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Hermaphroditism: What's not to Like?

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Abstract

Male and female social roles are largely predicated on the fact that male and female reproductive functions are separated in different individuals. This paper asks why gonochorism rather than hermaphroditism, is the rule among vertebrates. We argue that hermaphroditism may be unstable in the face of heterogeneity. Building on the Bateman principle – access to eggs, not sperm, limits reproductive success – and in line with Trivers-Willard, we show that low quality individuals will prefer to be all female. Moreover, without secondary sexual differentiation (SSD), males cannot exist in equilibrium. With sufficient SSD, however, males may outcompete hermaphrodites. As a result, while hermaphrodites may coexist with males and females, they mate among themselves only. The lack of interbreeding between hermaphrodites and gonochorists may form the basis for further speciation. Furthermore, while hermaphrodites strive to mate their male function and preserve their female function, equilibrium hermaphroditic mating is reciprocal. Reciprocal mating, in turn, makes hermaphrodites vulnerable to male-to-male violence, a form of SSD that may have contributed to the rarity of hermaphroditism.

1 Introduction

Sociobiology traces gender to the different roles of men and women in reproduction. While sexual reproduction clearly is an important reason for two sexes, our conception of gender is to a large extent predicated on male and female functions being separated in different individuals, that is, an organism is either male or female. However, separated sex functions is only one possibility.

Many plants and some animals (mainly invertebrate) are simultaneous hermaphrodites, that is, they combine both male and female functions in one organism. A hermaphrodite incurs the fixed costs of building both sex functions. On the other

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hand, if the organism itself is considered a fixed cost for the sex functions, hermaphroditism may be viewed as a low cost alternative. Moreover, unlike gonochorists, simultaneous hermaphrodites can reproduce with all mature conspecifics.[1]

Yet, hermaphroditism is rare among vertebrates and, phylogenically, it is in decline. The evolutionary basis for its rarity among evolved animals is not well understood. Ghiselin (1969) pointed to high search cost as a factor in hermaphroditism, e.g., from high dispersion or low (directed) mobility, an observation consistent with the prevalence of hermaphroditism among plants and slow moving animals (e.g., snails). Charnov (1979) pointed to limits on male reproductive success for understanding stability of hermaphroditism. More recent research has pointed to limited return to secondary sexual differentiation when the sex functions are bundled in one individual, e.g., Greeff and Michiels (1999). Moreover, Charnov (1982) suggested that giving up a sex function might be easier than assuming one, which could be part of the explanation for the decline of hermaphroditism. Yet another possibility is that intra-genomic conflict drives gonochorism, suggested by Hurst and Hamilton (1992).

This paper focusses on self-incompatible simultaneous hermaphroditism (SH) in animals. It proposes that such hermaphroditism is not stable in sufficiently heterogeneous populations, suggesting a possible reason for why hermaphroditism is rare among evolved animal species. The argument turns on the Bateman principle, namely that male reproductive success is limited by partner availability, while female reproductive success is not. Thus, it is closely related to Charnov (1979) who stressed the role of low mobility or population density in underpinning hermaphroditism. This paper explores an alternative route by focussing on the role of heterogeneity. Furthermore, this paper shows that reciprocal mating arises endogenously among simultaneous self-incompatible hermaphrodites, suggesting that hermaphroditism can only be sustained if reciprocal mating is stable.

This paper builds on Charnov, Maynard Smith, and Bull (1976), who formalized the conditions for dioecy and hermaphroditism under random mating. However, random mating better describes plants than animals, who, perhaps helped by their greater ability to search out and/or evade potential partners, have developed sophisticated strategies for mate choice. Our focus on non-random mating links our inquiry to the Trivers and Willard (1973) hypothesis that mammals should be able to influence the sex ratio of offspring according to parental condition.

2   Model

We consider a population of individuals who can be male, female or both. We index individuals by their quality, and assume that quality i is uniformly distributed on $[0, 1]$. Each individual i chooses the type that maximizes reproductive success (RS). RS depends on the number and quality of offspring. For tractability, we assume that

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[1]While the fixed costs of sex functions are not well known, at least the male reproductive system is potentially cheap, consisting chiefly of a duct to transport sex cells (Charnov (1979)).

offspring's quality is solely determined by the father's quality.[2]

Following Charnov (1979), we assume that each individual is endowed with a fixed amount of energy, 1, that can be devoted to reproduction. To build a female function the individual has to incur a fixed cost of a; to build a male function a fixed cost of b; $a, b > 0$ and $a + b < 1$. Hence, a female can spend $1 - a$ on reproduction, a male $1 - b$, and a hermaphrodite $1 - a - b$. We assume that sperm can be produced at zero marginal cost whereas the production of eggs is energy consuming. In particular, we assume that a female can produce $e_f \cdot r$ eggs out of an amount of energy r and normalize $e_f = 1$. Male reproductive success is constrained by partner ability. Let e_m (e_h in case of a hermaphrodite) be the energy devoted by a male to enhance eligibility (e.g., improve attractiveness, partner search, competitiveness). Thus, for a male, the budget constraint is $e_m \leq 1 - b$ and for a hermaphrodite $e_h \leq 1 - a - b$.

To calculate an individual's RS we have to consider how quality differences affect mating decisions. We abstract from sperm competition and assume that a male (male function) fertilizes all eggs of a partner.[3] Since the marginal cost of sperm is zero, a male (male function) is willing to mate with any female (female function). In contrast, an individual will be selective in terms of the sperm quality it accepts.

We restrict our analysis to the case of positive search cost. If there were no search cost, a male function would only be chosen by the highest quality individual (since we assume that quality is known at the time of "sex choice" and that sperm can be produced at zero marginal cost).

Definition 1 *A sub-population is a set of individuals who only mate with individuals in the same set.*

Definition 2 *We say that hermaphroditic mating is reciprocal if both female functions are mated.*

While two hermaphrodites who have mated reciprocally have exhausted their female functions, they can still use their male function in non-reciprocal matings with other hermaphrodites or pure females.

