Hermaphroditism: What’s not to Like?

Lena Edlund* and Evelyn Korn†

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Abstract

Male and female social roles are predicated on the fact that male and female reproductive functions are separated in different individuals. This paper asks why. That is, why is gonochorism, not hermaphroditism, the rule among vertebrates. We argue that (simultaneous) 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. We also show that without secondary sexual differentiation (SSD), there is no equilibrium with males. Only females and hermaphrodites. With sufficient SSD, however, males may outcompete hermaphrodites so that hermaphrodites only mate among themselves and thus for practical purposes form their own species. We also show that, while hermaphrodites strive to mate their male function and preserve their female function, equilibrium hermaphroditic mating is reciprocal. Reciprocal mating, in turn, makes hermaphrodites susceptible to male-to-male violence, suggesting that form of SSD 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 (Trivers 1972). 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

*Dept. of Economics, Columbia University. E-mail: le93@columbia.edu
†Dept. of Economics, Philipps-Universität Marburg. E-mail: korn@wiwi.uni-marburg.de
1Dioecy in plant species, or gonochorism in animal species.
organism. A hermaphrodite incurs the fixed costs of building both sex functions. On the other hand, if the organism itself is considered a fixed cost for the sex functions, hermaphroditism is a low cost alternative. Unlike gonochorists, simultaneous hermaphrodites can reproduce with all mature conspecifics. 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, perhaps inspired by 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 scope for 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.

This paper focuses 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). Charnov stressed the role of low mobility or population density in underpinning hermaphroditism. This paper takes a different view and concentrates on the impact of homogeneity in the persistence of hermaphroditism. Furthermore, this paper highlights the role of reciprocity in mating for sustaining hermaphroditism, the hypothesis being that reciprocal mating will arise endogenously in simultaneous self-incompatible hermaphrodites (as practised by, e.g., terrestrial snails).

The paper falls under sex allocation, which traces its origins to Darwin and Fisher’s sex ratio theory. Fisher noted that when offspring are equally related to mother and father (as in diploid species), sons and daughters are merely alternative routes to grandchildren. But as Charnov (1982) pointed out, the level of decision making could, in principle, equally be at the individual

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2 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).

3 They argued that sexes happen because there is conflict over which parent will contribute the mitochondria DNA. The solution found is that mother provides mitochondria. This may also explain why most animals are gonochoric. Mitochondria DNA only gets passed on through females. Therefore, mitochondria will find sperm a waste of resources and see to that the hermaphrodite only produced eggs. A possible objection to this is that this would be true of a gonochoric species as well. Mitochondria DNA does not die an immediate death in a son, but he is a dead end, so the problem is only removed one generation. Hypothetically, mitochondria DNA could find a way to insulate the female’s eggs so that they are only receptive to x-sperms.
level. This paper also builds on Charnov, Maynard Smith, and Bull (1976). They 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. The 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. It also ties in with one of the authors’ work on facultative sex ratios in human societies (Edlund 1999).

The remainder of the paper is organized as follows. Section 2 presents a theoretical model, and Section 3 concludes.

2 Model

We consider a population of individuals who face the following sex-choice: be male, female or both. Each individual chooses the type that maximizes reproductive success (RS). RS depends on the number and quality of offspring. For tractability, we assume that offspring’s quality is solely determined by the father’s quality, where individual quality $i$ is uniformly distributed on $[0, 1]$.$^4$

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 $e_m$ be the energy devoted 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 female (female function) it mates with.$^5$ As the marginal cost of sperm is zero, a male (male function) fertilizes all eggs of a female (female function) it mates with.

$^4$There are two ways to justify the assumption that only father’s quality matter. The first is that this is purely done for tractability and that qualitatively our results would stand as long as paternal quality matters at all for offspring quality, which seems like a reasonable assumption. The second tack would be to note that such a formulation is consistent with female quality varying less than male quality (not necessarily that female quality does not matter). Identical female (egg) quality may stem from the fact that female resources are scarce in reproduction. Thus, we would expect sexual selection to exert more pressure towards male differentiation than female such.

