



How to go extinct by mating too much: population consequences of male mate choice and efficiency in a sexual–asexual species complex

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Selection acting on individuals is not predicted to maximize population persistence, yet examples that explicitly quantify conflicts between individual and population level benefits are scarce. One such conflict occurs over sexual reproduction because of the cost of sex: sexual populations that suffer the cost of producing males have only half the growth rate compared to asexuals. Male behaviour can additionally impact population dynamics in a variety of ways, and here we study an example where the impact is unusually clear: the riddle of persistence of sperm-dependent sexual–asexual species complexes. Here, a sexually reproducing host species coexists with an ameiotically reproducing all-female sperm parasite. Sexual–asexual coexistence should not be stable because the proportion of asexually reproducing females will rapidly increase and the relative abundance of the sexually reproducing host species will decline. A severe shortage of males will lead to sperm limitation for sexual and asexual females and the system collapses. Male mate choice could reduce the reproductive potential of the asexual species and thus potentially prevent the collapse. In the gynogenetic (sperm-dependent parthenogenetic) Amazon molly *Poecilia formosa* and its host (*P. latipinna* or *P. mexicana*), males discriminate against asexual females to some extent. Using a population-dynamical model, we examine the population dynamics of this species complex with varying strengths of male discrimination ability and efficiency with which they locate females and produce sperm. The sexual species would benefit from stronger discrimination, thus preventing being displaced by the asexual females. However, males would be required to evolve preferences that are probably too strong to be purely based upon selection acting on individuals. We conclude that male behaviour does not fully prevent but delays extinction, yet this is highly relevant because low local extinction rates strongly promote coexistence as a metapopulation.

Since the 1960s group selection debate (Williams 1966) we have known that natural selection does not necessarily promote the evolution of traits that increase population or species persistence. However, good examples of clearly observable conflict between individual-level and population-level benefits are still scarce (except perhaps in microbial experimental populations in which extinction is common, Wagner 2006, Foster et al. 2007). One potential area where these conflicts have been suspected to have population consequences is that of sexual reproduction. The two-fold cost of sex, for instance, decreases the growth rate of sexual populations so much that it makes the maintenance of sex an “outstanding puzzle in evolutionary biology” (Williams 1975, see also Agrawal 2006), and sexual competition between males has often been invoked as a factor that might contribute to extinction risk over ecological or evolutionary time (Kokko and Brooks 2003, Morrow and Pitcher 2003, Le Galliard et al. 2005; but see Morrow and Fricke 2004, Worman and Kimbrell 2008). Nevertheless, the behaviour of males has thus far rarely been considered important as a determinant of population dynamics (Rankin and Kokko 2007). This is despite the

accumulating evidence that male behaviours can have important consequences on population dynamics and population fitness (Mysterud et al. 2002, Bauer et al. 2005, Fricke and Arnqvist 2007, Rankin and Kokko 2007, Rankin and Arnqvist 2008).

The behaviour of males might play a role in breeding systems that are otherwise hard to explain and that offer clear examples of stark conflict between individually selected behaviour and population-level performance such as population growth or persistence (Rankin et al. 2007). Gynogenesis, or sperm-dependent parthenogenesis (Beukeboom and Vrijenhoek 1998, Schlupp 2005), is an example where a species has evolved a reproductive system that at first sight appears to have no long-term prospects of persistence (Kiester et al. 1981). In a gynogenetic species, a ‘sperm-parasitic’ all-female species reproduces asexually yet sperm is required as a physiological stimulus to trigger embryogenesis. Since the species produces no sperm, it must coexist with a closely related sexual host species. When the ‘parasitic’ species reproduces, paternal genes are not incorporated into the offspring’s genome (Schlupp 2005). In the absence of sexual harassment by males directed towards asexual females

(Dagg 2006, Heubel and Plath 2008, Rankin 2008) or male mate choice, asexual females benefit from the two-fold growth rate of asexual lineages compared to sexual ones. Therefore, asexual females are expected to quickly out-compete their sperm-donating sexual 'host' species (Kiestler et al. 1981). But if this proceeds until the host species is ecologically displaced, there is no sperm available, and the asexual species become extinct soon after its sexual host (Clanton 1934, Hubbs 1964, Kiestler et al. 1981, Stenseth and Kirkendall 1985, Beukeboom and Vrijenhoek 1998, Schlupp 2005). The fact that a gynogenetic species complex can exist at all has therefore the potential to challenge our understanding of selection pressures that can either hamper or promote population or species persistence.