Characterization of Equilibria Equilibria can be summarized by the following partitioning of the unit interval: $i \in [0, \underline{j})$ are female; $i \in [\underline{j}, \bar{j}_1)$ are hermaphrodites who only mate with hermaphrodites; $i \in [\bar{j}_1, \bar{j}_2)$ are hermaphrodites who mate with hermaphrodites and females; and $i \in [\bar{j}_2, 1]$ are male, where $0 \leq \underline{j} \leq \bar{j}_1 \leq \bar{j}_2 \leq 1$. Depending on the parameter values (capturing search costs, resource constraints,

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[2]There are two ways to justify the assumption that only father's quality matter. First, our qualitative results stand as long as paternal quality matters *at all* for offspring quality. Second, this formulation is consistent with female quality varying less than male quality. Lower variation in female than male quality may stem from the fact that eggs are scarce in reproduction. Thus, we would expect sexual selection to exert more pressure towards male than female differentiation.

[3]Sperm competition may be crucial for understanding the existence of male-hermaphroditic populations: since hermaphrodites mate reciprocally, copulation alone cannot be the only determinant of male RS.

secondary sexual differentiation) some of the subintervals may be degenerate, such that purely gonochoric or mixed populations may result. However, there is no equilibrium with only hermaphrodites, except for the limit case of no male fixed cost ($b = 0$). Also, the lowest quality interval will always be female (unless $b = 0$). Moreover, no pure males can exist without secondary sexual differentiation. Lastly, reciprocity characterizes hermaphroditic mating.

2.1 Basic Specification

Here, we abstract from the role of secondary sexual differentiation (i.e., from analyzing e_m and e_h). Interestingly, this simplification precludes pure males in equilibrium. We relax this assumption in Section 2.2.

To preview results, equilibria will have the following structure: $i \in [0, \underline{j})$ are pure females, and $i \in [\underline{j}, 1]$ are hermaphrodites. All hermaphroditic mating is reciprocal. In addition, hermaphrodites of quality $i \in [\bar{j}_1, 1], \bar{j}_1 \geq \underline{j}$, will mate with pure females as well. Whether $\bar{j}_1 = \underline{j}$ or $\bar{j}_1 > \underline{j}$ will depend on parameter values.

Since there are search costs, females face a trade-off between mate quality and finding a mate. For a pure female this trade-off implies that she chooses a threshold quality $\bar{j}_1$ above which she accepts any male (or male function). Clearly, individuals $i < \bar{j}_1$ cannot be pure males. However, they may be hermaphroditic. We now turn to their mating behavior.

The hermaphroditic mating decision is complicated by the fact that the optimal mating strategy may involve "bundling" of the male and female functions. In particular, since a hermaphrodite seeks to mate its male function promiscuously while remaining selective with respect to its female function, hermaphroditic mating may be reciprocal in equilibrium.

Consider a hermaphrodite of quality $i < \bar{j}_1$. It is not accepted by a pure female. Consequently, it can either do without using its male function – in which case it might as well dispense with it altogether and spend the freed-up resources on eggs, i.e., be a pure female – or mate with other hermaphrodites. The reason the latter might be feasible is that hermaphrodites value access to eggs (unlike pure females). Thus, a necessary condition for individuals $i < \bar{j}_1$ to be hermaphroditic is that they mate reciprocally. Whether the mating is random or assortative will depend on search costs. If search costs are low, hermaphrodites will only accept sperm quality above a threshold value, resulting in assortative reciprocal mating. This is the case we will focus on.[4]

Search costs mainly impact the mating behavior of hermaphrodites (as opposed to gonochorists).[5] Hermaphrodites whose quality is below females' threshold $\bar{j}_1$ have to mate reciprocally in order to find a mate for their male function. Since search costs are low, the best type (close to $\bar{j}_1$) is only willing to mate its female

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[4]If search costs are high, a hermaphrodite has to seize any mating opportunity that allows RS through both male and female functions and random reciprocal mating results. However, the equilibria in this case are qualitatively similar to the low search cost case.

[5]This result is an artefact of our assumption that only paternal quality matters for offspring quality.

function to another hermaphrodite that is close to its own type. Therefore, it follows that these hermaphrodites mate assortatively.

The same applies to *hermaphroditic* mating above $\bar{j}_1$. By insisting on reciprocal mating, hermaphrodites ensure high quality sperm for their eggs. Thus, for high quality hermaphrodites reciprocal and assortative mating is a best response.

It is straightforward to see that this argument applies if $i > (\bar{j}_1 + 1)/2$ (if they were to mate non-reciprocally they would receive the average sperm quality $(\bar{j}_1 + 1)/2$ as opposed to quality i if mating were reciprocal).

Reciprocity is less obvious for individuals $i \in (\bar{j}_1, (\bar{j}_1+1)/2)$. They face a trade-off between sperm quality and mating opportunities for the following reason: the top hermaphrodites use their female function to buy reciprocity but they can still use their male function to fertilize other hermaphrodites (in addition to any females). However, that option exists for any hermaphrodite above $\bar{j}_1$ and is not important for the reasoning within the group of hermaphrodites. Thus, if hermaphrodites $i \in (\bar{j}_1, (\bar{j}_1 + 1)/2)$ were to mate nonreciprocally, they could receive higher sperm quality. But, as the top individuals' eggs are no longer available, the lower-quality hermaphrodites compete with all individuals above $\bar{j}_1$ for a reduced number of eggs. Thus, they can either mate reciprocally with a hermaphrodite of the same quality, or they mate non-reciprocally. In the latter case, their eggs would be fertilized by higher quality sperm, but they risk to mate their male function with pure females only. In other words, by giving up reciprocity, they are no longer guaranteed access to another hermaphrodite's eggs. For individuals below $(\bar{j}_1 + 1)/2$ but close to it, the gain in RS through female function (improved sperm quality) will not outweigh the loss in RS from male function (fewer fertilized eggs). Thus, reciprocal and assortative mating is optimal for individuals below but close $(\bar{j}_1 + 1)/2$. It then follows that it is also optimal for all hermaphrodites of lower quality. A formal proof is in the Appendix.

