

# Hermaphroditism: What's not to like? ☆

Lena Edlund<sup>a,\*</sup>, Evelyn Korn<sup>b</sup>

<sup>a</sup>*Department of Economics, Columbia University, USA*

<sup>b</sup>*Department of Economics, Philipps-Universität Marburg, Germany*

Received 22 June 2006; received in revised form 27 September 2006; accepted 31 October 2006

Available online 9 November 2006

## Abstract

Hermaphroditism is rare and phylogenically in decline among animal species. The evolutionary basis for this development is not well understood. This paper focusses on self-incompatible simultaneous hermaphroditism 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 (RS) is limited by partner availability, while female RS is not. We show that: low-quality individuals do better if female; secondary sexual differentiation may be important for understanding the existence of males; and that hermaphroditic mating is reciprocal. Reciprocity may be key to understanding promiscuity and attendant phenomena such as cryptic female choice, sperm competition and love darts—common features of hermaphroditic mating. We also argue that hermaphrodites are especially vulnerable to male violence, suggesting a reason for the rarity of trioecy. Finally, we propose that external fertilization, and the scope for streaking, may be one reason fish are the only simultaneously hermaphroditic vertebrates.

© 2006 Elsevier Ltd. All rights reserved.

*Keywords:* Sex allocation; Hermaphroditism; Evolution; Reciprocal mating

## 1. Introduction

Hermaphroditism is rare and phylogenically in decline among animal species. The evolutionary basis for this development is not well understood. While the lower search cost allowed by (simultaneous) hermaphroditism arguably is of greater importance for plants than animals (Ghiselin, 1969), hermaphroditism is not void of advantages for the latter. As Maynard Smith (1978) pointed out, the cost of sexual reproduction is the cost of males. If the male reproductive function did not require its own organism, substantial savings could be achieved (Charnov, 1979).<sup>1</sup> Why then is hermaphroditism not more common?

<sup>☆</sup>The authors thank Douglas Almond, Erwin Amann, and Christopher W. Petersen.

\*Corresponding author. Tel.: +1 212 854 4513; fax: +1 212 854 8059.

*E-mail addresses:* [le93@columbia.edu](mailto:le93@columbia.edu) (L. Edlund), [korn@wiwi.uni-marburg.de](mailto:korn@wiwi.uni-marburg.de) (E. Korn).

<sup>1</sup>A hermaphrodite incurs the costs of building two sex functions. While the fixed costs of sex functions are not well known, at least the male

One reason for an interest in mating system evolution is that our notion of gender is largely predicated on male and female reproductive functions being separated in different individuals, an observation which begs the question why such a separation has occurred.

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. In particular, we argue that low quality individuals can do better as pure females.

The argument turns on the Bateman principle, namely that male reproductive success (RS) is limited by partner availability, while female RS is not. Thus, it is closely related to Charnov (1979) who stressed the role of low mobility or population density in facilitating hermaphroditism. This

*(footnote continued)*

reproductive system is potentially cheap, consisting chiefly of a duct to transport sex cells.

paper explores an alternative route by focussing on the role of heterogeneity. Moreover, we show that reciprocal mating arises endogenously among simultaneous self-incompatible hermaphrodites.

We seek to complement the existing literature on the limitations of hermaphroditism. Charnov (1979) pointed to limits on male RS for understanding stability of hermaphroditism. More recent research has noted that hermaphroditism limits the returns to secondary sexual differentiation (SSD), e.g. Greeff and Michiels (1999a). 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 builds on Charnov et al. (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–Willard hypothesis (1973).

## 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 RS. RS depends on the number and quality of offspring. For tractability and in line with the Bateman principle, we assume that females differ with respect to the number of eggs they produce whereas males differ with respect to sperm quality.<sup>2</sup> Thus, if a male (male function) of quality  $i_m$  mates with a female (female function) who offers  $g(i_f)$  eggs, both parents will receive an RS of  $i_m \cdot g(i_f)$  from that mating.

Following Charnov (1979), we assume that each individual is endowed with a fixed amount of resources, 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 resource consuming. In particular, we assume that a female can produce  $g(i_f) = e_f \cdot i_f$  eggs, where  $e_f \leq 1 - a$  and  $i_f$  is the female's quality.<sup>3</sup> Male RS is constrained by partner availability. Let  $e_m$  be the amount of resources devoted by a male to enhance eligibility (e.g. improve attractiveness, partner search, competitiveness). Thus, for a

male, the budget constraint is  $e_m \leq 1 - b$ . Finally, we denote by  $e_{hf}$  the amount of resources a hermaphrodite devotes to egg production and  $e_{hm}$  the amount of resources devoted to improving RS through the male function and the budget constraint is that  $e_{hf} + e_{hm} \leq 1 - a - b$ .