Already in the early 1980s, Kiestler et al. (1981) showed that gynogenetic systems with random mating should not persist indefinitely. They consequently speculated that male mate choice might influence the dynamics of these systems, possibly preventing the excess proliferation of asexual forms that precedes extinction. Dewsbury (1982) discussed and reviewed examples of male mate choice in connection with the cost of sperm. Today, we know much more about the conditions under which male mate choice can arise (Bonduriansky 2001, Kokko and Monaghan 2001, Servedio and Lande 2006). Sperm is no longer viewed as entirely cheap to produce and available in limitless quantities, instead it is assumed to be one of the driving forces behind male mate choice and it often has to be strategically allocated (Reinhold et al. 2002, Wedell et al. 2002, Preston et al. 2003, Pound and Gage 2004, Byrne and Rice 2006, Ball and Parker 2007, Thomas and Simmons 2007). Sperm-dependent parthenogenesis can be considered as one of the most extreme cases in the difference of mate quality from the male's point of view. Here, males do not obtain any genetic offspring from mating with the asexual females, thus we can expect males to discriminate against these females.

Clearly, if males always discriminated against heterospecific gynogenetic females, the sexual species would never be displaced by the asexual females and the puzzle of coexistence would not arise. Strong male discrimination would thus bring about a population level benefit for later generations, but it is well known that one should not base evolutionary predictions on future group or population level benefits. Instead, theory predicts that male mate choice does not evolve under all conditions in which females vary in the direct benefits (number of genetic offspring) they offer to males (Johnstone et al. 1996, Kokko and Monaghan 2001, Kokko and Johnstone 2002, Servedio and Lande 2006). Selection cannot favour males who reject some mating opportunities if the rejection does not increase their reproductive success with the favoured female type (Kokko and Monaghan 2001, Servedio and Lande 2006). In the particular context of choosing between hetero- and conspecifics, a tendency to reject heterospecific females may remain weak for four mutually non-exclusive reasons.

Firstly, examining female species identity could take time and energy that a male could more usefully devote to courtship (Kawecki 1988). Secondly, distinguishing the two types of females may become very difficult for males because females may evolve counter-adaptations to avoid being discriminated against (Schlupp et al. 1991, Lima et al.

1996). Thirdly, male discrimination against asexual females may occasionally lead to loss of real reproductive opportunities through erroneous rejection of conspecifics (Schmeller et al. 2005, Hochkirch et al. 2007). Finally, mating with heterospecific asexual females may increase male attractiveness and mating success with conspecific sexual females via heterospecific mate-copying (Schlupp et al. 1994, Heubel et al. 2008).

On the other hand, in cases where gynogenetic females are in the process of displacing their host species such that sperm is beginning to become limiting, even slight discrimination against mating with asexual females might have a considerable effect on population dynamics. Even under sperm limitation, however, the response to selection for male discrimination ability might remain surprisingly weak. This is because an asexual female's success is little hampered as long as some males in the local population accept her as a mate, even if she is not their first choice. A male who allocates sperm prudently and prefers conspecific females will not pass on his genes to future generations if other, less discriminating males allow gynogenetic females to proliferate until all males are extinct (a 'tragedy of the commons', Rankin et al. 2007). However, since there is some evidence that some degree of male mate choice does exist in gynogenetic systems (Schlupp 2005), our aim is to consider a wide range of potential dynamics that a gynogenetic species complex can show, ranging from no discrimination by males to complete discrimination, and with widely varying values for male efficiency, by which we mean a male's ability to locate and fertilize many females without running out of sperm.

The system

Our model is inspired by a well known example of sperm-dependent sexual–asexual coexistence, the mating complex of Amazon mollies, *Poecilia formosa* (Schlupp 2005). Amazon mollies are all-female gynogenetic fish of the live-bearing family Poeciliidae. Their reproduction relies on closely related species that act as sperm donors (Hubbs and Hubbs 1932). The Amazon molly is probably derived from a single hybridisation event (Avisé et al. 1991, Scharl et al. 1995) and its range is from southeast Texas to northeast Mexico. *Poecilia formosa* is sympatric with its host species *P. latipinna* in Texas and in a few areas in northeast Mexico, while it is sympatric with another host *P. mexicana* in northeast Mexico (Darnell and Abramoff 1968, Schlupp et al. 2002). When sperm is not limiting, asexual and sexual females are equally fecund (Schlupp 2005, Schlupp et al. unpubl.), and there is no parental care. Thus the two-fold cost of sex applies.