We now state our first results:

Lemma 1 *Hermaphrodites mate reciprocally.*

Lemma 2 *If search costs are low, hermaphroditic mating is positive assortative.*

Based on these intermediate results we can describe the population structure that results if individuals choose whether to be male, female or both.

Proposition 1 *If there is no secondary sexual differentiation and search costs are low there are two kinds of Nash equilibria.*

1. *For any $a \in (0, 1)$ and $b := \mu(1 - a)$, $\mu \in (0, 1)$ there is a Nash equilibrium with the following structure:*

$$0 < \underline{j} = \bar{j}_1 < \bar{j}_2 = 1,$$

where $\underline{j} = \frac{2}{1-4\mu}(1 - \mu - \frac{1}{2}\sqrt{3 - 4\mu + 4\mu^2})$. For $\mu \in [1/2, 1]$, it is unique.

In words, all individuals of quality $i \in [0, \underline{j})$ choose to be female and accept any individual $i > \underline{j}$ as a partner, and all individuals of quality $i \in [\underline{j}, 1]$ choose to be hermaphrodites. Females accept all hermaphrodites as partners.

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2. *In addition, for any $a \in (0,1)$ and $b := \mu(1-a)$, $\mu \in [0,1/2)$, and for any $\bar{j}_1 \geq \frac{1}{3-4\mu}$ there is a Nash equilibrium with the following structure:*

$$0 < \underline{j} < \bar{j}_1 < \bar{j}_2 = 1,$$

where $\underline{j} := \frac{1+\bar{j}_1}{4(1-\mu)}$. In words, females only accept partners of quality $i \geq \bar{j}_1$, individuals of quality $i < \underline{j}$ are female, and individuals of quality $i \geq \underline{j}$ are hermaphroditic.

In sum, Proposition 1 says that females at the bottom and hermaphrodites at the top characterize equilibria. No equilibrium has only hermaphrodites and there are no pure males. The intuition for the former is that low quality individuals can do better as pure females. A proof is in the Appendix. Figure 1 depicts the equilibrium structure.
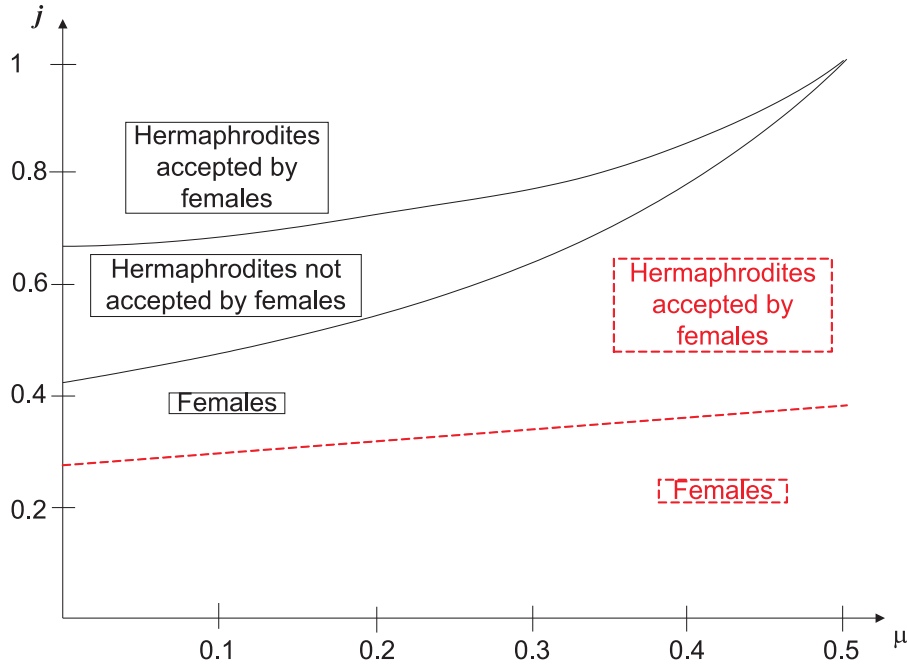
Notes: The dashed part of the figure depicts the distribution of types within the population from part 1 of Proposition 1. The dashed line is given by $\underline{j} = \frac{2}{1-4\mu}(1 - \mu - \frac{1}{2}\sqrt{3 - 4\mu + 4\mu^2})$. Individuals whose quality is below $\underline{j}$ choose to be female, individuals above $\underline{j}$ choose to be hermaphroditic. Females accept all hermaphrodites. This equilibrium exists for all $\mu \in [0,1]$.

The solid part of the figure depicts the distribution of types within the population from part 2 of Proposition 1. The exact distribution depends on the value of $\bar{j}_1$. The graph is based on $\bar{j}_1 = \frac{1 + \frac{1}{3-4\mu}}{2}$, i.e., a value in the middle of the admissible range. Here, all individuals above $\underline{j} = \frac{1+\bar{j}_1}{4(1-\mu)}$ choose to be hermaphrodites but females accept only those above $\bar{j}_1$.

Figure 1: Distribution of types without secondary sexual differentiation

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The lack of pure males is driven by the absence of secondary sexual differentiation which means that a pure male cannot access more females than a hermaphrodite (e.g., from being more attractive or faster). Therefore, hermaphrodites always have a higher RS than males of the same quality. Consequently, without secondary sexual differentiation the equilibrium population consists of females and reciprocal hermaphrodites (the latter mate reciprocally with each other and, obviously, non-reciprocally with the females).

2.2   Secondary Sexual Differentiation

Males were absent from the equilibria above. Secondary sexual differentiation (SSD) changes that.[6] The assumption that male sex cells are produced at zero marginal cost implies that high sperm quality is not scarce, and thus female RS hinges on the quantity of eggs produced. Male RS, on the other hand, increase with greater partner access, and partner access may be improved by investments in SSD.

