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The effect of cryptic female choice on sex allocation in simultaneous hermaphrodites

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Sex allocation theory for simultaneous hermaphrodites has focused primarily on the effects of sperm competition, but the role of mate choice has so far been neglected. We present a model to study the coevolution of cryptic female choice and sex allocation in simultaneous hermaphrodites. We show that the mechanism of cryptic female choice has a strong effect on the evolutionary outcome: if individuals remove a fixed proportion of less-preferred sperm, the optimal sex allocation is more female biased (i.e. more biased towards egg production) than without cryptic female choice; conversely, if a fixed amount of sperm is removed, sex allocation is less female-biased than without cryptic female choice, and can easily become male biased (i.e. biased towards sperm production). Under male-biased sex allocation, hermaphroditism can become unstable and the population can split into pure males and hermaphrodites with a female-biased allocation. We discuss the idea that the evolution of sex allocation may depend on the outcome of sexual conflict over the fate of received sperm: the sperm donor may attempt to manipulate or by-pass cryptic female choice and the sperm recipient is expected to resist such manipulation. We conclude that cryptic female choice can have a strong influence on sex allocation in simultaneous hermaphrodites and strongly encourage empirical work on this question.

Keywords: sex allocation; cryptic female choice; simultaneous hermaphroditism; sperm competition

1. INTRODUCTION

Simultaneous hermaphroditism (from here on hermaphroditism), i.e. having both sexes represented in the same individual at the same time, is the most common reproductive system in plants. In animals it is considerably less common, but hermaphrodites are widely distributed across the animal kingdom (Ghiselin 1969), and they represent a significant part of all animal species (6%, and about 30% if insects are disregarded (Jarne & Auld 2006)). Having both sexual functions at the same time leads to a dilemma: how to allocate resources between the production of eggs and sperm (or ejaculates)?

In general, the optimal sex allocation is that which leads to the highest total (male plus female) fitness (i.e. reproductive success). Male and female fitness is gained through different means: female fitness is determined by egg production (number and quality of eggs) and offspring quality and is expected to increase with the amount of resources available, whereas male fitness is gained through fertilizations and is expected to increase with the number of matings and the fertilization success per mating. This view suggests that male fitness strongly depends on the number of matings, while female fitness does not (Bateman's principle; Bateman 1948; Arnold 1994). Therefore, individual hermaphrodites may wish to mate mainly to donate sperm—not necessarily to receive it (Charnov 1979). This view of reproductive success for male and female roles appears to be correct for many species with separate sexes (Dewsbury 2005; Snyder & Gowaty 2007); whether it is also true for hermaphrodites is currently a matter of debate (see Leonard 1990, 2005; but see Pongratz & Michiels 2003 for empirical evidence in favour of Bateman's principle in hermaphrodites).

Assuming Bateman's principle applies to hermaphrodites, individuals may wish to donate sperm to many partners, but they may still be choosy about whose sperm they will allow to fertilize their own eggs. Both individuals in a mating pair would then want mostly to donate sperm, leading to a conflict over mating roles—both wanting to mate in the male role, but not necessarily in the female role. This conflict may escalate into, for example, hypodermic insemination, but another possible outcome is reciprocal mating where both individuals accept and donate sperm (Charnov 1979; Michiels 1998). In this scenario, individuals must accept sperm in order to be able to donate it, leading to a conflict of interest between their 'male role' and 'female role': wanting to mate as a male with an individual whose sperm one does not want to receive. One strategy to resolve this conflict would be for a hermaphrodite to mate and accept sperm, but to get rid of the unwanted sperm by post-copulatory cryptic female choice (Charnov 1979).

Cryptic female choice can be defined as any female-controlled process or structure leading to biased paternity

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(Eberhard 1996; Pitnick & Brown 2000). Although there is as yet no direct evidence for cryptic female choice occurring in hermaphrodites, there are good reasons to think it could play an important role. Many hermaphrodites have special organs for the specific purpose of digesting most, if not all, of their partner's sperm (e.g. Sluys 1989; Westheide 1999). The digested sperm may represent a nutrient source. There currently is no hard evidence for this, but see Greeff & Michiels (1999) for a model assuming this to be true. Moreover, sperm digestion may present hermaphrodites with a mechanism to influence paternity by preferentially digesting more sperm of some partners than of others.

If cryptic female choice occurs in hermaphrodites, this may affect how selection acts on their sex allocation. To understand why, one first needs to look at the effect of sperm competition on sex allocation. As female fitness depends mostly on the resources available for reproduction, it may often increase linearly with allocation to eggs. On the other hand, male fitness in hermaphrodites is expected to have a saturating gain curve (Charnov *et al.* 1976; Charnov 1979, 1996), with diminishing returns for higher male allocation. The reason for the saturating return is competition between related sperm (recently termed local sperm competition; see Schärer 2009), which in analogy to competition between related males in species with separate sexes (termed local mate competition; Hamilton 1967) is wasteful for the parental individual producing them. The precise shape of the male gain curve then determines the optimal sex allocation (Charnov 1979, 1996; Pen & Weissing 1999), and it is strongly influenced by the intensity of sperm competition (the degree to which an individual's sperm competes against related versus unrelated sperm): stronger sperm competition makes the gain curve reach its maximum more slowly, leading to an increased optimal male allocation.