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.<sup>4</sup> Since the marginal cost of sperm is zero, a male (male function) is willing to mate with any female (female function). In contrast, we would expect an individual to 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.** We say that a mating between two hermaphrodites  $A$  and  $B$  is reciprocal if hermaphrodite  $A$  mates its male as well as its female function with hermaphrodite  $B$ , and vice versa.

While two hermaphrodites who have mated reciprocally have exhausted their female functions, they can still use their male functions 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:  $i \in [0, j_0)$  are females,  $i \in [j_0, j_1)$  are hermaphrodites who mate exclusively with other hermaphrodites,  $i \in [j_1, j_2)$  are males, and  $i \in [j_2, 1]$  are hermaphrodites who mate with hermaphrodites and females, where  $0 \leq j_0 \leq j_1 \leq j_2 \leq 1$ . Depending on the parameter values (capturing search costs, resource constraints, SSD) some of the subintervals may be degenerate, resulting in a, for instance, purely gonochoric population. 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 SSD. Lastly, hermaphroditic mating will be reciprocal.

### 2.1. Base specification

Here, we abstract from the role of SSD (i.e. from analysing  $e_m$  and  $e_{hm}$ ). This simplification will preclude pure males in equilibrium. We relax this assumption in Section 2.2.

To preview results, equilibria have the following structure:  $i \in [0, j_0)$  are pure females, and  $i \in [j_0, 1]$  are hermaphrodites. All hermaphroditic mating is reciprocal. Hermaphrodites of quality  $i \in [j_1, 1], j_1 (= j_2) \geq j_0$ , will mate

<sup>2</sup>Qualitatively similar, and computationally simpler, results are obtained if only male quality matters for fitness. For realism, we present a formulation in which female quality also matters.

<sup>3</sup>Size may be a dimension of quality.

<sup>4</sup>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.

with pure females as well. Whether  $j_1 = j_0$  or  $j_1 > j_0$  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  $j_1$  above which she accepts any male (or male function). Clearly, individuals  $i < j_1$  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 will be reciprocal in equilibrium.

To see this, consider a hermaphrodite of quality  $i < j_1$ . 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  $i < j_1$  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 focus on.<sup>5</sup>

Hermaphrodites whose quality is below females’ threshold  $j_1$  have to mate reciprocally in order to find a mate for their male function. Since search costs are low, the best type (close to  $j_1$ ) is only willing to mate its female function to another hermaphrodite that is close to its own type. Therefore, it follows that these hermaphrodites mate assortatively.

Hermaphroditic (hermaphrodite-to-hermaphrodite) mating above  $j_1$  will also be assortative. It is straightforward to see that this argument applies if  $i > (j_1 + 1)/2$  (if they were to mate non-assortatively they would receive the average sperm quality  $(j_1 + 1)/2$  as opposed to quality  $i$  if mating were assortative).

Reciprocity is slightly less obvious for individuals  $i \in (j_1, (j_1 + 1)/2)$ . 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 may not access eggs from another hermaphrodite (i.e. they would only access eggs from pure females). For individuals just below  $(j_1 + 1)/2$ , the gain in RS through female function (improved sperm quality) will not outweigh the loss in RS from male function

(fewer fertilized eggs). In other words, reciprocal and assortative mating is optimal for individuals below but close to  $(j_1 + 1)/2$ . From that it follows that it will also be optimal for all hermaphrodites of lower quality. We provide a formal proof in the supplementary material.

We now state our first results:

**Lemma 1.** *Hermaphrodites mate reciprocally.*

Reciprocal mating is a prediction largely borne out by empirical studies of hermaphroditic mating, as are its corollaries: (female) promiscuity, sperm competition and cryptic female choice, further discussed in the concluding Section 3.

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

Some empirical evidence supports these results. When quality differences are measurable by humans, mating seems assortative. For instance, if egg production is linked to size, as in earthworms (Michiels et al., 2001) and tapeworms (Lüscher and Wedekind, 2002), behavior consistent with size assortative mating has been observed.