Since a male has no alternative uses for the energy endowment 1, we know that male investment in SSD, e_m, is:

$$e_m = 1 - \mu(1 - a).$$

A hermaphrodite can invest in eggs, and we will assume that it spends a fraction λ on eggs and the remaining energy on SSD, denoted e_h:

$$e_h = (1 - \lambda)(1 - a - b).$$

For a general analysis of the population structure, it would be necessary to consider λ as a choice variable of hermaphroditic individuals. However, we focus on understanding the role of SSD for gonochorism and therefore, we treat λ as a fixed parameter. Since hermaphrodites can spend less than males on SSD, they may give it up altogether in favor of egg production. Therefore a λ close to 1 seems therefore a reasonable assumption.

We parameterize the pure male's (male) advantage over a hermaphrodite by x, the ratio of the expected number of female partners of a male and a hermaphrodite respectively. The empirically relevant range is $x > 1$.

While females could gain RS by diverting resources into SSD, they do not have an incentive to do so in our set up. The reason is that there is no female competition for high quality males.

Again, we focus on the case of low search cost, i.e., hermaphrodites mate assortatively (and reciprocally).[7]

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[6]The concept was introduced by Darwin who defined it as traits that helped in the competition for mates, but are otherwise a burden, like the peacock's tail. He observed that secondary sexual differentiation is more pronounced among males, or in his words: "If masculine character [is] added to the species, we can see why young & Female [are] alike[.]" quoted in the Penguin Classics 2004 introduction to The Descent of Man. Secondary sexual differentiation being greater among males is consistent with the greater variable cost of female sex cells.

[7]Again, if search cost were high, hermaphrodites would mate randomly. This does not affect the qualitative characterization of the equilibria, only the values of the cut-off points.

Proposition 2 *For $a \in (0,1)$, $b = \mu(1-a)$, $\mu \in (0,1)$, $\lambda \in [0,1]$ there are the following Nash equilibria in pure strategies:*

1. *For $x \leq \frac{4\lambda^2(1-\mu)^2 - 4\lambda(1-\mu) + (2\lambda(1-\mu) - 1)\sqrt{4\lambda^2(1-\mu)^2 + 3 - 4\lambda(1-\mu)}}{2\lambda(1-\mu) - \sqrt{4\lambda^2(1-\mu)^2 + 3 - 4\lambda(1-\mu)}}$, there is an equilibrium with the following properties (cf. Proposition 1, part 1):*

$$0 < \underline{j} = \bar{j}_1 < \bar{j}_2 = 1,$$

   where

$$\underline{j} = \frac{2}{4\lambda(1-\mu) - 3}\left(\lambda(1-\mu) - \frac{1}{2}\sqrt{4\lambda^2(1-\mu)^2 + 3 - 4\lambda(1-\mu)}\right).$$

2. *For $\mu \leq 1 - \frac{1}{2\lambda}$, $x \leq 1 + \frac{8\lambda^2(1-\mu)^2(1-\bar{j}_1)}{1+\bar{j}_1}$, there is an equilibrium with the following properties (cf. Proposition 1, part 2):*

$$0 < \underline{j} < \bar{j}_1 < \bar{j}_2 = 1,$$

   where

$$\underline{j} = \frac{1+\bar{j}_1}{4\lambda(1-\mu)},$$

   and

$$\bar{j}_1 > \frac{1}{4\lambda(1-\mu) - 1}.$$

3. *For $\mu \leq 1 - \frac{1}{2\lambda}$, and $x > \max\{1 + \frac{8\lambda^2(1-\mu)^2(1-\bar{j}_2)}{1+\bar{j}_2}, \frac{1+\bar{j}_2}{1+\bar{j}_2 - 8\lambda^2(1-\mu)^2}\}$, there is an equilibrium with the following properties:*

$$0 < \underline{j} < \bar{j}_1 = \bar{j}_2 < 1,$$

   where

$$\underline{j} = \frac{1+\bar{j}_2}{4\lambda(1-\mu)}$$

   and

$$\bar{j}_2 > \max\{\frac{1}{4\lambda(1-\mu) - 1}, \frac{-1 + 8\lambda^2(1-\mu)^2}{1 + 8\lambda^2(1-\mu)^2}\}.$$

In words, females accept males above $\bar{j}_2$, individuals in $[0, \underline{j})$ are females, individuals in $[\underline{j}, \bar{j}_2)$, are hermaphrodites, and individuals in $[\bar{j}_2, 1]$ are males.

4. *If* $\mu > 1 - \frac{1}{2\lambda(\sqrt{3}-1)}$, *then there is for any* $x \geq \frac{1}{(1-2\lambda(\sqrt{3}-1)(1-\mu)}$ *an equilibrium with females and males only:*

$$0 < \underline{j} = \bar{j}_1 = \bar{j}_2 < 1,$$

where

$$\underline{j} = \frac{1}{\sqrt{3}}.$$

In words, all individuals in $[0, \underline{j})$ *are female and all individuals in* $[\underline{j}, 1]$ *are male. Females accept all males as partners.*

Proposition 2 describes a possible path towards gonochorism. Part 4 gives conditions for an immediate shift. In Part 3, using definition 1, the population splits into a sub-population of hermaphrodites and a sub-population of males and females. Within the sub-population of of hermaphrodites, the process may start anew, with the extremes turning gonochoric (females at the bottom and males at the top). Figure 2 illustrates parts 3 and 4 of the proposition.

Proposition 2 highlights the role of SSD for males, and that males and hermaphrodites are unlikely to co-exist in equilibrium. This suggests that for (simultaneous, self-incompatible) hermaphroditism to exist in "the long run," a species either lack "visible" heterogeneity (for instance from living in a habitat that is rich enough) or the scope for SSD is low (e.g., from low mobility).