$^5$Sperm competition may be crucial for understanding the existence of male-hermaphroditic populations, since hermaphrodites mate reciprocally, copulation alone can-
is willing to mate with any female (female function). In contrast, a female (female function) wants to receive the highest possible sperm quality for her eggs.

We restrict our analysis to situations with search cost. If there were no search cost, only the highest quality individual would choose to sport a male function (since we assume that quality is known at the time of "sex choice" and that sperm can be produced at zero marginal cost). Obviously, that is not an interesting equilibrium.

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

**Definition 2** We say that a hermaphrodite is reciprocal if it mates as a male and a female with the same hermaphrodite.

Note that 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.

To anticipate results, equilibria can be summarized by the following partitioning of the unit interval: $i \in [0, j)$ are female; $i \in [\tilde{j}, \tilde{j}_1)$ are hermaphrodites who only mate with hermaphrodites; $i \in [\tilde{j}_1, \tilde{j}_2)$ are hermaphrodites who mate with hermaphrodites and females; and $i \in [\tilde{j}_2, 1]$ are male, where $0 \leq \tilde{j} \leq \tilde{j}_1 \leq \tilde{j}_2 \leq 1$. Depending on the parameters under consideration (search costs, resource constraints, secondary sexual differentiation) some of the represented 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 $b = 0$. Also, the lowest quality interval will always be female (unless $b = 0$). Moreover, no pure males can exist without secondary sexual differentiation. Lastly, hermaphrodites will always mate reciprocally when mating with other hermaphrodites.

### 2.1 Basic Specification

In the basic specification, we abstract from the role of secondary sexual differentiation (i.e. from analyzing $e_m$). This is done for tractability, however, as an immediate upshot, no males can exist in equilibrium. We relax this restriction in Section 2.2.

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 $\tilde{j}$ above which she accepts any male (or male function). This means that investment in male function is wasted for individuals $i < \tilde{j}$. Consequently, a male function is useful for individuals $i > \tilde{j}$ only.\(^6\)

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\(^6\)There are additional restrictions for high quality individuals to be male. These restrictions are addressed later on.
A hermaphrodite can treat mating through its female and male functions separately, as long as RS through male and female functions are separable. This may however not be the case. Since hermaphrodites want to mate their male functions and preserve their female functions, a hermaphrodite may request reciprocal access to eggs.

Especially a hermaphrodite of quality $i < \bar{j}$ will not find a female that is willing to mate with its male function. Therefore, a hermaphrodite of quality $i < \bar{j}$ 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 – or use its female function as a currency for trading its male function. In that case reciprocal mating between hermaphrodites below the threshold quality $\bar{j}$ results. Whether hermaphrodites mate randomly or assortatively depends on the size of the search costs.

If search costs are relatively low, both partners will demand sperm of a certain quality for their eggs. In equilibrium that results in assortative reciprocal mating between hermaphrodites whose quality is below $\bar{j}$. If search costs are relatively high, a hermaphrodite has to seize any mating opportunity that allows to match its female and male part. In that case random reciprocal mating between hermaphrodites below the threshold quality $\bar{j}$ results.

2.1.1 Low search costs

Low search costs mainly impact the mating behavior of hermaphrodites. Hermaphrodites whose quality is below females’ threshold $\bar{j}$ have to mate reciprocally in order to find a mate for their male function. Since search costs are low, the best type (close to $\bar{j}$) is only willing to mate its female function to another hermaphrodite that is close to its own type. Therefore, it follows that these hermaphrodites also mate assortatively.

The same applies to those hermaphrodites that are above females’ threshold $\bar{j}$. They could mate their male function without using their female function as a currency for finding a mate. But they – as everybody else – prefer high quality mates for their female function. So, they use their female function as a currency in finding a high-quality mate. Thus, for high quality hermaphrodites reciprocal and assortative mating is a best response if search costs are low. This argument applies in an obvious way to those individuals whose own quality is above the average (with respect to the quality range above $\bar{j}$). For, if they mate non-reciprocally (and thus non-assortatively) they get the average sperm quality for their eggs, whereas they get their own quality by mating reciprocally.