Based on the above 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 SSD 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 exists a Nash equilibrium with the following structure:*

$$0 < j_0 = j_1 = j_2 < 1,$$

where  $j_0 = (1/(1 - 2\mu))(1 - \mu - \frac{1}{2}\sqrt{2 - 4\mu + 4\mu^2})$ . For  $\mu \in [\frac{1}{2}, 1]$ , it is unique.

*In words, all individuals of quality  $i \in [0, j_0)$  are female and accept any individual  $i > j_0$  as a partner, and all individuals of quality  $i \in [j_0, 1]$  are hermaphrodites. Females accept all hermaphrodites as partners.*

2. *In addition, for any  $a \in (0, 1)$  and  $b := \mu(1 - a)$ ,  $\mu \in [0, \frac{1}{2})$ , and for any  $j_1 \geq 1/(3 - 4\mu)$  there exists a Nash equilibrium with the following structure:*

$$0 < j_0 < j_1 = j_2 < 1,$$

where  $j_0 := (1 + j_1)/4(1 - \mu)$ . *In words, females only accept partners of quality  $i \geq j_1$ , individuals of quality  $i < j_0$  are female and individuals of quality  $i \geq j_0$  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 supplementary material. Fig. 1 depicts the equilibrium structure.

The lack of pure males is driven by the absence of SSD which means that a pure male cannot access more females

<sup>5</sup>If search costs are high, any mating opportunity that allows RS through both male and female functions is attractive and random reciprocal mating results. The equilibria in this case are qualitatively similar to the low search cost case.

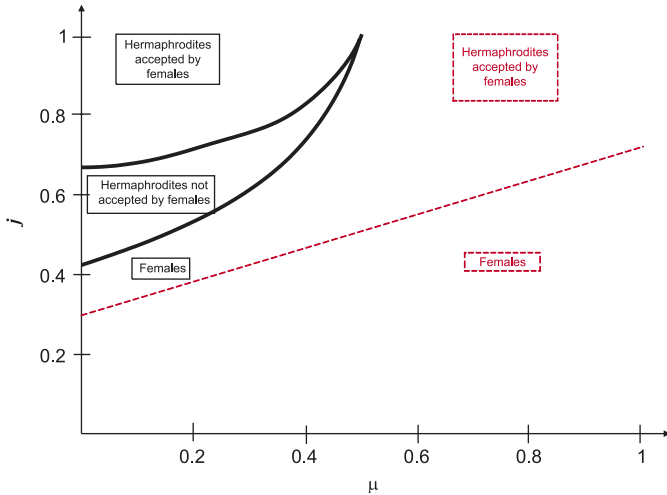


Fig. 1. Distribution of types without secondary sexual differentiation. Notes: The dashed part of the figure depicts the distribution of types within the population from part 1 of Proposition 1. The dashed line is given by  $j_0 = (1/(1 - 2\mu)) \left(1 - \mu - \frac{1}{2}\sqrt{2 - 4\mu + 4\mu^2}\right)$ . Individuals whose quality is below  $j_0$  choose to be female, individuals above  $j_0$  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  $j_1$ . The graph is based on  $j_1 = (1 + 1/(3 - 4\mu))/2$ , i.e. a value in the middle of the admissible range. Here, all individuals above  $j_0 = (1 + j_1)/4(1 - \mu)$  choose to be hermaphrodites but females accept only those above  $j_1$ .

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 SSD the equilibrium population consists of females and reciprocal hermaphrodites. The latter group mates reciprocally with each other and, obviously, non-reciprocally with females.

### 2.2. Secondary sexual differentiation

SSD will allow for males in equilibrium.<sup>6</sup> The assumption that male sex cells are produced at zero marginal cost implies that high-quality sperm is not scarce, and thus female RS depends on the quantity of eggs produced. Male RS, on the other hand, increases with greater partner access, and partner access may be improved by investments in SSD.

Since a male has no alternative use for the endowment 1, we know that male investment in SSD,  $e_m$ , is

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

<sup>6</sup>Darwin defined SSD as traits that helped in the competition for mates, but are otherwise a burden, like the peacock's tail. He observed that SSD 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. SSD being greater among males is consistent with the greater variable cost of female sex cells.