In the present study, we specifically address two aspects of male reproductive behaviour that may play significant yet potentially opposing roles in the context of sexual–sexual coexistence in gynogenetic species complexes. Firstly, we consider the effects of male efficiency. High male efficiency (i.e. the ability of a male to fertilize large numbers of females) is prevalent and selectively favoured among polygynous species (Birkhead and Møller 1998). Under gynogenesis it might be maladaptive for males to be able to fertilize large numbers of sexual and asexual females given

that the sufficient sperm supplies help the asexual females to reproduce faster than its host until both species become extinct, however this line of logic should not be followed blindly because it relies on a group benefit. Here we therefore simply quantify the effect of a large range of different efficiencies. Secondly, we attend to discrimination ability, the male's capacity to discriminate against matings with asexuals that incur no fitness benefits. Despite the four reasons (Introduction) why strong male mate choice might not evolve, some preferences for mating with conspecific sexual females could be expected given the vastly different fitness consequences of the two types of females as potential mates (Neiman 2004, but see Gumm and Gabor 2005, Schmeller et al. 2005).

There is evidence for male discrimination ability in such complexes (reviewed by Schlupp 2005). Empirical studies on male behaviour in this unisexual-bisexual species complex confirm that males do discriminate at several levels: they have mating preferences for conspecific females (Ryan et al. 1996, Gabor and Ryan 2001, Schlupp and Plath 2005), produce more sperm in the presence of such females (Aspbury and Gabor 2004), and transfer less sperm in matings with heterospecific females (Schlupp and Plath 2005, Riesch et al. 2008). However, most empirical and theoretical studies so far did not address specifically male discrimination ability in the context of population dynamics of coexistence (Moore and McKay 1971, Kiester et al. 1981, Kawecki 1988) and thus did also not comment on whether observed levels of discrimination are sufficiently strong for coexistence.

Methods

We built a population-dynamical model to investigate the conditions under which the asexual female may coexist with the sexual species. Consider a population of a sexual species, where there are $M(t)$ males and $F(t)$ sexual females in generation t . Additionally, there may be $A(t)$ asexual females of the gynogenetic species. We are interested in the dynamics of $M(t)$, $F(t)$ and $A(t)$ over time. Both asexual and sexual females need sperm from males to be fertile, and since there is potential for severe shortage of males and hence sperm limitation in such a system with fast reproducing asexuals that only produce female offspring (Hubbs 1964, Balsano et al. 1985, Heubel 2004), we assume that the fecundity of either species is dependent on the ratio of males to females. Denoting the fecundity of sexual females by $b(t)$ and that of asexuals by $b_A(t)$, we assume

$$b(t) = B \left(1 - \exp \left(-h \frac{M(t)}{F(t) + (1-D)A(t)} \right) \right) \quad (1a)$$

$$b_A(t) = B \left(1 - \exp \left(-h \frac{M(t)(1-D)}{F(t) + (1-D)A(t)} \right) \right) \quad (1b)$$

These functions (depicted in Fig. 1) capture the following assumptions. Females of either species can produce up to B offspring, but if there are no males ($M(t) = 0$), no offspring are produced. The fecundity function thus rises from 0 to B as the ratio of males to females increases, and the speed of this increase is controlled by the parameter h . The value of h describes male efficiency: large values imply that a small