However, reciprocity is not obvious for individuals below average (with respect to the quality range above $\bar{j}$) quality. 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 will still (try to) use their male function to fertilize other hermaphrodites – in addition to the females they fertilize; but that option exists for any hermaphrodite above
and is not important for the reasoning within the group of hermaphrodites.

Thus, if hermaphrodites below average (with respect to the quality range above $\bar{j}$) quality decide to mate nonreciprocally, they may receive high quality sperm. But, as the top individuals’ female functions are no longer available, the lower-quality hermaphrodites compete with all individuals above $\bar{j}$ for a reduced number of female functions. Accordingly, they have to compare two options: They can – by demanding reciprocity and same quality – content themselves with sperm of their own quality and secure that they can fertilize another hermaphrodite. Or they bear the risk not to find a hermaphroditic partner for their male function and gain the opportunity to receive high quality sperm. At least for those individuals who are below the average but close to it, the gain in sperm quality will not outweigh the loss in fertilized eggs. Thus, they will opt for reciprocal and assortative mating. But then the scarcity of eggs gets even more urgent for those individuals that are closer to $\bar{j}$. Thus, they are forced to mate reciprocally and assortatively if they want to fertilize another hermaphrodite.

**Lemma 1** If search cost are low, hermaphrodites mate reciprocally and positive assortatively.

Based on that intermediate result 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 $b := \mu(1 - a)$ there exists a Nash equilibrium with the following structure: All individuals of quality $i \in [0, \bar{j})$ choose to be female and accept any individual $i > \bar{j}$ as a partner, and all individuals of quality $i \in [\bar{j}, 1]$ choose to be hermaphrodites, where $\bar{j} = \frac{2}{1-4\mu}(1 - \mu - \frac{1}{2}\sqrt{3 - 4\mu + 4\mu^2})$. For $\mu \in [1/2, 1)$, it is unique.

2. In addition, for any $a \in (0, 1)$ and $b := \mu(1 - a)$, $\mu \in [0, 1/2)$, and for any $\bar{j} \geq \frac{1}{3-4\mu}$ there exists a Nash equilibrium with the following structure: Females only accept partners of quality $i \geq \bar{j}$, individuals of quality $i < \bar{j} := \frac{1+\bar{j}}{4(1-\mu)}$ are female, and individuals of quality $i \geq \bar{j}$ are hermaphrodite.

In sum, Proposition 1 says that females at the bottom and hermaphrodites at the top characterize equilibria. The proof also establishes that an all hermaphroditic population is not an equilibrium, since low quality individuals will do better as females. Moreover, note that there are no males.

The lack of pure males is mainly 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 considered more attractive or being faster). Therefore, hermaphrodites always have a higher RS than males of the same
quality. Consequently, without secondary sexual differentiation the population will – in equilibrium – consist of females and reciprocal hermaphrodites (the latter mate reciprocally with each other and, obviously, non-reciprocally with the females).

2.1.2 High search costs

Here, again, equilibrium structure depends on the mating behavior of hermaphrodites and on the quality thresholds chosen by females. If there are hermaphrodites below females’ threshold quality \( \bar{j} \), they have to mate reciprocally in order to find a partner for their male function. As search costs are high, they will accept each hermaphrodite they meet as a partner. Thus, random mating results.

As in the low-search-cost case, hermaphrodites above \( \bar{j} \) do not need their female function as a currency for access to females for their male functions. However, under high search cost it does not pay to search for partners of similar quality. Therefore, high-quality hermaphrodites face two alternatives. They can either mate reciprocally with random partners (within the group of high-quality hermaphrodites) or mate their female and male functions separately. As both choices lead to the same (expected) RS, but non-reciprocal mating carries the risk of leaving the male function without a partner, random reciprocal mating is a (weakly but risk dominant) best response.

Lemma 2 If search cost are high, hermaphrodites mate reciprocally and randomly.

Thus, we can state:

Proposition 2 If there is no secondary sexual differentiation and search costs are high there are two kinds of Nash equilibria.