3 Discussion

The paper has argued that hermaphroditism is not stable in the face of population heterogeneity. The reasons are three fold. First, low quality individuals would do better as pure females if there are fixed costs associated with a sex function. Second, females prefer high quality individuals as mating partners. Thus, low and high quality individuals interbreed, whereas intermediate individuals only mate among themselves. Third, if there is sufficient scope for secondary sexual differentiation, it pays for the high quality individuals to be pure males. In that case two sub-populations form: a gonochoric sub-population consisting of (low-quality) females and (high-quality) males and a sub-population of hermaphrodites. The remaining hermaphrodites are less heterogeneous, but within this group the selection process may start anew. By this logic, a hermaphroditic species may turn gonochoric – unless heterogeneity is absent or there is no scope for secondary sexual differentiation (from anything that caps male reproductive capacity, low mobility being a case in point).

Phylogenically, hermaphroditism has given way to gonochorism, and irreversibility of the latter may be one reason. Charnov (1982):241 wrote "At least one constraint hypothesis suggests itself. It may be easier to change from hermaphroditic to
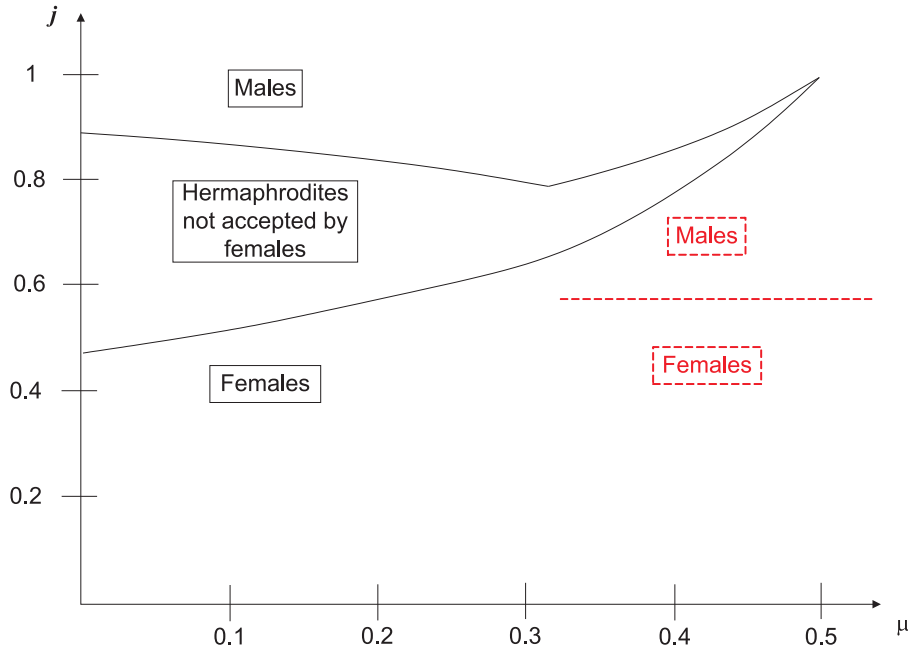
Notes: The figure is based on the assumption that only males invest into secondary sexual differentiation, i.e., $\lambda = 1$.

The dashed part of the figure depicts the distribution of types within the population from part 4 of Proposition 2. The dashed line is given by $\underline{j} = \frac{1}{\sqrt{3}}$. Individuals whose quality is below $\underline{j}$ choose to be female, individuals above $\underline{j}$ choose to be males. This equilibrium only exists for $\mu \in [.317, 1]$.

The solid part of the figure depicts the distribution of types within the population from part 3 of Proposition 2. The exact distribution depends on $\bar{j}_2$. The graph assumes that $\bar{j}_2$ is in the middle of the admissible range. Here, individuals between $\underline{j} = \frac{1 + \bar{j}_2}{4(1-\mu)}$ and $\bar{j}_2$ choose to be hermaphrodites but females accept only males.

Figure 2: Distribution of types with secondary sexual differentiation

dioecious than the reverse. A hermaphrodite need only suppress the development or use of one sex function; suppression early in development may automatically free resources for the other sex function. Under dioecy, an individual becoming a hermaphrodite must build and operate the other sex function. Until the other function works, selection must operate against diverting resources there." The development of SSD, facilitated by gonochorism (dioecy) may be another reason the process might not easily reverse. Once in place, the existence of SSD may make the male function of a hermaphrodite uncompetitive and thus redundant.

Male violence is a particularly interesting form of SSD. Our results suggest that hermaphrodites are particularly vulnerable to male-to-male violence. Since hermaphrodites mate reciprocally, a hermaphrodite's female function is not available to pure males, and thus a hermaphrodite is, in the eyes of a pure male, for practical purposes a male rival only. Note that male-to-male violence is more debilitating to the hermaphroditic population than the gonochoric even at similar fatality rates.

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This follows because the death of a pure male does not affect the number of eggs produced, whereas the death of a hermaphrodite does. Although "male" violence among hermaphrodites does occur (e.g., marine flatworms, see Michiels and Newman (1998)), we would expect such violence to be non-lethal.

It has been noted that reciprocal mating results in weaker sexual selection (cf. strict monogamy among gonochorists). Our paper points to the possibility that hermaphroditism is only stable if the scope for sexual selection is low (i.e., low heterogeneity). This is consistent with the Charnov's observation that reciprocal mating does not preclude effective polygyny (for an example of sperm competition and counter strategies, see Haase and Karlsson (2004)).

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Appendix

Proof of Lemmas 1 and 2:

Consider a group of hermaphrodites that mate with each other as males and females and are, in addition, willing to use their male function when mating with individuals from another group (females or other hermaphrodites). Reproductive

success from outside the group is a fixed revenue for all individuals. It is therefore unmentioned in what follows.

Let the worst quality within this group be j_1, the best quality j_2. Individuals can use three different mating strategies within the group of hermaphrodites:

(1) Random, non-reciprocal mating

(2) Random, reciprocal mating

(3) Assortative, reciprocal mating

Assortative, non-reciprocal mating is not a meaningful strategy as the female function does not contribute to offspring quality. To show that under low search costs individuals will choose assortative, reciprocal mating, we show first that random, non-reciprocal mating is dominated by random, reciprocal mating and then that assortative, reciprocal mating constitutes a Nash equilibrium.