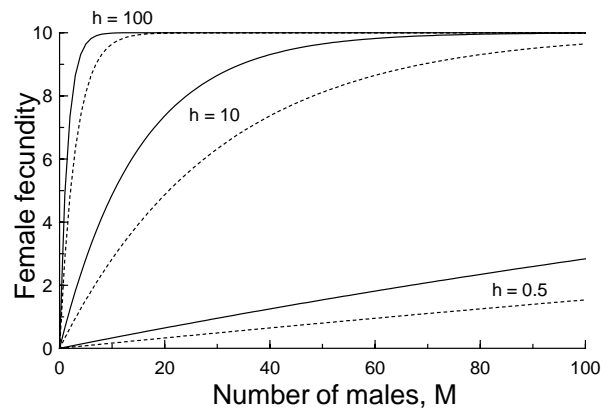


Figure 1. Examples of the shape of the fecundity function for sexual (solid line) and asexual (dotted line) females in a population of 100 females of each type (i.e. $F=A=100$), when male numbers vary from 0 to 100, males are moderately discriminating ($D=0.5$), and $B=10$. When male efficiency h is high, either type of female reaches their maximum fecundity under most conditions despite male discrimination, while very low h indicates severe sperm limitation for both types of female.

number of males are capable of securing the fecundity of a large number of females ($h=100$ in Fig. 1), while small values indicate severe sperm limitation even in situations where the sex ratio in the sexual species is 1:1 and the sexual species is not outnumbered by asexuals (these conditions are captured in Fig. 1 at $h=0.5$ and $M=100$).

The parameter D indicates whether, and to what extent, males can discriminate against asexual females that offer them no genetic offspring. If $D=0$, there is no male mate choice (males never discriminate between sexual and asexual females, a case that has been previously investigated by Kiester et al. 1981), while if $D=1$ they always reject the latter. Intermediate values describe situations in which asexual females' attractiveness to males is reduced by a fraction D compared to sexual females. Note the biologically correct assumption that if male efficiency h is high (or if there are very many males), asexual fecundity is not compromised even if males discriminate against them to some extent: in such a case, there is a surplus of sperm available for all females, and foregoing some matings is not limiting the fecundity in mixed populations (Fig. 1 with $h=100$, for all values $M > 20$).

The 'fecundity' in Fig. 1 refers to all offspring, male or female, thus B does not differ between the sexual and asexual species. Female-to-female reproduction is typically halved in sexual species, however, because of the two-fold cost of sex (Agrawal 2006). More generally, if a proportion of r of the offspring are male in the sexual species, then the population dynamics of males, females and asexuals can be described as

$$\begin{aligned} M(t+1) &= f(N(t)) r b(t) F(t) \\ F(t+1) &= f(N(t)) (1-r) b(t) F(t) \\ A(t+1) &= f(N(t)) b_A(t) A(t) \end{aligned} \quad (2)$$

Here, $f(N(t))$ describes density dependence where $N(t) = M(t) + F(t) + A(t)$. This formulation assumes that all fish contribute to ecological competition to an equal degree, e.g. by consuming resources equally over their lifetime. Thus, our model investigates ecological coexistence in the absence of

partial niche differentiation. Partial niche differentiation has been suggested as an alternative mechanism promoting coexistence in gynogenetic species complexes (Schley et al. 2004). The choice of the function $f(N)$ matters little for our predictions on persistence times, as it scales the absolute numbers of fish but not the relative numbers that are important to predict whether the sexual host is ecologically displaced (Eq. 2). To provide a simple example, here we use $f(N) = 1/(1 + \alpha N)^\beta$ according to (Hassell et al. 1976) and (Bellows 1981). Here, the parameter α scales the intensity of competition and β influences the type of density dependence.

Results

Our model shows that permanent coexistence between the asexual and sexual species is possible in the absence of any niche differentiation (Schley et al. 2004) or spatial structure (Kokko et al. 2008). Coexistence can be simply based on the ability of males to discriminate against sperm-parasitic asexual females (Fig. 2). Asexual females reproduce faster (Eq. 2) if $b_A > b(1 - r)$. This condition is easily fulfilled if the sexual species has a 1:1 primary sex ratio (so that $r = 0.5$) and if sperm is not limiting, such that $b_A \approx b$. However, sperm eventually does become limiting to both sexual and asexual females as the proportion of males continually diminishes (Eq. 1). If males discriminate against asexual females, this reproductive limitation damages the reproduction of sperm-dependent asexuals before that of sexual females. When $b_A(t) = b(t)(1 - r)$, the frequency of asexual females no longer increases, and an equilibrium with stable coexistence has been reached.