This effect of sperm competition on fitness via the male function has been considered the most important factor determining hermaphrodite sex allocation (reviewed in Schärer 2009). However, the payoff for male investment can also be influenced by a female-controlled process like cryptic female choice. This then could in turn affect the evolution of sex allocation, but this question has not been included in models for hermaphrodite sex allocation so far. Two published models have gone some way in this direction. The first, by Greeff & Michiels (1999), considered the effect of sperm digestion on sex allocation, and they concluded that the reduction of an individual's competitive potential through sperm digestion leads to a higher investment into sperm. In their model there was no choice, however; an equal proportion of incoming sperm of all partners was being digested. The second model, by Greeff *et al.* (2001), looked at the effect on optimal sex allocation of skewed paternity owing to random effects and found that greater skews lead to lower male allocation.

Some theoretical models exist on cryptic female choice in organisms with separate sexes, which might give some indication of what to expect in hermaphrodites. In separate-sexed species, a male must divide his resources between acquiring mates and investment per mating, and there are two models predicting how males should allocate their resources when females can exercise cryptic female choice. In the model by Ball & Parker (2003), females remove a fixed proportion of the sperm of 'unwanted' males, and the results suggest that males should allocate more to sperm when favoured, and decrease it when disfavoured. The second model, by Greeff & Parker (2000), considers sperm allocation of males that do not know if they are favoured or disfavoured. This model has two contrasting results, depending on whether females remove a fixed proportion or a fixed amount of the unwanted sperm: when females remove a fixed proportion, males should invest less in sperm per mating; when they remove a fixed amount, they should invest more.

The dilemma faced by hermaphrodites is similar, trading off fertilization per mating to another fitness component; but it is still different from the trade-off for males in separate-sexed species. How these results would translate to the sex allocation question in hermaphrodites is not immediately clear. Using a combination of mathematical modelling and individual-based simulations, we investigate this question for the first time here.

2. METHODS AND RESULTS

We used two modelling approaches to study two scenarios: first, a simplified analytical model to study the effect of cryptic female choice on sex allocation, while keeping cryptic female choice constant; and second, a more complex individual-based simulation model to study the coevolution of sex allocation and cryptic female choice.

Both models consider a population of simultaneous hermaphrodites with non-overlapping generations. Individuals mate randomly, in pairs, and always mate reciprocally (following the assumption that, according to Bateman's principle, both want to donate sperm; Charnov 1979), and only reproduce after all matings are done. Individuals only differ in two genetically determined traits: sex allocation and a form of cryptic female choice. Sex allocation refers to the proportion of an individual's fixed resource budget invested into the male as opposed to the female function—that is, there is a direct trade-off between male and female investment. Thus, sex allocation can vary continuously between 'pure males' (100% allocation to male) and 'pure females' (100% allocation to female function). As in Ball & Parker (2003), we assume that each individual is randomly assigned one of the two non-heritable 'types' at birth with equal probability. Each individual mates a fixed number of times at random but each type 'prefers' the sperm of its own type and exercises cryptic female choice by removing a certain amount or all of the sperm of the opposite type, in accordance with their genetically determined cryptic female choice trait. Any remaining sperm is stored, and after all matings are done, all stored sperm compete over fertilization in a fair raffle (i.e. the probability of fertilization of a given egg = amount of sperm transferred/total amount of sperm in storage).

Following the approach of Greeff & Parker (2000), we consider two types of cryptic female choice: (i) a fixed proportion of incoming sperm is removed, regardless of ejaculate size; and (ii) a fixed amount, possibly all, of incoming sperm is removed.

(a) *Analytical model*

First we assume that the mode and strength of cryptic female choice is fixed, and we use an analytical ESS approach to

study the evolution of sex allocation. Specifically, we derive an expression for the fitness of a rare mutant in a monomorphic resident population and use this to find candidate evolutionary equilibria (e.g. Pen & Weissing 2002).

The total fitness of a rare mutant with sex allocation x (proportion of resources allocated to the male as opposed to the female function) in a resident population with sex allocation $\hat{x}$ is given by the sum of fitness through female function (F) and the fitness through male function (M)

$$W(x,\hat{x}) = F + M. \tag{2.1}$$

Fitness through female function is the number of eggs produced, which we assume is proportional to the proportion of total resources allocated to eggs: $F = 1 - x$. Thus, fitness through female function increases linearly with allocation to eggs.

Fitness through male function equals the total number of eggs produced by successfully fertilized mating partners, and this depends on the type of cryptic female choice exercised by the mating partners, which we explain in the next two sections.