1. For any \( a \in (0, 1) \) and \( b := \mu(1-a) \) there exists a Nash equilibrium with the following structure: All individuals of quality \( i \in [0, \bar{j}) \) choose to be female and accept any individual \( i > \bar{j} \) as a partner and all individuals of quality \( i \in [\bar{j}, 1] \) choose to be hermaphrodites, where \( \bar{j} = \frac{1}{3\mu}(-1 + \mu + \sqrt{1-2\mu+4\mu^2}) \). For \( \mu \in [1/2, 1) \), it is unique.

2. In addition, for any \( a \in (0, 1) \) and \( b := \mu(1-a) \), \( \mu \in [0, 1/2) \), and for any \( \bar{j} = \frac{1}{3-4\mu} \) there exists a Nash equilibrium with the following structure: Females only accept partners of quality \( i \geq \bar{j} \), individuals of quality \( i < \bar{j} := \frac{1+\mu\bar{j}}{3(1-\mu)} \) are female, and individuals of quality \( i \geq \bar{j} \) are hermaphrodite.

Proposition 2 shows that under high search costs equilibria have the same basic structure as under low search costs: Females are found at the bottom of
the quality scale and hermaphrodites at the top. Independent of the magnitude of search costs there is an additional property. If the fixed cost of a male function is relatively low, there is another equilibrium that shows a segregation within the group of hermaphrodites. Females only mate with the best-quality male functions (whose carriers also sport a female function owing to the lack of SSD). Given that a male function is cheap, it pays for individuals of intermediate quality to form a (hermaphroditic) group on their own and to mate within that group.

This latter case of low fixed costs for a male function is the more interesting one with respect to the role of SSD - which we are going to analyze in the subsequent section. For, in that case there remains a considerable amount of energy that can be spent on SSD or – for hermaphrodites – on egg production.

2.2 Secondary Sexual Differentiation

Males were absent from the equilibria in the Section 2.1. Allowing for secondary sexual differentiation will change that. This 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. Our (extreme) assumption that male sex cells are produced at zero marginal cost mean that good sperm quality is not scarce, and hence a female improves her RS by producing more sex cells. The male on the other hand, improves his RS by investing in features that improves partner access. The rewards from so doing is that he can outcompete hermaphrodites, and possibly other males.

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

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

A hermaphrodite, however, can invest in eggs, and for we will assume that it spends a fraction $\lambda$ of its energy on egg production and the remaining energy on $e_h$:

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

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.

As in the case without secondary sexual differentiation, search cost determine the equilibrium sorting and thus curb of points for the female, hermaphroditic and male, segments. If search cost are low, hermaphrodites mate
assortatively. But if males can outcompete hermaphrodites, the result that in equilibrium there are no males does not hold any more.

**Proposition 3** For $a \in (0,1)$, $b = \mu(1-a) \mu \in (0,1)$, low search costs, $\lambda \in (0,1]$ being the fraction of energy a hermaphrodite spends on egg production, and $x \in [1, \infty)$, where $x$ is the ratio between expected number of females per male and expected number of females per (by females accepted) hermaphrodite, there are the following Nash equilibria in pure strategies:

1. If $x \leq \frac{4 \lambda^2 (1-\mu)^2 - 4 \lambda (1-\mu) + (2 \lambda (1-\mu) - 1) \sqrt{4 \lambda^2 (1-\mu)^2 + 3 - 4 \lambda (1-\mu)}}{2 \lambda (1-\mu) - \sqrt{4 \lambda^2 (1-\mu)^2 + 3 - 4 \lambda (1-\mu)}}$, then an equilibrium as in Proposition 1, part 1, leading to a females/hermaphrodites population results. The threshold quality in this equilibrium is

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

   There are no males in equilibrium.

2. If $\mu \leq 1 - \frac{1}{2 \lambda}$, $\bar{j} > \frac{1}{4 \lambda (1-\mu) - 1}$, $x \leq 1 + \frac{8 \lambda^2 (1-\mu)^2 (1-\bar{j})}{1+\bar{j}}$, an equilibrium as in Proposition 1, part 2: a females/hermaphrodites population. Here, $\bar{j} = \frac{1+\bar{j}}{4 \lambda (1-\mu)}$. There are no males in equilibrium.