However, reaching this solution requires that the discrimination ability D begins to limit asexual reproduction sufficiently faster than that of sexuals. The condition $b_A(t) = b(t)(1 - r)$ is impossible to fulfil if the discrimination ability falls below 0.5. In that case discrimination cannot overcome the two-fold cost of sex at any male density. Thus, under such conditions no population of either sexual or asexual fish can be maintained regardless of the efficiency of males, h (Fig. 2). On the other hand, male efficiency h is not irrelevant either. A high enough h is necessary for a population of any kind to exist.

The parameter region with persistent populations of any kind is thus characterized by at least moderately large values of both male efficiency h and male discrimination ability D (Fig. 2). This region is clearly split into two. The first region (uppermost part of Fig. 2) is characterized by a high male efficiency h and relatively low discriminatory level D , and here asexual fish persist together with some (but often very small numbers of) sexual fish. In another region (middle part of Fig. 2), with a higher discrimination D and relatively lower male efficiency h , sexual fish reach high population sizes and asexual ones are absent.

These results imply that coexistence of sexual fish and their asexual relatives is not impossible, but as a whole, the parameter region in which permanent local coexistence is possible can be characterized as rather small (shaded area in Fig. 3). If, for example, males are moderately efficient at fertilizing many females (e.g. $h = 10$ in Fig. 3), asexuals are wiped out both when the male discrimination ability is too low (asexuals then outcompete the sexual host that they

depend on), and when it is too high (asexuals are then driven extinct due to sperm shortage). The range of values of discrimination, D , allowing coexistence is at its widest when males fertilize females very efficiently ($h = 100$ in Fig. 2), but under these conditions there will also be extremely few sexual individuals at equilibrium. This suggests that local perturbations, e.g. naturally occurring sudden changes in water level or temperature, might drive such a system extinct even if coexistence is possible in a deterministic setting.

The parameter space where deterministic coexistence is possible is not the only interesting region of Fig. 2–3. Host–parasite systems are well known to persist at larger spatial scales even if local coexistence is difficult or impossible (Holyoak and Lawler 1996, Lawler et al. 1999, Ellner et al. 2001, Bonsall et al. 2002). In a complementing paper (Kokko et al. 2008), we showed that large-scale coexistence in a gynogenetic species is possible despite local extinction,

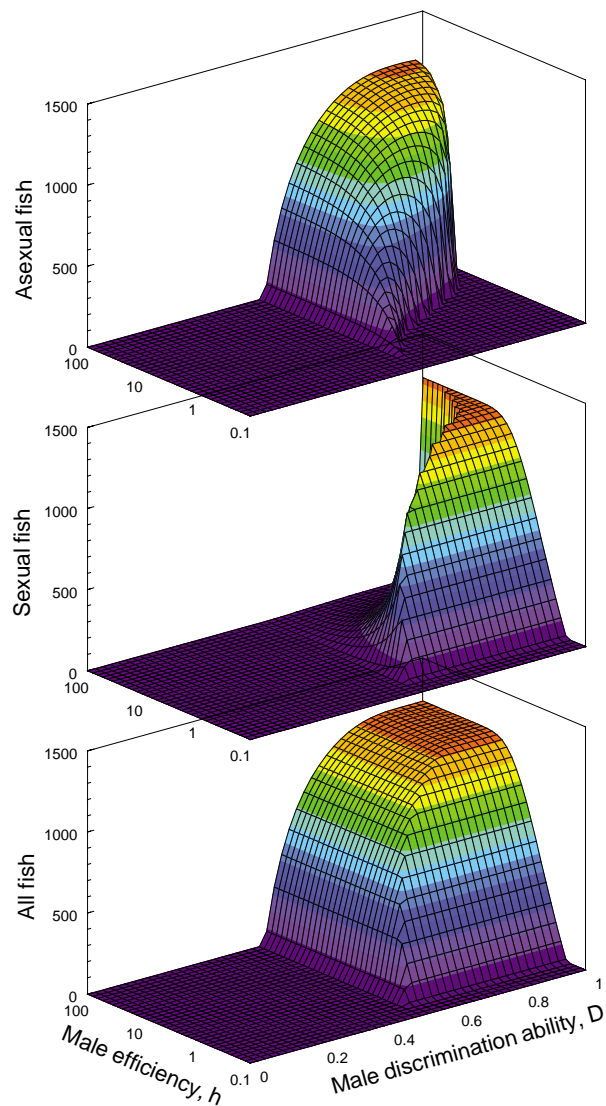


Figure 2. Equilibrium sizes of a population of asexual females, sexual fish (half of them male), and all fish together, for different values of male mate choice (discrimination ability D) and male efficiency h . Other parameters: $B = 10$, $r = 0.5$, $\alpha = 0.001$, $\beta = 2$; note that the values of α and β , as well as the choice of the density dependent function in general, only scale the y-axis.