Thus, we compare RS from the first two alternatives. If (all) individuals mate randomly, they receive sperm of quality $\frac{j_1+j_2}{2}$ in expectation. This quality is independent of reciprocity. Thus, without search costs there is no difference between both strategies. If we account for search costs, mating reciprocally reduces search costs as well as the risk of not finding a partner. Random, non-reciprocal mating is therefore dominated by random, reciprocal mating. Random, non-reciprocal mating is thus canceled from the strategy space under consideration.

To show that assortative mating constitutes a Nash equilibrium needs more considerations. First, it is clear that individuals whose quality is above $\frac{j_1+j_2}{2}$ prefer to mate assortatively – if search costs are sufficiently low – as they have an RS of

$$2j(1-a-b)$$

if mating assortatively and of

$$j(1-a-b) + \frac{j_1+j_2}{2}(1-a-b)$$

if mating randomly. The former value is higher than the latter as long as $j > \frac{j_1+j_2}{2}$.

Individuals of quality $j \in \left[j_1, \frac{j_1+j_2}{2}\right]$ would receive sperm of – in expectation – higher quality under random mating than under assortative mating. But, as those individuals of quality above $\frac{j_1+j_2}{2}$ will mate assortatively and reciprocally, the number of male and female functions that are to be randomly matched is off balance. For, individuals above $\frac{j_1+j_2}{2}$ have used their female function for reciprocal mating but are still willing to use their male function again. Therefore, if individuals of lower quality (below $\frac{j_1+j_2}{2}$) accept sperm from those individuals who have already used their female function for reciprocal mating, they will forego mating opportunities for their own male function.

Therefore, individuals of quality $j \in \left[j_1, \frac{j_1+j_2}{2}\right]$ face three alternatives:

(a) Mate randomly and reciprocally (and, thus, forego high quality sperm) which leads to RS of

$$j(1-a-b) + \frac{j_1 + \frac{j_1+j_2}{2}}{2}(1-a-b),$$

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(b) mate randomly and non-reciprocally (and accept sperm from all individuals above j_1) which leads to RS of

$$\frac{j_1 + j_2}{2}(1 - a - b) + j(1 - a - b)\underbrace{\frac{\frac{j_1+j_2}{2} - j_1}{j_2 - j_1}}_{=1/2}$$

as there are excess male functions and therefore the probability of finding a mate for ones own male function is smaller than 1 for an individual of quality $j \in [j_1, \frac{j_1+j_2}{2}]$, (c) mate assortatively which leads to RS of

$$2j(1 - a - b).$$

Comparing alternatives (a) and (b) we find that for individuals of lower quality (below $\frac{j_1+j_2}{2}$) random, reciprocal mating dominates random, non-reciprocal mating – that includes all male functions – as long as $j_1 > 1/3j_2$. This condition holds in all scenarios considered throughout the paper as individuals of quality $j \leq 1/3$ will always choose to be purely female and j_2 cannot exceed 1. Therefore, alternative (b) can be ignored.

Comparing alternatives (a) and (c) we find that – ignoring search costs – assortative mating is the better strategy for all individuals of quality above $\frac{3j_1+j_2}{4}$. If we account for search costs this threshold would be even smaller.

Thus, we have shown that individuals in $[\frac{3j_1+j_2}{4}, j_2]$ will mate assortatively. Individuals in $[j_1, \frac{3j_1+j_2}{4}]$ again face the behavioral alternatives (a), (b), and (c) with the corresponding – mutatis mutandis – RS. Alternative (b) can again be excluded if $j_1 > 1/3j_2$. From comparison of (a) and (b) we get that individuals of quality above $\frac{7j_1+j_2}{8}$ prefer to mate assortatively.

Taking that argument ad infinitum we can show that all individuals above j_1 prefer to mate assortatively if the best individuals within the group do so. This behavior is a best response for high quality individuals if search costs are low – which we assumed. q.e.d.

Proof of Proposition 1:

Part 1: We assume that individuals of quality $i < \underline{j}$ choose to be female and to accept males of quality $i > \underline{j}$. Then there are $\underline{j}$ females and $1 - \underline{j}$ males and hermaphrodites. Accordingly, the RS of a hermaphrodite of quality i is given by

$$2(1 - a - b)i$$

from reciprocal mating and

$$(1 - a)i\frac{\underline{j}}{1 - \underline{j}}$$

from its male function. The RS of a female is

$$(1 - a)\frac{1 + \underline{j}}{2}.$$

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To determine the threshold $\underline{j}$, an individual of quality $\underline{j}$ has to be indifferent between being female and being hermaphroditic. Using $b = \mu(1 - a)$ we obtain

$$(1 - a)\frac{1 + \underline{j}}{2} = 2(1 - a - b)\underline{j} + (1 - a)\underline{j}\frac{\underline{j}}{1 - \underline{j}}, \quad \underline{j} \in [0, 1]$$

$$\Leftrightarrow \quad \underline{j} = \frac{2}{1 - 4\mu}(1 - \mu - \frac{1}{2}\sqrt{3 - 4\mu + 4\mu^2})$$

which exists and is in $[0, 1]$ for all $\mu \in [0, 1]$ except for $\mu = 1/4$, where the function has a removable pole. Thus, being female and accepting all male functions above $\underline{j}$ is a best response to all individuals above $\underline{j}$ being hermaphrodites and vice versa. Therefore, $\underline{j} = \bar{j}_1$. As there is no SSD, being pure male does not provide an advantage in fertilizing eggs but goes at the cost of not having RS from own eggs; therefore $\bar{j}_2 = 1$.