A hermaphrodite can invest in eggs, and we will assume that it spends a fraction  $\lambda$  of its endowment on eggs and the remaining resources on SSD:

$$e_{hf} = \lambda(1 - a - b)$$

and

$$e_{hm} = (1 - \lambda)(1 - a - b).$$

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

As noted above, while females could gain RS by diverting resources towards SSD, they do not have an incentive to do so in our setup. 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).<sup>7</sup>

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

#### 1. Females and hermaphrodites:

(a) For any  $\mu$  and

$$x \leq 1 + 4\lambda(1 - \mu) \frac{\lambda(1 - \mu) - 1 + \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1}}{\lambda(1 - \mu) - \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1}},$$

there is an equilibrium with the following properties (cf. Proposition 1, part 1):

$$0 < j_0 = j_1 = j_2 < 1,$$

where  $j_0 = (1/(2\lambda(1 - \mu) - 1))(\lambda(1 - \mu) - \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1})$ .

In words, all individuals in  $[0, j_0)$  are females and all individuals in  $[j_0, 1]$  are hermaphrodites. Females accept all hermaphrodites as partners.

(b) For  $\mu \leq 1 - 1/2\lambda$ ,  $j_1 > 1/(4\lambda(1 - \mu) - 1)$  and

$$x \leq 1 + \frac{(4\lambda(1 - \mu))^3(1 - j_1)j_1}{(1 + j_1)^2},$$

there is an equilibrium with the following properties (cf. Proposition 1, part 2):

$$0 < j_0 < j_1 = j_2 < 1,$$

<sup>7</sup>Again, if search costs were high, hermaphrodites would mate randomly. This does not affect the qualitative characterization of the equilibria, only the values of the cut-off points.

where

$$j_0 = \frac{1 + j_1}{4\lambda(1 - \mu)}$$

In words, all individuals in  $[0, j_0)$  are females and all individuals in  $[j_0, 1]$  are hermaphrodites. Females accept hermaphrodites above  $j_1$ .

2. Females, males, and hermaphrodites who mate with females:

(a) For any  $\mu$  and

$$1 + 4\lambda(1 - \mu) \frac{\lambda(1 - \mu) - 1 + \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1}}{\lambda(1 - \mu) - \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1}} < x$$

$$< 1 + 4\lambda(1 - \mu) \frac{(2\lambda(1 - \mu) - 1) \left( \lambda(1 - \mu) - 1 + \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1} \right)}{\left( \lambda(1 - \mu) - \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1} \right)^2},$$

there is an equilibrium with the following properties:

$$0 < j_0 = j_1 < j_2 < 1,$$

where

$$j_0 = \frac{1}{2\lambda(1 - \mu) - 1} \left( \lambda(1 - \mu) - \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1} \right)$$

and

$$j_2 = \frac{xj_0 - 1 + \sqrt{(xj_0 - 1)^2 + j_0^2(x - 1)^2/\lambda(1 - \mu)}}{2(x - 1)}$$

In words, all individuals in  $[0, j_0)$  are females, all individuals in  $[j_0, j_2)$  are males and individuals in  $[j_2, 1]$  are hermaphrodites. Females accept all males and hermaphrodites as partners.

(b) For  $\mu \leq 1 - 1/2\lambda$ ,  $j_1 > 1/(4\lambda(1 - \mu) - 1)$  and

$$1 + \frac{(4\lambda(1 - \mu))^3(1 - j_1)j_1}{(1 + j_1)^2} < x < 1 + \frac{(4\lambda(1 - \mu))^3(1 - j_1)}{(1 + j_1)^2},$$

there is an equilibrium with the following properties:

$$0 < j_0 < j_1 < j_2 < 1,$$

where  $j_0 = (1 + j_1)/4\lambda(1 - \mu)$  and  $j_2 = (xj_1 - 1 + \sqrt{(xj_1 - 1)^2 + (j_0^2(x - 1)^2/\lambda(1 - \mu))})/2(x - 1)$ .

In words, females accept males (male functions) above  $j_1$ , individuals in  $[0, j_0)$  are females, individuals in  $[j_0, j_1)$  are hermaphrodites, individuals in  $[j_1, j_2)$  are males and individuals in  $[j_2, 1]$  are hermaphrodites who mate among themselves and with females.

3. Females, males, and hermaphrodites who mate among themselves only:

For  $\mu \leq 1 - 1/2\lambda$ ,  $j_1 > \max\{1/(4\lambda(1 - \mu) - 1), -1 - \frac{1}{2}(4\lambda(1 - \mu))^3 + \frac{1}{2}\sqrt{8(4\lambda(1 - \mu))^3 + (4\lambda(1 - \mu))^6}\}$ ,  $j_0 = (1 + j_1)/4\lambda(1 - \mu)$  and

$$x > \frac{(1 + j_1)^2}{(1 + j_1)^2 - (1 - j_1)(4\lambda(1 - \mu))^3},$$

there is an equilibrium with the following properties:

$$0 < j_0 < j_1 < j_2 = 1.$$

In words, females accept males above  $j_1$ , individuals in  $[0, j_0)$  are females, individuals in  $[j_0, j_1)$  are hermaphrodites and individuals in  $[j_1, 1]$  are males.