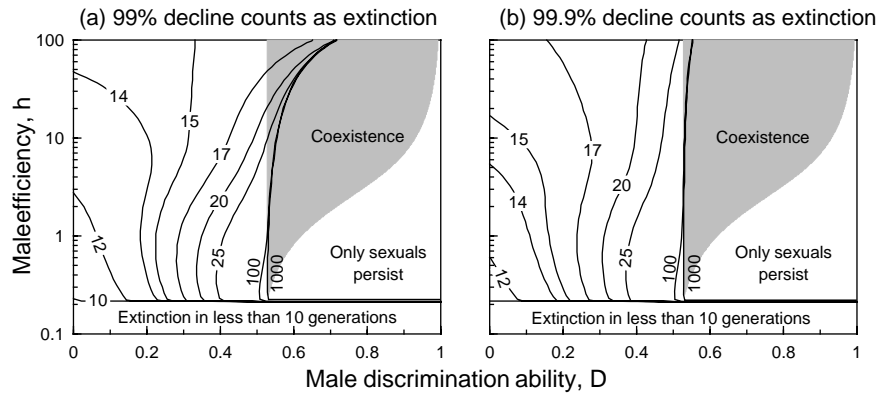


Figure 3. The same model as in Fig. 2, now indicating time to extinction (in generations) in cases where the asexual species drives its host to quasi-extinction. Quasi-extinction is observed when the number of sexual females (also equal to the number of males) is less or equal than (a) 1% and (b) 0.1% of the original equilibrium number of sexual females in the absence of asexual females.

and that this possibility is strongly enhanced if local extinctions occur at a relatively slow rate. Therefore, one should be interested in comparing these rates for different scenarios, and not simply categorize every locally extinct population in Fig. 2 and 3 as equally doomed when viewing prospects for coexistence in a broader spatial context.

For this reason, we derived quasi-extinction times (Ginzburg et al. 1982) for populations that start at equilibrium with only the sexual species present (denoting these numbers F^* , M^*), and then introduce 1% asexual individuals such that $F(0) = F^*$, $M(0) = M^*$, and $A(0) = 0.01 F^*$. Following the dynamics of Eq. 2, we recorded the number of generations after which the sexual host $F(t)$ has declined to a fraction 0.01 or 0.001 of its original numbers. We used quasi-extinction times rather than time to actual extinction because the latter is not reached in finite time in our deterministic model, which allows males to comprise an arbitrarily small fraction of the population. In practice populations with a very small proportion of males left will eventually fail to produce any surviving mature males.

Such an analysis suggests that prolonged coexistence is indeed difficult when male efficiency h is very high, unless male mate choice, D , is very strong. An intriguing feature of Fig. 3 is that isoclines for a finite time to quasi-extinction overlap somewhat with the shaded area that indicates that local coexistence should be possible (the effect is especially strong when using a 99% decline as the definition of quasi-extinction, Fig. 3a). This means that even though coexistence is possible in this region, it is in practice hard to achieve because the population equilibrates with extremely few sexuals (Fig. 2). When discrimination ability D falls below 0.5, local coexistence is impossible. However, Fig. 3 also indicates that extinctions are not immediate in this region. While neither species can persist indefinitely in these areas, extinction typically takes 10 to 20 generations (and up to 100 or more near $D = 0.5$). Thus, even moderate discriminatory abilities of males are sufficient to slow down extinction rates considerably.