3. If $\mu \leq 1 - \frac{1}{2 \lambda}$, $\bar{j} > \max \left\{ \frac{1}{4 \lambda (1-\mu) - 1}, \frac{-1 + 8 \lambda^2 (1-\mu)^2}{1+\bar{j}}, \frac{1+\bar{j}}{1+\bar{j} - 8 \lambda^2 (1-\mu)^2} \right\}$, then there is an equilibrium where females accept males above $\bar{j}$, individuals in $[0, \bar{j})$, $\bar{j} = \frac{1+\bar{j}}{4 \lambda (1-\mu)}$ are females, individuals in $[\bar{j}, \bar{j})$, are hermaphrodites, and individuals in $[\bar{j}, 1]$ are males.

4. If $\mu > 1 - \frac{1}{2 \lambda (\sqrt{\lambda} - 1)}$, then there is for any $x \geq \frac{1}{(1 - 2 \lambda (\sqrt{\lambda} - 1))(1-\mu)}$ an equilibrium with females and males. Here, all individuals in $[0, \bar{j})$ are females and all individuals in $[\bar{j}, 1]$ are males where $\bar{j} = \frac{1}{\sqrt{\lambda}}$. Females accept all males as partners. There are no hermaphrodites in equilibrium.

Proposition 3 describes a possible path towards gonochorism. Either there is fast crowding out of hermaphrodites or the population splits into a population of hermaphrodites and a population of males and females and the two groups do not interbreed. Within the group of hermaphrodites, the process starts anew, with the extremes turning gonochoric (females at the bottom and males at the top). Using definition 1 we would say that females and males form a new (gonochoric) species.

Proposition 3 highlights the role of SSD for males, and the unlikely co-existence of males and hermaphrodites in equilibrium. This suggests that for 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 that the scope for SSD is low.
If search cost are high, hermaphrodites mate randomly. Again, males can enter the population if they can outcompete hermaphrodites by the use of SSD. The results under high search costs are similar to those under low search costs.

3 Discussion

The paper shows that heterogeneous hermaphroditic species show a tendency towards gonochorism. This process has three main sources. (1) Low quality individuals prefer to be female as an investment into the scarce resource in reproduction (eggs) secures RS. In contrast, investment into sperm bears the risk of being wasted as there might be no other individual that accepts low quality sperm. If there are fixed costs for either sex, low quality individuals will give up their male function. (2) Females prefer high quality individuals as mating partners. Thus, bottom- and top-end individuals interbreed, whereas intermediate individuals need to form a mating group on their own. (3) If there is sufficient scope for secondary sexual differentiation, it pays for the top individuals to turn male. In that case two new species form: a gonochoric species consisting of (low-quality) females and (high-quality) males and a species of (intermediate-quality) hermaphrodites. The remaining hermaphrodites are thus less heterogeneous, but within this group the selection process starts anew.

The analysis shows that secondary sexual differentiation is not an additional means that has been developed by males to gain an advantage in male-to-male competition. The existence of SSD is necessary for males to exist. This is in line with Darwin’s comment cited above.

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. This follows because the death of a pure male does not affect the number of eggs produced by pure females, while the death of a hermaphrodite implies a reduction in the number of eggs produced by hermaphrodites.

There is scope for male violence among hermaphrodites and it does occur (for an account from marine flatworms, see Michiels and Newman (1998)). But in contrast to some male-to-male violence in gonochoric species these assaults are not lethal as they aim at fertilizing the other individual’s eggs while preventing own eggs from being fertilized. Killing the other individual would thus not advance own RS.

Phylogenically, hermaphroditism has given way to gonochorism, and irreversibility of the latter may be on reason. Charnov (1982):241 wrote “At
least one constraint hypothesis suggests itself. It may be easier to change from hermaphrodite to 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.” If so, and if initially homogeneous populations become more diverse (e.g., offspring quality is father quality plus noise), this would suggest that the hermaphroditic population (initially distributed on $I_h = (j_1, j_2)$) eventually experiences a similar “defection” to gonochorism as described in Proposition 2.1.

Sexual selection among hermaphrodites will be weaker because of reciprocal mating. As Charnov pointed out, with sperm competition, reciprocal mating does not preclude effective polygyny. However, as the example of spermatophores among marine slugs suggest, attempts to “cheat” are countered Haase and Karlsson (2004).