(i) *Fixed proportion of sperm removed*

Each individual mates n times, and each time the probability is 1/2 that the partner is of the same type, in which case the partner will not remove any sperm and store an amount proportional to x, the mutant's allocation to sperm. Conversely, if a partner is of the opposite type, it will remove a fraction r of the sperm and store an amount proportional to $(1 - r)x$. Each partner will mate with $n - 1$ other individuals (all of them residents, since mutants are assumed rare), and $i = 0, \ldots, n - 1$ will be of the same type as the partner, which happens with probability $p_i = 1/2^{n-1}\,\mathrm{binom}(n - 1, i)$. Thus, if the partner is of the same type as the mutant, the mutant-stored ejaculate of size x will compete with an amount of sperm given by

$$c_i^{\mathrm{s}} = i\hat{x} + (n - 1 - i)(1 - r)\hat{x}. \tag{2.2}$$

The superscript s stands for 'same' type. If the partner of the mutant is of the opposite type, the amount of competing sperm is given by

$$c_i^{\mathrm{o}} = i(1 - r)\hat{x} + (n - 1 - i)\hat{x}. \tag{2.3}$$

Now the superscript denotes 'opposite' type. Combining, we find the following expression for the mutant's fitness through its male function:

$$M = n(1 - \hat{x}) \sum_{i=0}^{n-1} p_i \left[\frac{1}{2} \frac{x}{x + c_i^{\mathrm{s}}} + \frac{1}{2} \frac{(1 - r)x}{(1 - r)x + c_i^{\mathrm{o}}} \right]. \tag{2.4}$$

Inserting these expressions in equation (2.1), we arrive at the fitness function for the mutant. Candidate evolutionary equilibria x^* are then found by solving

$$\left. \frac{\partial W}{\partial x} \right|_{x=\hat{x}=x^*} = 0. \tag{2.5}$$

Stability of solutions to equation (2.5) was checked by verifying $\partial^2 W/\partial x^2 < 0$ (evolutionary stability) and $\partial/\partial x^* \left(\partial W/\partial x|_{x=\hat{x}=x^*}\right) < 0$ (convergence stability). All solutions were both evolutionarily stable and convergence stable (Geritz *et al.* 1998). Closed-form solutions are available but are neither very pleasing to the eye nor very informative. Figure 1*a* shows the solution graphically for different values of n and r. In general, the stable level of allocation to sperm is higher for higher numbers of matings (more sperm competition), as expected from the mating group size model (Charnov 1982), and more severe (higher r) cryptic female choice leads to a lower sex allocation.

(ii) *Fixed amount of sperm removed*

Instead of removing a fraction r of incoming sperm of the opposite type, we now assume that an absolute amount r is removed. This changes the expression for male fitness as follows:

$$M = n(1 - \hat{x}) \sum_{i=0}^{n-1} p_i \left[\frac{1}{2} \frac{x}{x + c_i^{\mathrm{s}}} + \frac{1}{2} \frac{\max(x - r, 0)}{\max(x - r, 0) + c_i^{\mathrm{o}}} \right]. \tag{2.6}$$

The expressions for the amount of competing sperm are now given by

$$\begin{aligned} c_i^{\mathrm{s}} &= i\hat{x} + (n - 1 - i)\max(\hat{x} - r, 0), \\ c_i^{\mathrm{o}} &= i\max(\hat{x} - r, 0) + (n - 1 - i)\hat{x}. \end{aligned} \tag{2.7}$$

The results are shown in figure 1*b*. It turns out that there are always two equilibria for a given combination of n and r. There is an upper equilibrium sex allocation that is always slightly higher than the amount removed by a partner of the opposite type, and a lower equilibrium that is independent of r and identical to the $r = 1$ equilibrium in the fixed proportion model. Upper equilibria can easily be male biased in the sense that more resources are allocated to the male than to the female function. Both upper and lower equilibria are always evolutionarily stable and convergence stable. However, it can be shown with pairwise invasibility plots that for high r-values the upper equilibrium's basin of attraction becomes quite small, and in simulations the population tends to end up in the lower equilibrium (results not shown). Conversely, for small r-values, the lower equilibrium has a small basin of attraction, and the population is more likely to end up in the upper equilibrium.

Thus, in contrast to the fixed proportion model, cryptic female choice in the fixed amount model can lead to an increased allocation to sperm.

(b) *Simulation model*

We used an individual-based simulation approach to model the coevolution of sex allocation and cryptic female choice (C++ code available upon request). As in the analytical model, individuals go through all matings before reproduction. Mating itself is modelled slightly differently: two random individuals are chosen from the population to mate; this is repeated nN times, so n is the average instead of the exact number of matings. For reproduction, for each offspring an individual is chosen with a probability proportional to its energy available for egg production; a father is then chosen from its sperm donors based on each donor's amount of sperm in storage (fair raffle sperm competition).