4. Females and males:

If  $\mu \geq 1 - 1/(2 - \sqrt{2})4\lambda$ , then there is for any

$$x \geq 1 + 4\lambda(1 - \mu) \frac{(2\lambda(1 - \mu) - 1) \left( \lambda(1 - \mu) - 1 + \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1} \right)}{\left( \lambda(1 - \mu) - \frac{1}{2}\sqrt{(2\lambda(1 - \mu) - 1)^2 + 1} \right)^2}$$

an equilibrium with females and males only:

$$0 < j_0 = j_1 < j_2 = 1,$$

where  $j_0 = \frac{1}{\sqrt{2}}$ . In words, all individuals in  $[0, j_0)$  are females and all individuals in  $[j_0, 1]$  are males. Females accept all males as partners.

The parts in Proposition 2 are organized in ascending order with respect to  $x$  (the scope for SSD) (Fig. 2). In part 1, SSD is so low as to not make a difference, and equilibria are as in the case without SSD. In parts 2 and 3,  $x$  is high enough to allow for males. Since hermaphrodites mate reciprocally, males need access to females, and as  $x$  increases, hermaphrodites become more marginalized. In the case described in part 3, they no longer mate with females (only among themselves). For sufficiently high  $x$ , described in part 4, hermaphrodites are eliminated.<sup>8</sup> Proposition 2 suggests that for (simultaneous, self-incompatible) hermaphroditism to exist in “the long run”, a species must either lack functional heterogeneity (for

<sup>8</sup>The attentive reader may have noted that the population sex ratio in this case is female biased. Unbalanced sex ratios is a common prediction for models where the average RS differs from the marginal RS (as in Trivers and Willard, 1973, see e.g. Charnov et al., 1981).

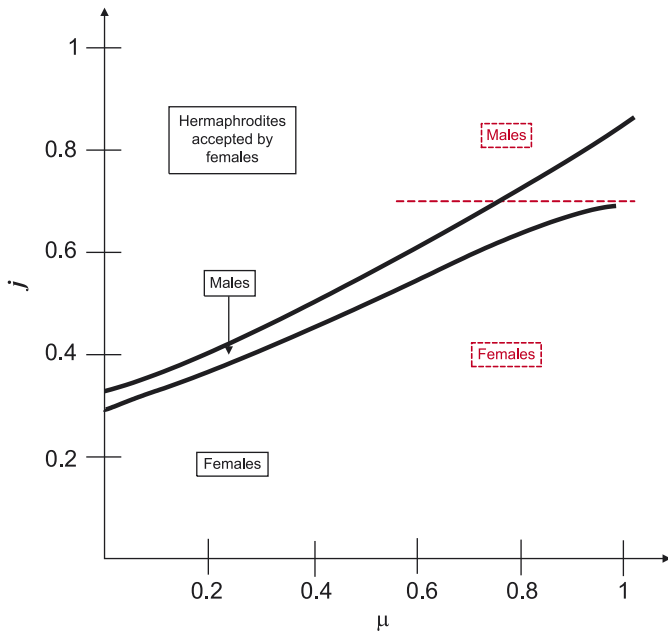


Fig. 2. Distribution of types with secondary sexual differentiation. *Notes:* The figure is based on the assumption that only males invest in secondary sexual differentiation, i.e.  $\lambda = 1$ . The dashed part of the figure depicts the distribution of types within the population from part 4 of Proposition 2. The dashed line is given by  $j_0 = \frac{1}{\sqrt{2}}$ . Individuals whose quality is below  $j_0$  choose to be female, individuals above  $j_0$  choose to be males. This equilibrium only exists for  $\mu \in [.573, 1]$ . The solid part of the figure depicts the distribution of types within the population from part 2(a) of Proposition 2. The exact distribution depends on  $x$ . The graph assumes that  $x$  is in the middle of the admissible range. Here, individuals between  $j_0 = (1/(1-2\mu))\left(1 - \mu - \frac{1}{2}\sqrt{(1-2\mu)^2 + 1}\right)$  and  $j_2 = \left(xj_0 - 1 + \sqrt{(xj_0 - 1)^2 + j_0^2(x-1)^2/(1-\mu)}\right)/2(x-1)$  choose to be males. All individuals above  $j_2$  choose to be hermaphrodites. Females accept all hermaphrodites and males.

instance, from living in a habitat that is rich enough) or the scope for SSD is low (e.g. from low mobility).