Discussion

We have shown that two behavioural adaptations of males, i.e. male efficiency (fertilization ability) and mate choice

(discrimination ability), can stabilize a gynogenetic species complex. They can do so even if one assumes an absence of two factors that have been argued to aid coexistence prospects: partial niche differentiation (Schley et al. 2004) and host–parasite dynamics with spatial structure (Kokko et al. 2008). The proliferation of an asexual species is bound to lead to sperm limitation, but if there is sufficiently strong male mate choice, reproduction of asexual females will be affected more strongly than sexual females. They will suffer from sperm limitation before the reproductive output of the sexual species is severely damaged. If males additionally have been selected for high male efficiency (i.e. for avoiding being sperm-limited when encountering a female – a selection pressure typically argued to be strong, Birkhead and Møller 1998), then the region of coexistence is wider. However, our model also shows that particular combinations of male efficiency and male mate choice are required for gynogenetic coexistence, and it is not guaranteed that selection acting on individuals will produce values of these traits that are favourable for long-term persistence. We will first consider male mate choice (discrimination ability D) in this respect, then their efficiency h .

Population consequences of male mate choice

Male mollies of the host species do not completely reject Amazon molly females: if they did, no Amazon molly would ever be able to reproduce. Empirical data, however, show enormous temporal and spatial variation and plasticity in male mate discrimination ability D : male mate preference for sexual over asexual females varies seasonally in terms of association preference (Heubel and Schlupp 2008) and sperm transfer (Riesch et al. 2008), and among populations depending on the species complex and the strength of sexual-asexual sympatry (Ryan et al. 1996, Gabor and Ryan 2001). Male mate discrimination may conflict with preferences for large body size (Gumm and Gabor 2005) or female receptivity (Schlupp et al. 1991) and be weakened by social effects such as mate-copying (Schlupp and Ryan 1997) or presence of potential competitors (Plath et al. 2008). This result is in good line with theoretical predictions that male mate choice, even if good for the species, may fail to become strong when based

on individual-level selection (Schmeller et al. 2005, Servidio and Lande 2006). For individual males, the cost of erroneously rejecting a conspecific female often overrides the cost of wasting time, energy, or sperm by accepting a large proportion of heterospecific asexual females (Kawecki 1988, Schmeller et al. 2005). This is especially relevant in the context of two other known mechanisms, namely heterospecific mate-copying and cyclic receptivity of females. Firstly, males mating with asexual females while being watched by sexual females become more attractive and thus increase their chances of mating with the latter (Schlupp et al. 1994, Heubel et al. 2008). Secondly, only a fraction of females, sexual and asexual alike, may be receptive at any given time. For males, it may be more urgent to detect the females' reproductive status than their reproductive mode (Schlupp et al. 1991).

Our model indicates that the sexual species would, at a species level, always benefit from stronger male discrimination. Discrimination levels of $D = 0.5$ or above are required before local sexual populations cannot be out-competed by sperm-parasitic asexual females, and even sexuals can be driven to extremely low numbers unless D is close to 1 (the precise value required depends on male efficiency h , below). A value of $D = 0.5$ implies that if males encounter sexual and asexual females equally often, they mate with the latter only half as often as with the former. Experimental findings support this view: mean discrimination levels ($1 - \text{ratio of [mean number of copulation attempts directed towards asexual females] to [mean attempts towards sexual females]}$), the empirical equivalent of D (0 equals random mating, 1 is perfect discrimination against asexuals) show that indeed $D > 0.5$ on average (0.75 ± 0.35 mean \pm SD; min 0.0; max 0.98; $n = 28$; Ryan et al. 1996, Gabor and Ryan 2001, Schlupp and Plath 2005). These observations confirm that even though there is high variation in D , there is on average a fairly strong male preference for conspecific sexual females with most published values of D well above 0.5.

Even with high discrimination ability D , however, our model predicts that sexuals will often be driven to such low numbers that extinction can easily follow due to demographic or other sources of stochasticity. Indeed, there is evidence that extinction of mollies regularly occurs over local scales (Kokko et al. 2008). On the other hand, any increase in male mate choice D , regardless of the selective process that produces it, is always beneficial at the population level. It slows down extinctions, and we have previously shown that even minor delays in extinction time scales can be important because gynogenetic species complex can persist at a metapopulation scale despite local extinctions (Kokko et al. 2008). Local populations that have time to colonize other habitats before going extinct enhance the persistence prospects of the entire metapopulation, and if male behaviour prolongs the time to extinction, even moderately, it promotes coexistence at the metapopulation level.