To introduce a selection pressure on choice, we assumed that being choosy has both costs and benefits. To model costs we assumed that if y is the amount of sperm removed, then the total amount of resources available for egg production are reduced according to a power function $(cy)^a$ (note that when $c < 0$ sperm removal may yield extra resources). Benefits of choosiness were implemented by assuming that offspring from matings between opposite types have a relative viability of $v < 1$ compared with

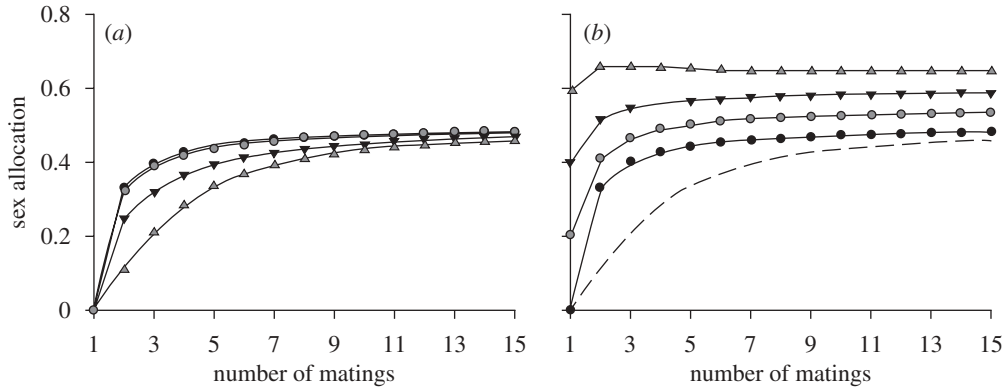

Figure 1. ESS sex allocation, dependent on number of matings, for different degrees of cryptic female choice. (*a*) Fixed proportion model. Filled circle, no cryptic choice; open circle, 50 per cent removal; filled triangle, 90 per cent removal; open triangle, 100 per cent removal. (*b*) Fixed amount model. In (*b*), two equilibria are present for each value of *r*: a low equilibrium, where sex allocation evolves to below the amount removed; and a high equilibrium where sex allocation is higher than the amount removed. Filled circle, no cryptic choice; open circle, 0.2 removed; filled triangle, 0.4 removed; open triangle, 0.6 removed; dash line, low equilibrium.

offspring from same-type matings. Thus, by removing sperm from 'incompatible' partners, the expected viability of offspring is increased. In the examples shown, we set $v = 0.8$.

The population size in the simulations was $N = 10\,000$ diploid individuals. The loci coding for sex allocation (x) and cryptic female choice (r) were assumed to be unlinked, and for the choice locus alleles had additive effects. For the sex-allocation locus, we assumed that the allele with the greater x-value was dominant, allowing for dimorphic (instead of trimorphic) populations in the case of evolutionary branching (Geritz *et al.* 1998). However, qualitatively similar results are obtained with additive allele action (data not shown). Mutations occurred with a frequency of 1 per cent per allele per generation and mutation sizes were drawn from a normal distribution with mean zero and a standard deviation of 1 per cent.

(i) *Fixed proportion of sperm removed*

A typical result is shown in figure 2. For a sufficiently low cost/benefit ratio (low c, high v), selection favours cryptic female choice ($r > 0$). Whether maximal choosiness (r close to 1) evolves depends on how costs increase with the amount of sperm removed. For linear or decelerating costs ($a \leq 1$) maximal or zero r-values evolve, while for accelerating costs ($a > 1$) choosiness evolves to intermediate values. The coevolving sex allocation evolved entirely as predicted by the analytical model: higher choosiness leads to lower investment into sperm.

(ii) *Fixed amount of sperm removed*

For relatively low mating rates (n), cryptic female choice appears to evolve according to the same principles as for the fixed proportion model (figure 3*a*), and the evolved sex allocation behaves as predicted by the analytical model. However, for higher mating rates, when sex allocation is more likely to be male biased ($x^* > 0.5$) according to the analytical model, branching of the sex allocation trait occurs: part of the population allocates nearly all resources to sperm and the rest have strongly female-biased sex allocation (figure 3*b*). For very low costs of choice, evolutionary cycling occurs (figure 4).

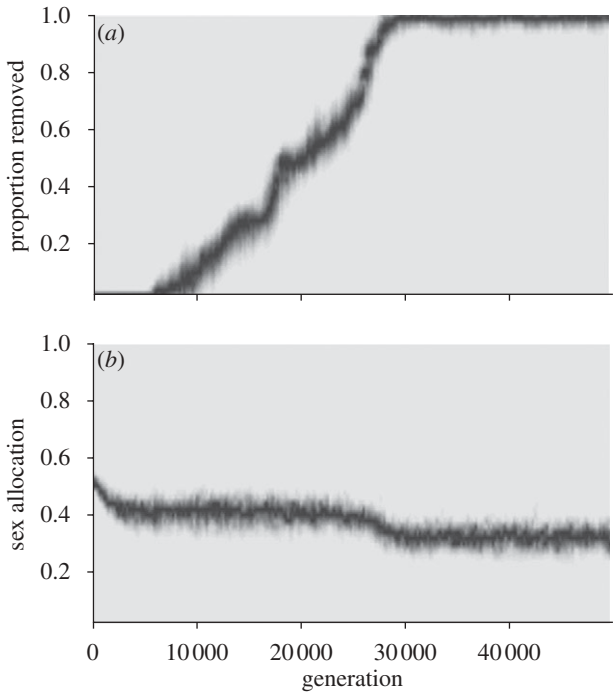

Figure 2. (*a*) Coevolution of cryptic female choice and (*b*) sex allocation. Typical individual-based simulation results for the fixed proportion model; grey intensity represents the frequency of phenotypes in the population. Note that cryptic choice was not 'allowed' to evolve in the model until sex allocation had reached equilibrium after 5000 generations. Per capita number of matings $n = 4$. Cost of choice parameters: $c = 0.8$, $a = 4$.