Also, note that there are no equilibria with only males and hermaphrodites. Androdioecy (hermaphrodites and males) has been documented among freshwater shrimp (Weeks et al., 2006), and seabasses but is otherwise rare. In the case of the former, androdioecy might be linked to self-compatibility, where pure males protect against inbreeding depression. Seabasses are further discussed below.

### 3. Summary and discussion

Hermaphroditism is rare among animals, and mainly confined to invertebrates. The paper has argued that (simultaneous, self-incompatible) hermaphroditism is not stable in the face of population heterogeneity. The proposed reason is that if female fecundity is more constrained than male fecundity, for instance, from female sex cells being costlier than male sex cells, then low-quality individuals do better as pure females. Obviously, this does

not rule out hermaphroditism. However, if there is sufficient scope for SSD, high-quality individuals can do better as pure males. By this logic, a hermaphroditic species may turn gonochoric—unless there is little heterogeneity or scope for SSD. SSD is low among hermaphrodites, already noted by Darwin. Low SSD is commonly considered an outcome of hermaphroditism, e.g. (Greeff and Michiels, 1999a). This paper has argued that it is not only an outcome of, but also a condition for, hermaphroditism. SSD also offers a suggestion to why the process from hermaphroditism to gonochorism might be irreversible, thus adding to Charnov's (1982) observation that the disposal of a function may be more easily achieved than its adoption: SSD may raise the fixed costs associated with each gender role.

Male violence is an 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 a hermaphroditic than to a gonochoric population even at similar fatality rates. 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.

Other than predicting the rarity of hermaphroditism, for which there is ample prima facie evidence, our model predicts hermaphroditic mating to be reciprocal. Reciprocity has been widely observed, and it has an interesting corollary: promiscuity. While it takes two to tango, the promiscuity of the female function provides the starkest contrast to gonochores and reciprocity sheds light on it and correlates such phenomena as cryptic female choice and male counter strategies such as love darts and sperm competition, further discussed below.

#### 3.1. Reciprocal mating

Reciprocity, in our model and empirically, is an equilibrium outcome, not a physiological necessity, see e.g. Michiels and Streng (1998).

The reciprocity often takes the form of two matings with the same partner, one in, say, the female role, closely followed by one in the male role. However, repeated, alternating, inseminations have been observed, and have been called sperm trading (Leonard and Lukowiak, 1984). If sperm are abundant and eggs scarce, why trade sperm? The answer may lie in the observation that while internal fertilization means that it is sperm that are transported, the trade is actually in its dual: the acceptance of sperm, as Michiels and Streng (1998) showed for the flatworm, *Dugesia polychroa*.

Egg trading—the conditional release of eggs—is common among seabasses, first documented by Fischer (1980), for a survey see Petersen (2006). Fertilization is also external among polychaetes, for whom a similar system has been observed, e.g. Sella (1985), Sella et al. (1997) and Sella and Lorenzi (2000). Small clutches of eggs are released sequentially, following the partners reciprocation in kind, presumably to control the level and ratio of matings in the male and female roles, respectively.

*(Female) promiscuity:* An obvious consequence of reciprocity is that the female and the male functions would be equally promiscuous. The same force that makes the male (latently) promiscuous among gonochores may drive promiscuity among hermaphrodites. In a hermaphrodite, the male function can gain from promiscuity. To obtain a partner for it, access to own female function may be used as currency. The female function can thus by being promiscuous (or rather, as promiscuous as the male function) aid the organism's RS through the male function.

As a direct consequence, we would also expect hermaphrodites to be more promiscuous than gonochores, because no side is limiting.<sup>9</sup>

As with gonochores, female RS may not be maximized through promiscuity, and the tension between the interest of the male and the female routes to offspring may have been an important reason for the development of cryptic female choice among hermaphrodites with internal fertilization. Examples of male counter strategies may include the employment of love darts, e.g. Haase and Karlsson (2004), and sperm competition, e.g. Greeff and Michiels (1999b).