Part 2: However, all hermaphrodites being assortatively reciprocal does not imply that females accept all hermaphrodites as partners. We now describe the conditions for an equilibrium where individuals below $\underline{j}$ are female and females choose a different threshold quality $\bar{j}_1$. If there are hermaphrodites below $\bar{j}_1$ their RS only comes from reciprocal matings and is given by

$$2(1 - a - b)i.$$

Female RS is now given by

$$(1 - a)\frac{1 + \bar{j}_1}{2}$$

and RS of a hermaphrodite above $\bar{j}_1$ by

$$2(1 - a - b)i + (1 - a)\frac{\underline{j}}{1 - \bar{j}_1}.$$

The lower threshold is again given by indifference between female and hermaphroditic (without additional matings) RS. Using $b = \mu(1 - a)$ we get:

$$(1 - a)\frac{1 + \bar{j}_1}{2} = 2(1 - a - b)\underline{j}$$

$$\Leftrightarrow \quad \underline{j} = \frac{1 + \bar{j}_1}{4(1 - \mu)}. \tag{1}$$

To provide a basis for an equilibrium, $\underline{j}$ and $\bar{j}_1$ have to meet two conditions:
(1) $\underline{j} \leq \bar{j}_1$ which implies that

$$\frac{1}{3 - 4\mu} \leq \bar{j}_1, \quad \text{and} \quad \mu < \frac{3}{4}$$

the condition on $\bar{j}_1$ given in the proposition.
(2) $\bar{j}_1 \leq 1$ which – following from the first condition – implies $\frac{1}{3-4\mu} \leq 1$. This condition holds if $\mu \leq 1/2$. Again, there is no room for males: $\bar{j}_2 = 1$. q.e.d.

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Proof of Proposition 2:
A hermaphrodite spends $\lambda \cdot e$ on eggs and $(1 - \lambda) \cdot e$ on matings.
The RS of a male of quality i is given by

$$i(1 - a)d_m,$$

where d_m denotes the expected number of a male's female partner, and the RS of a hermaphrodite of quality i under assortative mating is given by

$$2\lambda(1 - a - b)i + i(1 - a)d_h = 2\lambda(1 - \mu)(1 - a)i + i(1 - a)d_h,$$

where d_h denotes the expected number of a hermaphrodite's female partner. Comparing these expressions we obtain

$$
\begin{aligned}
i(1 - a)d_m \quad &\gtreqless \quad 2\lambda(1 - \mu)(1 - a)i + i(1 - a)d_h \\
\Leftrightarrow \quad d_m \quad &\gtreqless \quad 2\lambda(1 - \mu) + d_h.
\end{aligned}
\tag{2}
$$

That is, the difference in male and hermaphroditic success is independent of individual quality. Therefore, a pure strategy equilibrium will either result in females and hermaphrodites or in females and males. Thus, to prove the proposition's claims it suffices to show under which conditions a population with hermaphrodites who mate with females is stable against male invasion and under which conditions a female-male population is stable against hermaphroditic invasion. Thus, independent of equilibrium structure we have $\bar{j}_1 = \bar{j}_2$.

For the female-hermaphrodite equilibria, the population structures are similar to those of Proposition 1:

(1) Females accept all hermaphrodites as partners and all individuals below $\underline{j}$ are female and all individuals above $\underline{j}$ are hermaphrodites. The individual of quality $\underline{j}$ is indifferent between being female or hermaphroditic, which defines threshold quality $\underline{j}$ as

$$\underline{j} = \frac{2}{4\lambda(1 - \mu) - 3}\left(\lambda(1 - \mu) - \frac{1}{2}\sqrt{4\lambda^2(1 - \mu)^2 + 3 - 4\lambda(1 - \mu)}\right).$$

For $\lambda = 1$ this expression is equal to that in proposition 1.

(2) Females accept only hermaphrodites above $\bar{j}$, which leads to a three-layer population structure: All individuals below $\underline{j}$ are female, individuals in $[\underline{j}, \bar{j}_1)$ are hermaphrodites that do not mate with females, and in $[\bar{j}_1, 1]$ there are hermaphrodites that do mate with females.

Since individual $\underline{j}$ needs to be indifferent between being female, earning a RS of $(1 - a)(\bar{j}_1 + 1)/2$, and being a hermaphrodite who mate reciprocally and assortatively only, earning a RS of $2\lambda(1 - \mu)(1 - a)\underline{j}$, we obtain

$$\underline{j} = \frac{1 + \bar{j}_1}{4\lambda(1 - \mu)}.$$

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For males to be able to invade, they need to do better than the hermaphrodites who mate with females. The expected number of matings with females for a hermaphrodite is $d_h = \frac{f}{h^*}$ where h^* varies according to the equilibrium. A male that invades the population mates with $d_m = x d_h$ females (cf. page 7). Therefore, from (2) we know that a male can invade the population if

$$x \frac{f}{h^*} > 2\lambda(1-\mu) + \frac{f}{h^*}. \tag{3}$$

If females accept all hermaphrodites as partners, condition (3) takes the form

$$x \frac{\underline{j}}{1-\underline{j}} > 2\lambda(1-\mu) + \frac{\underline{j}}{1-\underline{j}}. \tag{4}$$

If females only accept the top hermaphrodites as partners, then condition (3) takes the form

$$x \frac{\underline{j}}{1-\bar{j}_1} > 2\lambda(1-\mu) + \frac{\underline{j}}{1-\bar{j}_1}, \tag{5}$$

where $\underline{j}$, $\bar{j}_1$ have to be substituted according to the threshold values from proposition 1. Inequalities (4) and (5) lead to the equilibria in parts 1 through 3 of Proposition 2.

We now turn to proving the specific parts of the proposition.

Part 1.

Here (4) is the relevant inequality with $\underline{j} = \frac{2}{4\lambda(1-\mu)-3}(\lambda(1-\mu) - \frac{1}{2}\sqrt{4\lambda^2(1-\mu)^2 + 3 - 4\lambda(1-\mu)})$. Therefore a female/hermaphroditic population is stable (i.e., males cannot invade) if

$$
\begin{aligned}
x \frac{\underline{j}}{1-\underline{j}} &\leq 2(1-\mu) + \frac{\underline{j}}{1-\underline{j}} \\
\Leftrightarrow x &\leq 1 + (1-\mu)2\frac{1-\underline{j}}{\underline{j}} \\
\Leftrightarrow x &\leq \frac{4\lambda^2(1-\mu)^2 - 4\lambda(1-\mu) + (2\lambda(1-\mu)-1)\sqrt{4\lambda^2(1-\mu)^2 + 3 - 4\lambda(1-\mu)}}{2\lambda(1-\mu) - \sqrt{4\lambda^2(1-\mu)^2 + 3 - 4\lambda(1-\mu)}}
\end{aligned}
$$

which proves the claim. If $\lambda = 1$ the relevant threshold is given by $x \leq \frac{\sqrt{3-4\mu+4\mu^2}+4\mu^2-2\mu\sqrt{3-4\mu+4\mu^2}-4\mu}{2-2\mu-\sqrt{3-4\mu+4\mu^2}}$.