3. DISCUSSION

The results of our model suggest that cryptic female choice can have a strong effect on sex allocation in hermaphrodites. Similar to the results of Greeff & Parker (2000) for gonochorists, the effect of cryptic female choice depends strongly on the mechanism of sperm removal. If a fixed proportion of sperm is removed, the result is always a lower sex allocation compared with populations without cryptic female choice. If a fixed amount is removed, the result is either a higher (sometimes even male biased)

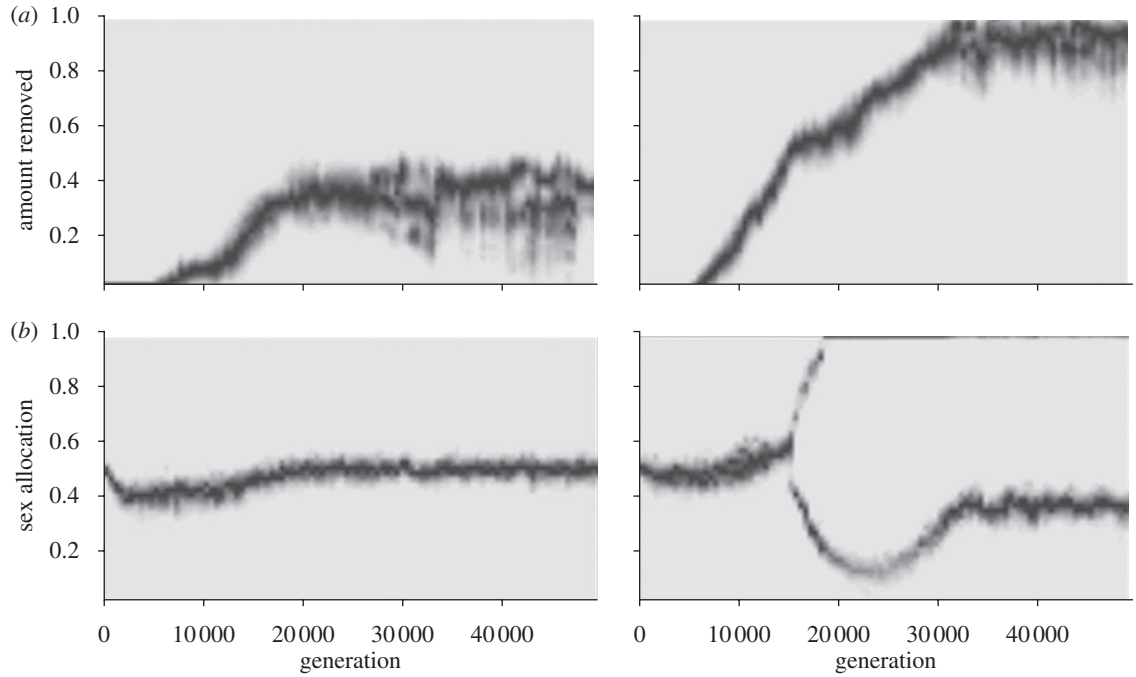

Figure 3. (*a*) Evolution of cryptic female choice and (*b*) sex allocation. Typical individual-based simulations for the fixed amount model. Left panels: $n = 4$, $c = 0.3$, $a = 3$. Right panels: $n = 10$, $c = 0.05$, $a = 2$.

