nicholson–Bailey host–parasite model with self-limitation in the host in two ways: (i) it decreases fluctuations in population density and (ii) it moves the system onto stable limit cycles for population growth rates that would result in complex dynamics in the absence of sexual reproduction (e.g. Fig. 1). In particular, we have demonstrated that low-to-intermediate frequencies of sex are typically sufficient for a simplification of the dynamics (e.g. Fig. 2). Whereas most previous models have focused on the effects of sex on the dynamics of single species, here we have investigated how sex affects the population dynamics of two interacting species (see also Doebeli & Koella, 1994; Doebeli, 1997).

Previous theoretical work has demonstrated that one-locus two-allele genetics leading to complete mixing through sexual reproduction can simplify ecological dynamics when compared to asexual systems (e.g. Doebeli & Koella, 1994; Doebeli & De Jong, 1999). It is worth noting that in these models, as well as in ours, the effects of sex on population dynamics are due to segrega-

tion, not recombination, since only a single locus is considered. Similarly, Ruxton (1995) has compared an asexual with a sexual system in which mating is assortative. He showed that when mating occurs only between individuals of the same genotype, the production of homozygous offspring from two heterozygous parents leads to a coupling of populations of different genotypes that simplifies the dynamics of the system. Furthermore, he showed that the addition of small amounts of random mating across genotypes reduced the propensity of the sexual system to exhibit chaos even further. However, sexual reproduction does not always stabilize population dynamics. Most models investigating the effect of sex on population dynamics are one-sex models, considering only the female sex explicitly. Although this is a common assumption of demographic models, it is to a certain extent unrealistic and restrictive. Consequently, two-sex demographic models have been developed (e.g. Caswell, 1989). As shown by Lindström & Kokko (1998) the direct role of males in reproduction and density dependence does not necessarily stabilize population dynamics. In such two-sex models, sexual reproduction can even lead to destabilization, e.g. when particular mating systems are considered (Lindström & Kokko, 1998; Ranta *et al.*, 1999).

Here we have set aside the complications arising in two-sex models and instead we have concentrated on the question of how much sex is needed to achieve a qualitative change in the dynamic behaviour of a general model. Thus, whereas previous models have focused on the effects of full sexual reproduction on population dynamics, we have explored the consequences of the whole range of partial sexual reproduction, from fully asexual to fully sexual populations. In agreement with earlier results we generally find a simplification of the dynamics that is due to the coupling of genotype subpopulations through sexual reproduction. However, our results suggest that the stabilization of population dynamics does not require full sexual reproduction. In our model the simplifying effects of sex can be observed already for low-to-intermediate frequencies of sex (e.g. Figs 2 and 3). This suggests that organisms with partial sexual reproduction may potentially benefit both from stable population

dynamics and from a reduced two-fold cost of sex by reproducing asexually most of the time, but occasionally reproducing sexually. Since we are considering periodic sexual reproduction, the organisms to which our model might apply could be protozoans, unicellular algae, digenean trematodes, monogonot rotifers, cladocerans, aphids or other species with occasional sex (e.g. Hebert, 1987). Examples for host–parasite systems in which both species may have periodic sex may be cyclical parthenogenetic *Daphnia* and their microparasites (e.g. microsporidians) which are likely to be occasionally sexual. Host–parasite systems that combine both sexual and asexual reproduction include trematode parasites (e.g. *Microphallus* spp., *Uvulifer* spp.), having asexual and sexual life history stages, that infect both asexual and sexual populations of snail hosts (*Potamopyrgus antipodarum*) or fish (*Poeciliopsis monacha*), respectively (e.g. Lively, 1990; Lively *et al.*, 1990).

There seem to be some interesting analogies between our findings and previous theoretical studies on the evolutionary and ecological consequences of sex. These studies often suggest that most of the evolutionary and ecological “benefits” of sexual reproduction may already be obtained if only a small proportion of offspring are produced by sexual means (Charlesworth *et al.*, 1993; Green & Noakes, 1995; Hurst & Peck, 1996; Peck *et al.*, 1997). For instance, Lynch & Gabriel (1983) have demonstrated that periodic sex can allow for much higher rates of phenotypic evolution than full sexuality, and work by Bell (1988) suggests that a very low rate of sex (i.e. recombination) may be enough to overcome the accumulation of deleterious mutations (i.e. Muller’s ratchet). Similarly, it is conceivable that the simplification of population dynamics through “a bit of sex” may be evolutionarily advantageous if it leads to a reduction of the variance in fitness, thereby increasing geometric mean fitness (Hamilton, 1980). That individual selection can favour sexual over asexual reproduction because sexuals have simpler dynamics than asexuals has been shown by Doebeli (1995). However, it remains unclear at present how general the phenomenon of “a bit of sex” being as advantageous as “a lot” is. If it is general, the question arises why partial sexual reproduction is

not more common (Green & Noakes, 1995; Hurst & Peck, 1996; Peck & Waxman, 2000).

What are the mechanistic causes for the stabilizing effects of sexual reproduction on population dynamics? Intuitively, sexual reproduction blurs the deterministic details of interactions between phenotypes leading to chaos by evening out the fluctuations in their densities. In the mathematical sense, stabilization of the population dynamics through sex can, for instance, be due to a reduction of the number of attractors and/or due to an enlargement of their basins of attraction. Such a stabilizing mechanism has been investigated by Doebeli (1995) who analysed the effects of sex on the dynamics of a single-species model of population growth introduced by Hassell (1975). Variability was introduced by assuming that different phenotypes (or genotypes) have different dynamical behaviours, ranging from stable equilibria to chaos. In the asexual case, the system displays many different attractors which can display many different dynamic behaviours, depending on the point in the set of equilibria from which the system is perturbed away. In this model, sex drastically reduces the number of attractors and thus the number of asymptotic behaviours. Sex enlarges the basins of attraction so that the dynamics become less dependent on the initial conditions. This is because sexual reproduction induced shifts of the system along the set of equilibrium points (Doebeli, 1995). In our model, however, it is less clear why sex leads to a simplification of the dynamics, and in particular why low-to-intermediate frequencies of sex can be more stabilizing than high frequencies of sex. Identifying the mechanisms for the stabilizing effects of sex in the Nicholson–Bailey model used here would likely require an analytical approach, e.g. identifying the attractors of the system and studying their stability using local stability analysis. However, such an analytical approach is not feasible in our rather complicated model, because the dynamics are often complicated, i.e. periodic, quasi-periodic or chaotic. As a consequence, we are unable to offer clear mechanistic explanations for the effects of sex on population dynamics that we have observed.

In conclusion, our results clearly support the intuitive idea that sex can have a stabilizing

influence on population dynamics. Together with other work (e.g. Doebeli & Koella, 1994; Ruxton, 1995; Doebeli, 1997), our study shows that the stabilizing effects of sex may be a rather general phenomenon, reducing the tendency of chaos in many predator-prey, host-parasite and single-species (e.g. intraspecific competition) models of population growth framed in nonlinear difference equations. However, as we have demonstrated here, intermediate levels of mixing through sexual reproduction may lead to simpler dynamics than the complete mixing in fully sexual populations, and often “a bit of sex” may be as stabilizing as “a lot”.

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