Assuming that individual females (female functions) bear 50 % sons and 50 % daughters, the gonochoric population will have an initial boost in quality from males being of higher quality than hermaphrodites. In subsequent generations, assuming sufficient weight on paternal quality (at least as high as mother’s) in offspring quality, sexual selection will be stronger in gonochoric species.

References


Haase, Martin and Anna Karlsson, “Mate Choice in a Hermaphrodite: You Won’t Score with a Spermatophore,” Animal Behaviour, 67

7Obviously, this result hinges crucially on the weight given paternal quality in offspring quality.


**Appendix**

**Proof of Proposition 1:**

**Part 1:** We assume that individuals of quality \( i < j \) choose to be female (which has to be reconfirmed later on) and to accept males of quality \( i > j \). Then there are \( j \) females and \( 1 - j \) males and hermaphrodites. Accordingly, the RS of a hermaphrodite of quality \( i \) is given by

\[
2(1-a-b)i
\]

from reciprocal mating and

\[
(1-a)i\frac{j}{1-j}
\]

from its male function. The RS of a female is

\[
(1-a)\frac{1+j}{2}.
\]

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

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

\[
\Leftrightarrow j = \frac{2}{1-4\mu}(1-\mu - \frac{1}{2}\sqrt{3-4\mu + 4\mu^2})
\]

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.

**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 females choose a threshold quality \( \bar{j} \). If – differing from part 2 of the proof – there are hermaphrodites below \( \bar{j} \) their RS only comes from reciprocal matings and is given by

\[
2(1-a-b)i.
\]
Female RS is now given by

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

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

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

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

$$(1 - a) \frac{1 + \bar{j}}{2} = 2(1 - a - b)\bar{j} \iff \bar{j} = \frac{1 + \bar{j}}{4(1 - \mu)}. \tag{1}$$

To provide a basis for an equilibrium, $\bar{j}$ and $\bar{j}$ have to meet two conditions:

1. $\bar{j} \leq \bar{j}$ which implies that
   $$\frac{1}{3 - 4\mu} \leq \bar{j}, \quad \text{and} \quad \mu < \frac{3}{4}$$

   the condition on $\bar{j}$ given in the proposition.

2. $\bar{j} \leq 1$ which – following from the first condition – implies $\frac{1}{3 - 4\mu} \leq 1$.

   This condition holds if $\mu \leq 1/2$.

   q.e.d.

**Proof of Proposition 2:**

Analogous to the proof of Proposition 1.

**Proof of Proposition 3:**

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

$$i(1 - a)d_m$$

and the RS of a hermaphrodite of quality $i$ under assortative mating is given by

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

Comparing these expressions we obtain

$$i(1 - a)d_m \geq 2\lambda(1 - \mu)(1 - a)i + i(1 - a)d_h \iff d_m \geq 2\lambda(1 - \mu) + d_h. \tag{2}$$

That is, the difference in male and hermaphrodite 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 herma-
phroditic invasion.

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

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

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

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

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

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

\[
\hat{j} = \frac{1 + \hat{j}}{4\lambda(1-\mu)}.
\]

For males to be able to invade, they need to do better than the hermaphro-
dites who mate with females. The expected number of matings with females
for a hermaphrodite is \( d_h = \frac{\hat{j}}{h^*} \) where \( h^* \) varies according to the equilibrium.

A male that invades the population mates with \( d_m = xd_h \) females. Therefore,
from (2) we know that a male can invade the population if

\[
x \frac{\hat{j}}{h^*} > 2\lambda(1-\mu) + \frac{\hat{j}}{h^*}, \tag{3}
\]

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

\[
x \frac{j}{1-j} > 2\lambda(1-\mu) + \frac{j}{1-j}, \tag{4}
\]

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

\[
x \frac{\bar{j}}{1-\bar{j}} > 2\lambda(1-\mu) + \frac{\bar{j}}{1-\bar{j}}, \tag{5}
\]

where \( \hat{j}, \bar{j} \) 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 3.
We now turn to proving the specific parts of the proposition.