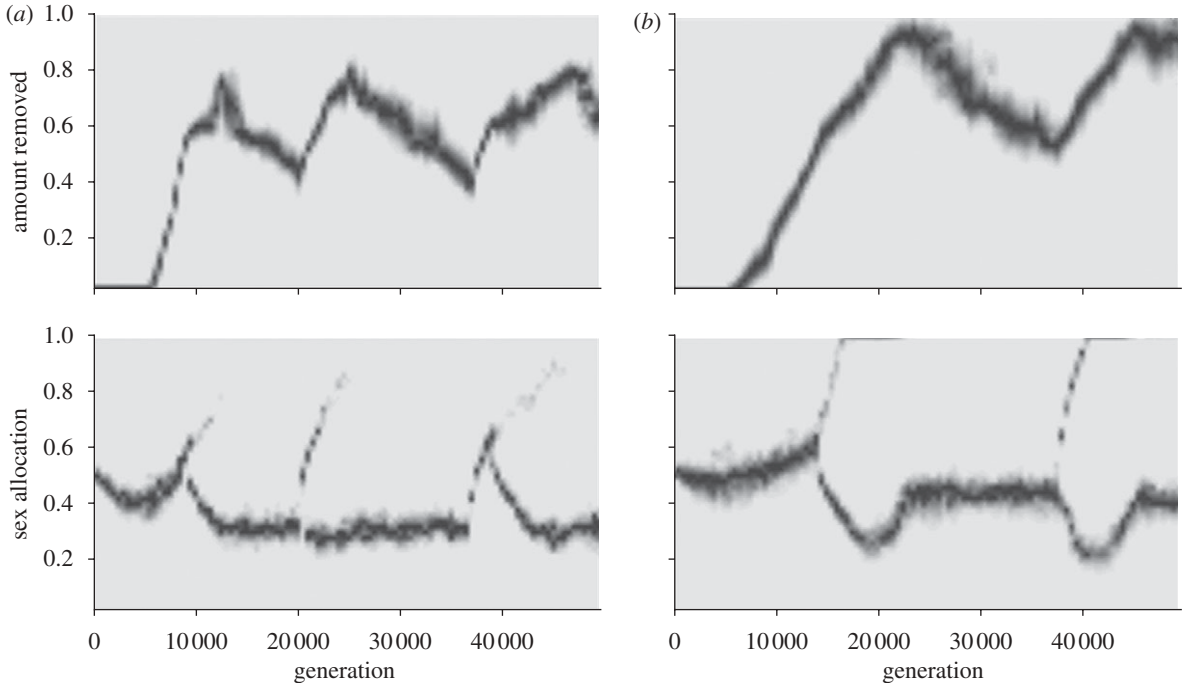

Figure 4. Coevolutionary cycling of cryptic female choice and sex allocation. Typical individual-based simulations for the fixed amount model, with very low costs of choice ($c \approx 0$). (*a*) $n = 4$. (*b*) $n = 10$.

allocation or lower allocation to sperm, depending on the initial conditions. Interestingly, with the fixed amount mechanism, branching of the sex allocation strategy, and even evolutionary cycling, can occur when the mating rate is sufficiently high.

The different outcomes we find for removing a fixed proportion and a fixed amount are in line with Greeff & Parker (2000); however, they contradict the earlier model results by Greeff & Michiels (1999), where removing a fixed proportion resulted in a higher sex allocation. Moreover, in their model, an equal proportion of every competitor was removed; the same scenario would not affect sex allocation in our model at all. This is probably due to the fact that in Greeff & Michiel's model, sperm removal decreases the competitive ability of one's own sperm, but does not fully take into account that competitors' sperm numbers will also be affected. In other words, sperm removal affects the ability to displace the sperm already in storage, but the amount of sperm in storage is not affected by the sperm removal process.

Both removing an amount and removing a proportion may be considered plausible assumptions. For example, if

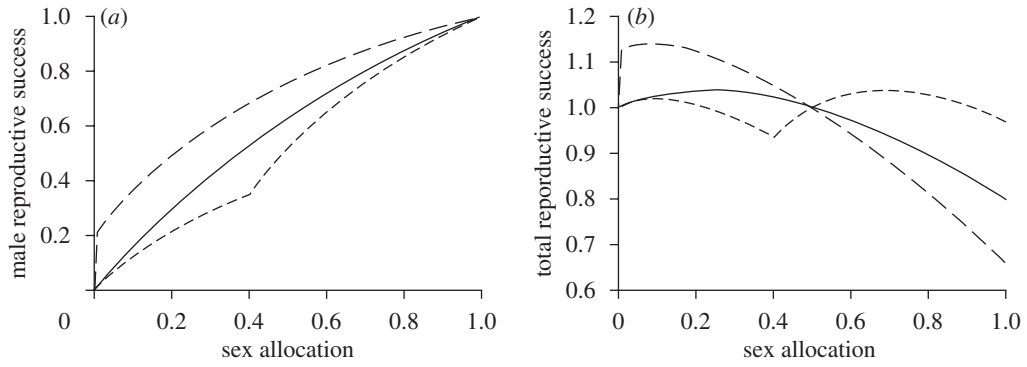

Figure 5. Examples of (*a*) male fitness gain curves and (*b*) the resulting total (male and female) fitness of a mutant introduced into a simulated population with sex allocation $\hat{x} = 0.5$ and $n = 4$ matings per individual. No cryptic female choice (solid line); fixed proportion model, 100 per cent removed (long dashes); fixed amount model, 0.4 removed (short dashes). Male reproductive success is normalized as a fraction of the maximal possible male fitness (i.e. fitness for $x = 1$) for clarity.

a digestive or storage organ with limited capacity is used for removing the unwanted sperm, this will in effect remove a fixed amount; and a scenario where the unwanted sperm is killed chemically or by phagocytosis in the reproductive tract will probably remove a fixed proportion. Another factor that could play a role is whether sperm is removed before or after storage and mixing with the sperm already present; if sperm removal takes place after sperm is in storage and mixed, this would likely remove a proportion rather than an amount.