Part 2.

Here (5) is the relevant inequality, where $\underline{j} = \frac{1+\bar{j}_1}{4\lambda(1-\mu)}$; the proposed three-layer population only exists if $\mu \leq 1 - \frac{1}{2\lambda}, (\lambda > \frac{1}{2})$ and $\bar{j}_1 \geq \frac{1}{4\lambda(1-\mu)-1}$. The condition for a purely female/hermaphroditic population to be stable is

$$
\begin{aligned}
x \frac{\underline{j}}{1-\bar{j}_1} &\leq 2(1-\mu) + \frac{\underline{j}}{1-\bar{j}_1} \\
\Leftrightarrow x &\leq 1 + (1-\mu)2\frac{1-\bar{j}_1}{\underline{j}} \\
\Leftrightarrow x &\leq 1 + \frac{8\lambda^2(1-\mu)^2(1-\bar{j}_1)}{1+\bar{j}_1}
\end{aligned}
$$

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which proves the claim.

Part 3.

The three-layer equilibrium with females and hermaphrodites can be invaded if (5) holds which implies that

$$x > 1 + \frac{8\lambda^2(1-\mu)^2(1-\bar{j}_1)}{1+\bar{j}_1}.$$

In that case males had an incentive to replace those hermaphrodites whose quality is above $\bar{j}_1$; females' and intermediate hermaphrodites' incentives are not modified by that change as their RS only depends on the fact that there are male functions above $\bar{j}_1$ and is independent of the provider's sex choice.

Thus, if $x > 1 + \frac{8\lambda^2(1-\mu)^2(1-\bar{j}_1)}{1+\bar{j}_1}$ there can be an equilibrium with females below $\underline{j}$, purely reciprocal hermaphrodites in $[\underline{j}, \bar{j}_1)$, and males above $\bar{j}_1$. As $\bar{j}_1 = \bar{j}_2$ and $\bar{j}_2$ denotes the threshold between hermaphrodites and males, we replace $\bar{j}_1$ by $\bar{j}_2$ for the remainder of the proof. This equilibrium however could be invaded by hermaphrodites. Now, the considerations leading to (5) have to be undertaken from male perspective.

If there are males only above $\bar{j}_2$, their average number of matings is $d_m = \frac{f}{m}$. A hermaphrodite invading this population would have $d_h = \frac{1}{x}d_m$ matings with females according to (2). Thus, a hermaphrodite can invade the population if

$$
\begin{aligned}
d_m &< 2\lambda(1-\mu) + d_h \\
\Leftrightarrow \quad \frac{f}{m} &< 2\lambda(1-\mu) + \frac{1}{x}\frac{f}{m} \\
\Leftrightarrow \quad (1-\frac{1}{x})\frac{\underline{j}}{1-\bar{j}_2} &> 2\lambda(1-\mu)
\end{aligned}
$$

If we substitute $\underline{j}$ we get

$$x\left(\frac{1+\bar{j}_2}{4\lambda(1-\mu)(1-\bar{j}_2)} - 2\lambda(1-\mu)\right) < \frac{1+\bar{j}_2}{(1-\bar{j}_2)4\lambda(1-\mu)}$$

where the bracket is positive as long as $\bar{j}_2 > \frac{-1+8\lambda^2(1-\mu)^2}{1+8\lambda^2(1-\mu)^2}$. Thus, if $\bar{j}_2$ sufficiently high, hermaphrodites can invade the population if

$$x < \frac{1+\bar{j}_2}{1+\bar{j}_2 - 8\lambda^2(1-\mu)^2(1-\bar{j}_2)}$$

which proves the claim.

Part 4. As we have already shown that males will invade a two-layer population if $x > \frac{4\lambda^2(1-\mu)^2-4\lambda(1-\mu)+(2\lambda(1-\mu)-1)\sqrt{4\lambda^2(1-\mu)^2+3-4\lambda(1-\mu)}}{2\lambda(1-\mu)-\sqrt{4\lambda^2(1-\mu)^2+3-4\lambda(1-\mu)}}$, it remains to show when a female/male population would be stable. Hermaphrodites cannot invade a female/male population if

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$$\frac{f}{m} \geq 2\lambda(1-\mu) + \frac{1}{x}\frac{f}{m}$$

$$\Leftrightarrow \qquad \frac{\underline{j}}{1-\underline{j}} \geq 2\lambda(1-\mu) + \frac{1}{x}\frac{\underline{j}}{1-\underline{j}} \qquad (6)$$

where $\underline{j}$ needs to be determined. Female RS is given by

$$(1-a)\frac{1+\underline{j}}{2}$$

and RS of an individual of quality i is given by

$$(1-a)i\frac{\underline{j}}{1-\underline{j}}.$$

Therefore the threshold quality $\underline{j}$ can be determined by the indifference condition

$$(1-a)\frac{1+\underline{j}}{2} = (1-a)\underline{j}\frac{\underline{j}}{1-\underline{j}}$$

$$\Leftrightarrow \qquad \underline{j} = \frac{1}{\sqrt{3}}.$$

If we substitute $\underline{j}$ into inequality (6), we see that it can only hold (even if $x \to \infty$) if $\mu > 1 - \frac{1}{2\lambda(\sqrt{3}-1)}$. If we solve (6) for x, we get that hermaphrodites cannot invade the population if $x \geq \frac{1}{(1-2\lambda(\sqrt{3}-1)(1-\mu)}$. q.e.d.