**Part 1.**
Here (4) is the relevant inequality with
\[ j = \frac{2}{4 \lambda (1 - \mu) - 3} (\lambda (1 - \mu) - \frac{1}{2} \sqrt{4 \lambda^2 (1 - \mu)^2 + 3 - 4 \lambda (1 - \mu)}). \]

Therefore a female/hermaphroditic population is stable (i.e., males cannot invade) if
\[ x \leq \frac{2(1 - \mu) + \frac{j}{1 - j}}{1 - \frac{j}{1 - j}} \]
\[ \equiv x \leq 1 + (1 - \mu) \frac{1 - \frac{j}{1 - j}}{\frac{j}{1 - j}} \]
\[ \equiv x \leq \frac{4 \lambda^2 (1 - \mu)^2 - 4 \lambda (1 - \mu) + (2 \lambda (1 - \mu) - 1) \sqrt{4 \lambda^2 (1 - \mu)^2 + 3 - 4 \lambda (1 - \mu)}}{2 \lambda (1 - \mu) - \sqrt{4 \lambda^2 (1 - \mu)^2 + 3 - 4 \lambda (1 - \mu)}} \]

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
\[ j = \frac{1 + \bar{j}}{4 \lambda (1 - \mu)}, \]

the proposed three-layer population only exists if \( \mu \leq 1 - \frac{1}{4 \lambda}, (\lambda > \frac{3}{2}) \) and \( \bar{j} \geq \frac{1}{4 \lambda (1 - \mu)}. \) The condition for a purely female/hermaphroditic population to be stable is
\[ x \leq \frac{2(1 - \mu) + \frac{j}{1 - j}}{1 - \frac{j}{1 - j}} \]
\[ \equiv x \leq 1 + (1 - \mu) \frac{1 - \frac{j}{1 - j}}{\frac{j}{1 - j}} \]
\[ \equiv x \leq \frac{8 \lambda^2 (1 - \mu)^2 (1 - \bar{j})}{1 + \bar{j}} \]

which proves the claim.

**Part 3.**

The three-layer equilibrium with females and hermaphrodites can be invaded if (5) holds which implies that
\[ x > 1 + \frac{8 \lambda^2 (1 - \mu)^2 (1 - \bar{j})}{1 + \bar{j}}. \]

In that case males had an incentive to replace those hermaphrodites whose quality is above \( \bar{j} \); 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 \( \bar{j} \) and is independent of the provider’s sex choice.

Thus, if \( x > 1 + \frac{8 \lambda^2 (1 - \mu)^2 (1 - \bar{j})}{1 + \bar{j}} \) there can be an equilibrium with females below \( \bar{j} \), purely reciprocal hermaphrodites in \([\bar{j}, \tilde{j})\), and males above \( \tilde{j} \). 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 \( \bar{j} \) 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

\[
d_m < 2\lambda(1 - \mu) + d_h
\]

\[
\Leftrightarrow \quad \frac{f}{m} < 2\lambda(1 - \mu) + \frac{1}{x} \frac{f}{m}
\]

\[
\Leftrightarrow \quad (1 - \frac{1}{x}) \frac{j}{1 - \bar{j}} > 2\lambda(1 - \mu)
\]

If we substitute \( \bar{j} \) we get

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

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

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

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

\[
n \geq \frac{2\lambda(1 - \mu)}{(1 - a)\frac{1 + j}{2}}
\]

\[
\Leftrightarrow \quad \frac{j}{1 - \bar{j}} \geq \frac{2\lambda(1 - \mu)}{x \frac{j}{1 - \bar{j}}}
\]

where \( \bar{j} \) needs to be determined. Female RS is given by

\[
(1 - a)\frac{1 + j}{2}
\]

and RS of an individual of quality \( i \) is given by

\[
(1 - a)i\frac{j}{1 - \bar{j}}
\]

Therefore the threshold quality \( \bar{j} \) can be determined by the indifference condition

\[
(1 - a)\frac{1 + j}{2} = (1 - a)\frac{j}{1 - \bar{j}}
\]

\[
\Leftrightarrow \quad \bar{j} = \frac{1}{\sqrt{3}}
\]
If we substitute $j$ 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.