Why removing a fixed proportion should lead to a lower sex allocation, and removing a fixed amount to a higher sex allocation, is not hard to grasp intuitively. If a proportion is removed, any extra sperm produced to counteract cryptic female choice will be partly removed as well, leading to a reduced payoff for producing extra sperm. Conversely, if a fixed amount is removed, all sperm produced in excess of the threshold value will count fully in sperm competition, giving a high payoff for the same costs. Another way of expressing the difference is by looking at the effect of cryptic female choice on the male fitness gain curve (shown in figure 5). Without cryptic female choice, the male gain curve is saturating, becoming less so (more approximately linear) for higher mating rates (and therefore leading to a higher optimal sex allocation). Removing a fixed proportion makes the gain curve more rapidly saturating, leading to an optimal sex allocation that is more female-biased. Removing a fixed amount, on the other hand, has a very different effect: the gain curve for this scenario consists of two gain curves superimposed on one another. If an individual's ejaculate size is smaller than the amount removed by sperm recipients, reproductive success is only gained in matings with the right type (in incompatible matings, all sperm is removed). For ejaculate sizes larger than the amount removed, the gain curve for matings with the wrong type is again saturating. By 'connecting' the two curves, the shape drawn in figure 5*a* is obtained. This looks similar to an S-shaped gain curve, which has been shown before to select for higher (or even male biased) sex allocation (Pen & Weissing 1999). Also, the male gain curves without cryptic choice and for the fixed proportion model are both saturating, leading to the stability of hermaphroditism, whereas the sigmoid-shaped curve of the fixed amount model is partly concave, and can lead to branching into two sex allocation strategies (Charnov 1979).

What happens to total fitness is shown in figure 5*b*. The more strongly saturating gain curve in the fixed proportion model shifts the optimum to the left. In contrast, the curve of the fixed amount model again has a more complex shape, this time with two optima, as there are two ways to respond to cryptic female choice. Increased sex allocation yields higher male fitness (with consequent lower female fitness). Alternatively, decreased sex allocation means fertilizations will only be gained in 50 per cent of the matings, but female fitness is much higher to compensate. We can explain why it leads to a higher sex allocation for low mating rates and to branching for higher mating rates. As cryptic female choice evolves, the right-hand ('male biased') optimum moves to the right. There is also a female-biased optimum, but this can be difficult to reach because the intermediate sex allocation values yield a much lower fitness. However, higher mating rate leads to a less saturating male gain function, rendering the fitness 'valley' less deep, thus making it easier for the 'female-biased' fitness optimum to be reached. Therefore, branching is more likely for high mating rates, or when mutational step size is sufficiently large. All our simulations use a small mutational step size (0.01; see § 2), and this might be an unrealistic assumption, especially as sex allocation is not a completely genetic trait, and can change plastically to adapt to local social or environmental circumstances (Schärer & Ladurner 2003; Brauer *et al.* 2007; reviewed in Schärer 2009).

In the fixed amount model, for sufficiently low costs of cryptic choice, coevolutionary cycles between sex allocation and cryptic female choice may occur. With the outcome depending so strongly on the assumption that there are costs, it is important to consider how likely it is that removing sperm does in fact incur costs. Some mechanisms for removing sperm must be developed, and resources must be spent on building these mechanisms, so it seems unlikely there are no costs at all. For example, if male counteradaptations preventing sperm removal have evolved, which have to be overcome for sperm removal to take place, this will probably cause some costs to be present (Parker 2006). However, it is also possible that hermaphrodites digest the received ejaculate to gain energy. If this is the case, cryptic female choice may have no net costs, and it may even have net benefits. Even though there is no direct evidence for this, it may not be an unreasonable expectation; many

hermaphrodites can digest sperm, and presumably they gain something by it. Extracting energy from digested sperm could be an adaptation resulting from attempting to reduce costs associated with cryptic female choice, and may allow to turn these costs into a net benefit. Thus, both scenarios are plausible, and experiments to test for sperm digestion in general, and energetic benefits of sperm digestion in particular, are needed.

Our model is based on Bateman's principle being true in hermaphrodites, and especially on the idea that individuals are more willing to mate in the male role. There is some debate about whether or not this is the case (Leonard 2005); if not, that would render the scenario of our model less plausible. Moreover, one may argue that, if cryptic female choice occurs, mating in the male role becomes more risky owing the possibility of sperm being wasted. Consequently, individuals may become less willing to mate in the male role, reducing the driving force behind the evolution of cryptic female choice. On the other hand, sperm donors also have higher fitness gains per mating when they are the favoured type, as they face lower sperm competition; and if sperm removal incurs costs, mating in the female role also becomes risky. A preference for the female role or reluctance to mate in the male role need not be the result. What would happen to the preferred mating role under cryptic female choice is an interesting question that needs further investigation, but is beyond the scope of this paper.

(a) *Other possible evolutionary outcomes*

We have seen that cryptic female choice can lead to a coevolutionary arms race between a sperm donor trying to gain fertilizations (by increasing sex allocation) and the recipient trying to prevent them (by increasing cryptic female choice). The most natural interpretation is cryptic female choice by sperm removal and a male response of increased sperm production to counteract the removal. Sperm donors may evolve different mechanisms for counteracting cryptic female choice, e.g. by making their sperm more difficult to digest or remove (e.g. by using spermatophores or more complex sperm morphology) or by using substances to manipulate the sperm recipient into accepting their sperm (Charnov 1979; Parker 2006). Our model only considers increased male allocation as a response. However, male allocation in our model reflects the energy spent on male reproduction in general. This is not necessarily only the part spent on sperm production, although this is the easiest interpretation. So an increase in sex allocation does not necessarily equal increased sperm production; more resources are spent on trying to gain fertilizations, both by sperm production and by other means. This suggests, again, that we should be careful to draw conclusions on what we would be likely to find in nature. For the fixed amount scenario, our model predicts an increase in sex allocation; even if this is correct, increased sperm number is not necessarily what one would expect to see, and all components of male allocation, such as investment into prostatic fluids, should be taken into account.