*High investment in sperm:* Our model assumed that mating in the male function has zero marginal cost. However, investment in sperm can be substantial among hermaphrodites, as indeed would follow from reciprocity and the ensuing promiscuity. Our assumption was done for simplicity rather than realism. Our model turns on asymmetrical parental investment, and could in principle allow for male investment to exceed female as such (males and females would swap places in the described equilibria). The perhaps more interesting thought experiment is that of symmetric parental investments. If investments were to equalize, this would undermine sex asymmetries in mating, and thus imply monogamy. Monogamy, in terms of our model, stabilizes hermaphroditism.

*Exceptions to reciprocity:* Fish present an interesting exception to the rule of reciprocity. Among seabasses (Petersen, 2006) and the goby (St. Mary, 1994) gender roles are assigned based on size, where large fish mate more often in the male role and obtain higher RS through their male function. If size indicates quality, perhaps because bigger is older, and old age can be a signal of quality (survived), this would fit the basic premise of our model (and Trivers and Willard, 1973). Then, this begs the question how hermaph-

roditism can be stable? Why do large fish maintain their female function, and why do small fish not shed their male function? Part of the answer is that some do. Among two of the seven species of seabasses for which data exist, large fish guard harems and are behaviorally and gonadally pure males. Among the remaining species, hermaphroditism is maintained despite size biasing RS in favor of one gender (the male in four out of five cases) (Petersen, 2006).

Egg trading has been proposed as a reason for large fish to maintain egg production (Petersen, 1995). However, egg trading has been shown to be asymmetrical and larger fish get away with trading fewer eggs, casting doubt on this hypothesis (Petersen, 2006).

We propose that external fertilization and the possibility of streaking may be key to understanding hermaphroditism in the face of heterogeneity and gendered roles in mating, where the smaller fish mates in the female role and the bigger fish in the male role, e.g. St. Mary (1994) and Oliver (1997).

If bigger fish are of higher quality (for instance, observed to be socially dominant), then they can mate polygynously in the male role. Analogously, lower quality—smaller—fish would mate in the female role. But smaller fish may also be quicker (or more difficult to detect). This would give smaller fish an advantage as streakers, which could be a reason to maintain a male function despite only mating in the female function when in a couple.<sup>10</sup> Streaking may also explain why large fish maintain a female role. Conceivably, a large fish could be even larger if it gave up its female function. However, the gain in terms of male RS might be limited by the presence of streakers, since larger fish may also be even more vulnerable to streaking. Thus, streaking may be important for understanding hermaphroditism in the face of unilateral matings and size-dependent gender roles. Moreover, since streaking is conditional on external fertilization, this form of male cheating may be one reason for why fish are the only vertebrates with SH, a novel observation to the best of our knowledge.

We end with a puzzle. Unilateral mating has been observed for the freshwater snail (*Physa*) (DeWitt, 1996). Here fertilization is internal and the adopted gender in a mating is size dependent, the smaller snail mates in the male role and the larger snail in the female role. Attempts by larger individuals to inseminate smaller individuals are met with shell shaking, which deters the would-be partner (shell shaking attracts predators). Dewitt argued that the reason for this asymmetry is that a relatively small suitor has more to gain reproductively than a relatively large suitor, and thus, the deterrence effect of shell shaking is less effective, and not employed, in the pairing of a small “male” snail and a large “female” snail acting in the female role. Size asymmetry thus makes for unilateral mating. There remains the question why the snails do not mate size assortatively. One possibility might be high search

<sup>9</sup>Consider humans, if men are latently promiscuous and women are not, heterosexual matings would not be promiscuous (while male homosexual matings would be).

<sup>10</sup>Switching costs may explain why “sequential” hermaphrodites may be gonadally simultaneous hermaphrodites (St. Mary, 1994).

cost, but that would suggest mating to be reciprocal in the first place.

### Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:[10.1016/j.jtbi.2006.10.031](https://doi.org/10.1016/j.jtbi.2006.10.031).