Population consequences of the efficiency of males

Our model shows that the efficiency of males (their ability to mate frequently without becoming sperm depleted) has a rather complicated relationship to the stability of a

gynogenetic species complex. First, consider cases where the species complex will deterministically collapse because there is little or no male mate choice (low D). The expected time to extinction will then depend on male efficiency. High efficiency h slows down extinction when males almost completely lack discrimination abilities, while the opposite is true if males have developed this ability to some extent: close to $D = 0.5$, extinctions occur much more slowly when sperm production is inefficient (low h , Fig. 3). Indeed, inefficient male fertilization appears to be a real problem in the Amazon molly complex: Hubbs (1964) found only partially fertilized asexual and sexual females. This seems to be especially a problem in populations with very low frequencies of males, a situation that is fairly common in mixed sexual-asexual populations in the Amazon molly complex (Balsano et al. 1981, Heubel 2004). Recently, Riesch et al. (2008) showed that particularly asexual females suffer severely from sperm limitation. As before, a long time to extinction helps explain how the gynogenetic species complex can persist as a whole.

Second, it is also possible that the male efficiency promotes gynogenesis not by slowing down extinction rates of both species, but by allowing the asexual females to exist where otherwise only the sexual species could. When there is strong male mate choice, increasing male efficiency h tends to shift solutions from a region of sexual-only persistence to one of coexistence. Such coexistence is often characterized by very small numbers of the sexual species and a large number of asexuals, with sperm depletion affecting reproduction in both species. Such skewed sexual:asexual ratios are well supported by empirical data (Hubbs 1964, Heubel 2004), and mixed sexual-asexual populations face the risk of sperm depletion (Hubbs 1964, Monaco et al. 1981, Riesch et al. 2008). Interestingly, empirical findings indicate that also male sperm production may respond differentially towards the presence of sexual and sperm-parasitic asexual females (Aspbury and Gabor 2004). In general, sperm is not an unlimited resource in such systems (Monaco et al. 1981, Kirkendall 1990, Pilastro and Bisazza 1999). Rather counterintuitively, if sperm depletion selects for more discriminating males then poor male function can favour coexistence, and similar effects are also found in systems with coexisting sexual and asexual hermaphroditic plants (Britton and Mogie 2001).

If male efficiency is further increased (which can be argued to be selectively advantageous, given sperm limitation), 'coexistence' is based on such small numbers of the sexual host species that the situation is more appropriately characterized as quasi-extinction. Throughout these shifts in male efficiency h , an adaptation that is probably advantageous for individual males (increasing h) ultimately damages the persistence prospects of the sexual species that the male belongs to.

Summing all our results together, male adaptations are important. However, it appears unlikely that male adaptations have evolved to reach the particular combination of traits that stabilize sperm-dependent sexual-asexual mating complexes. As such, this is not surprising, as it is a good illustration that natural selection does not act with 'foresight' and maximize species persistence, especially when the selective environment does not remain constant: the mating dynamics changes radically over a few generations from no

sperm limitation to persistence-threatening levels of limitation as the number of asexual females increases. Another implication of selective pressures that do not guarantee persistence is that the ecological and evolutionary stability of any gynogenetic complex found in nature is far from trivial (Kokko et al. 2008). However, a strong result from our model is that even modest levels of male mate choice can significantly prolong the time that the two species can co-occur before local extinction occurs. Together with spatial structure (Kokko et al. 2008) and/or niche differentiation (Balsano et al. 1981, Schley et al. 2004) this can contribute substantially towards explaining stability as a whole.

Note, however, that our models consider ecological persistence but not the long-term evolutionary fate of Amazons, which is still under debate (Schlupp 2005). Genetic models of asexual disadvantage predict long-term benefits of sexually reproducing and recombining organisms compared to costs incurred by asexuals due to accumulation of deleterious mutations in the genome of the asexuals (Muller 1964, Crow and Kimura 1965, Maynard Smith 1978, Kondrashov 1988, Lynch and Gabriel 1990). Theoretically, asexual lineages are expected to go extinct after approximately 10 000–100 000 generations (Lynch and Gabriel 1990). With Amazons, however, this seems not to be the case: asexual and sexual females have been coexisting for more than 100 000 generations (Schartl et al. 1995). Nevertheless, solving the ecological conundrum of coexistence is a necessary first step towards understanding the longer-term prospects.

Acknowledgements – Funding was provided by the Academy of Finland. DJR is currently funded by SNSF-grant 3100A0-105626 (to M. Taborsky). Jan Engelstädter kindly commented on the manuscript.

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