One obvious way to gain more fertilizations, investing in finding more mates, is present in Ball & Parker (2003) but not included in our model, where the number of matings is fixed. It is not immediately obvious exactly how this option would affect the results of our model, as the situation is different for reciprocal matings between hermaphrodites than for separate sexes. A strategy to obtain more matings for one individual would also increase the number of matings for others, and some individuals would gain more mates without any extra investment, perhaps making this investment less profitable and less likely to evolve. This is an interesting issue that demands further exploration in the future.

Other alternative responses to cryptic female choice can be imagined. Hypodermic insemination could evolve to bypass the female control in the reproductive tract altogether (Charnov 1979; Michiels 1998; Michiels & Newman 1998). Another possibility is the evolution of a mechanism to recognize the type (or quality) of each potential partner precopulatorily, and to refuse to mate with or donate sperm to unwanted partners. These possibilities are not included in our model, and may lead to different results. For example, as hypodermic insemination bypasses both sperm displacement in the reproductive tract and cryptic female choice, it may lead once more to a situation with fair raffle sperm competition, where higher sperm competition leads to higher sex allocation (Schärer & Janicke in press).

(b) *How reasonable is the 'two types' model?*

To model cryptic female choice, we have followed Ball & Parker (2003) by dividing the population into two types of individuals, and individuals favouring or disfavouring their partners based on a random, non-genetic trait. Realistically, it must be assumed that individuals must have some reason for disfavouring certain partners, especially if costs are involved—that is, some genetic benefit for their offspring must offset the costs. Possibilities for this may be genetic quality (good genes selection) or compatibility of the immune system (with more similar—or more dissimilar—partners giving higher quality offspring). The reason we disregarded the mechanism and made a rather simple model is that, whatever the mechanism for causing variability in partner desirability, the end result will be a population in which individuals will favour some partners over others. This is the scenario we wanted to investigate, and the specifics of what causes partners to vary were not the focus of our study.

There are a number of other simplifying assumptions in the model that may influence the outcome. Mating is assumed to be always reciprocal, as often happens in nature (Michiels 1998); individuals are assumed to be willing to mate all the time. Cryptic female choice makes mating in the male role more costly and risky, making the assumption that individuals will mate indiscriminately as males somewhat questionable. Some hermaphrodites indeed appear to have some mate choice as a sperm donor (Vreys & Michiels 1998; Michiels & Bakovski 2000; Haase & Karlsson 2004). Another important assumption is that individuals play the same strategy throughout their life, both in sex allocation and in strength of cryptic female choice. Realistically, one may expect an individual to treat the sperm of its first partner differently (i.e. not to remove anything if it is unsure whether there will be more matings). It seems logical that individuals should make their decision on whether or not to keep sperm based on how much they already have in storage; this also is not included in the model.

A last important assumption is that sperm removal can be perfect, i.e. individuals are capable of removing all incoming sperm if they want to. This is especially the case in the fixed amount model, where it is assumed that individuals can always remove the specified amount, regardless of how much they receive (and in cases where they receive less than the amount they can remove, they remove everything). If sperm removal is imperfect, however, and some sperm always survives to compete for fertilization, this could reduce the need to increase allocation to sperm if the amount left is large enough to still compete successfully. This could then reduce the strength of the patterns seen for the fixed amount model. Whether this is expected to be the case, however, is again still an open question.

Interestingly, our simulations give two results that are rarely predicted by theoretical models: male-biased sex allocation (fixed amount, low mating rate) and androdioecy, the stable coexistence of males and hermaphrodites (fixed amount, high mating rate). Androdioecy is rare in nature (see Weeks *et al.* 2006 for an overview of androdioecy in animals), and the fact that most models can predict it only under very restrictive assumptions has been invoked as an explanation for this (Lloyd 1975; Charlesworth & Charlesworth 1978; Charlesworth 1984). However, androdioecy may be more rare in plants than its counterpart (gynodioecy, the coexistence of females and hermaphrodites), but this is not the case in animals, where gynodioecy is also extremely rare. Our model presents one mechanism by which androdioecy could evolve and remain stable for many generations, although given the rarity of androdioecy its explanatory power may be limited.

In conclusion, our models suggest that cryptic female choice, if present in hermaphrodites, can have a significant effect on the evolution of sex allocation. Unfortunately, there are at present no empirical data available to test the predictions of our model, as very little is known about cryptic female choice in hermaphrodites. However, given the widespread finding of sperm digestion, our results make it likely that cryptic female choice is an important factor to understand hermaphrodite sex allocation.

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