### References

- Charnov, E.L., 1979. Simultaneous hermaphroditism and sexual selection. *Proc. Natl Acad. Sci. USA* 76 (5), 2480–2484.
- Charnov, E.L., 1982. *The Theory of Sex Allocation*. Princeton University Press, Princeton, NJ.
- Charnov, E.L., Maynard Smith, J., Bull, J.J., 1976. Why be an hermaphrodite? *Nature* 263 (5573), 125–126.
- Charnov, E.L., Los den Hartogh, R.L., Jones, W.T., van den Assem, J., 1981. Sex ratio evolution in a variable environment. *Nature* 289 (5793), 27–33.
- DeWitt, T.J., 1996. Gender contests in a simultaneous hermaphrodite snail: a size-advantage model for behaviour. *Anim. Behav.* 51 (2), 345–351.
- Fischer, E.A., 1980. The relationship between mating system and simultaneous hermaphroditism in the coral-reef fish, *Hypoplectrus nigricans* (Serranidae). *Anim. Behav.* 28, 620–633.
- Ghiselin, M.T., 1969. The evolution of hermaphroditism among animals. *Q. Rev. Biol.* 47, 189–208.
- Greeff, J.M., Michiels, N.K., 1999a. Low potential for sexual selection in simultaneously hermaphroditic animals. *Proc. R. Soc. London* 266, 1671–1676.
- Greeff, J.M., Michiels, N.K., 1999b. Sperm digestion and reciprocal sperm transfer can drive hermaphrodite sex allocation to equality. *Am. Nat.* 153 (4), 421–430.
- Haase, M., Karlsson, A., 2004. Mate choice in a hermaphrodite: you won't score with a spermatophore. *Anim. Behav.* 67 (2), 287–291.
- Hurst, L., Hamilton, W., 1992. Cytoplasmic fusion and the nature of sexes. *Proc. R. Soc.* 1320 (247), 189–207.
- Leonard, J.L., Lukowiak, K., 1984. Male–female conflict in a simultaneous hermaphrodite resolved by sperm-trading. *Am. Nat.* 124 (2), 282–286.
- Lüscher, A., Wedekind, C., 2002. Size-dependent discrimination of mating partners in the simultaneous hermaphroditic cestode *Schistocephalus solidus*. *Behav. Ecol.* 13 (2), 254–259.
- Maynard Smith, J., 1978. *The Evolution of Sex*. Cambridge University Press, Cambridge.
- Michiels, N.K., Newman, L.J., 1998. Sex and violence in hermaphrodites. *Nature* 391 (6668), 647.
- Michiels, N.K., Streng, A., 1998. Sperm exchange in a simultaneous hermaphrodite. *Behav. Ecol. Sociobiol.* 42 (3), 171–178.
- Michiels, N.K., Hohner, A., Vorndran, I.C., 2001. Precopulatory mate assessment in relation to body size in the earthworm *Lumbricus terrestris*: avoidance of dangerous liaisons? *Behav. Ecol.* 12 (5), 612–618.
- Oliver, A.S., 1997. Size and density dependent mating tactics in the simultaneously hermaphroditic seabass *Serranus subligarius* (Cope, 1870). *Behaviour* 134 (7–8), 563–594.
- Petersen, C.W., 1995. Reproductive-behavior, egg trading, and correlates of male mating success in the simultaneous hermaphrodite, *Serranus tabacarius*. *Environ. Biol. Fishes* 43 (4), 351–361.
- Petersen, C.W., 2006. Sexual selection and reproductive success in hermaphroditic seabasses. *Integrative Comp. Biol.* 46 (4), 439–448.
- Sella, G., 1985. Reciprocal egg trading and brood care in a hermaphroditic polychaete worm. *Anim. Behav.* 33 (3), 938–944.
- Sella, G., Lorenzi, M.C., 2000. Partner fidelity and egg reciprocation in the simultaneously hermaphroditic polychaete worm *Ophryotrocha diadema*. *Behav. Ecol.* 11 (3), 260–264.
- Sella, G., Premoli, M.C., Turri, F., 1997. Egg trading in the simultaneously hermaphroditic polychaete worm *Ophryotrocha gracilis* (Huth). *Behav. Ecol.* 8 (1), 83–86.
- St. Mary, C.M., 1994. Sex allocation in a simultaneous hermaphrodite, the blue-banded goby (*Lythrypnus dalli*): the effects of body size and behavioral gender and the consequences for reproduction. *Behav. Ecol.* 5 (3), 304–313.
- Trivers, R.L., Willard, D.E., 1973. Natural selection of parental ability to vary the sex-ratio of offspring. *Science* 179, 90–92.
- Weeks, S.C., Sanderson, T.F., Reed, S.K., Zofkova, M., Knott, B., Balaraman, U., Pereira, G., Senyo, D.M., Hoeh, W.R., 2006. Ancient androdioecy in the freshwater crustacean *Eulimnadia*. *Proc. R. Soc. London Ser. B* 273 (1587), 725–734.