Sex in Simultaneous Hermaphrodites

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Mating in the leopard slug (*Limax maximus*)

from the BBC nature documentary ‘Life in the Undergrowth’
Summary: Sex in Simultaneous Hermaphrodites

- distribution of hermaphroditism
- advantages of hermaphroditism
- sexual selection
  - Bateman’s principle
  - male and female cross-terms
- sexual conflict
  - conditional egg trading in the hamlets
  - conditional sperm exchange in internal fertilisers
  - cryptic female choice
  - rejection or digestion of received sperm
  - sperm trading
  - bypassing female control (hypodermic impregnation)
  - manipulation of cryptic female choice
  - preventing the partner from mating again

Distribution

- hermaphroditism occurs in about 70% (24 of 34) animal phyla
- it is frequent or dominant in 14 phyla
- the 10 purely gonochoristic phyla contain relatively few species
- only 5-6% are hermaphrodites (but 30% when insects are excluded)
- hermaphroditism is rare in vertebrates
- there is a strong phylogenetic component in the distribution

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<th>Phylum</th>
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modified from Jarne & Auld 2006
Advantages

- reproductive assurance (Darwin 1876)
  - if one does not find a partner, one can still self-fertilise
  - but many simultaneous hermaphrodites actually do not self-fertilise!

- low density (Tomlinson 1966, Ghiselin 1969)
  - every partner you meet is a potential mating partner

- local mate competition (Charnov 1979, Charnov 1982)
  - limited male-male competition

- local sperm competition (Schärer 2009)
  - competition between related sperm

- these factors generally favour a female-biased sex allocation
Advantages

- simultaneous hermaphrodites probably often have a higher female than male investment
  - → the fitness return per unit of male investment is higher

Sexual selection

- Darwin (1871) doubted that sexual selection occurs in simultaneous hermaphrodites
  - ‘with animals belonging to the lower classes, the two sexes are not rarely united in the same individual, and therefore secondary sexual characters cannot be developed [...] Moreover it is almost certain that these animals have too imperfect senses and much too low mental powers to appreciate each other's beauty or other attractions, or to feel rivalry'

- but Darwin was only aware of pre-copulatory sexual selection
  - in simultaneous hermaphrodites there indeed is little evidence for traits involved in pre-copulatory sexual selection
    - but consider for a moment how we usually identify pre-copulatory secondary sexual characters in gonochoristic organisms
  - most sexual selection appears to be post-copulatory (i.e. sperm competition and cryptic female choice)
    - Parker’s (1970) recognition of sperm competition paved the way to a better understanding of sexual selection in simultaneous hermaphrodites
Sexual selection

- Bateman’s principle
  - in a female, reproduction tends to be limited by the number (and quality) of eggs she produces, which is often limited by the amount of resources she has
  - in a male, reproduction tends to be limited by the number (and quality) of eggs he fertilises, which is often limited by the number of females he can mate with

- → males will tend to want to mate more often than females
  - eager males and choosy females
  - sexual conflict between males and females over the optimal mating rate

- Charnov (1979) was the first to explicitly consider Bateman’s principle in simultaneous hermaphrodites
  - ‘I propose here that “Bateman’s principle” is also valid for these organisms — that fertilized egg production by an individual is limited not by the ability to get sperm, but by resources allocated to eggs. This is a strong assumption [...]. However, if it is approximately true, then [this] has several important implications for reproductive biology’

- → hermaphrodites will tend to prefer mating in the male sex role
  - simultaneous hermaphrodites often mate to give, rather than receive, sperm
  - sexual conflict between the sperm donor and sperm recipient should be intense
Sexual selection

- chain and ring mating in sea slugs

Sexual selection

- an individual's male and female mating success may not be independent of each other

(A) Strictly reciprocal mating

(B) Relaxed reciprocal mating

(C) Unilateral mating

Figure 4: Arbitrary examples illustrating how hermaphrodite mating modes can generate collinearity between male and female mating success (MS). When MS is defined at the level of copulations, individual $MS_m$ and $MS_f$ (and the variances of their underlying data distributions) will be identical in systems with strictly reciprocal mating (A). The link between $MS_m$ and $MS_f$ (and their population variances) becomes weaker when reciprocal mating is not obligatory (B). In systems with unilateral matings (C), $MS_m$ and $MS_f$ are no longer mechanically connected. Depending on circumstances, they may thus show positive, neutral (as plotted here), or negative covariance.

Anthes et al. 2010
Sexual selection

- an individual’s male and female mating success may affect its male and female reproductive success differently

![Bateman gradients](image)

Figure 3: Arbitrary example illustrating the interactive nature of Bateman gradients in hermaphrodites. Male reproductive success ($RS_m$; A) and female reproductive success ($RS_f$; B) are represented as partial regression planes on male and female mating success ($MS_m$ and $MS_f$). The graphs exemplify positive Bateman gradients for each sex ($\beta_{mm}$ and $\beta_{mf}$) that are reduced by some costs of matings via the other sex function ($\beta_{mf}$ and $\beta_{mm}$). The overall Bateman gradient is steeper for the male function ($\beta_{mm} > \beta_{mf}$), but male RS is depressed more strongly through female matings than vice versa ($\beta_{mf} < \beta_{mm}$).

Anthes et al. 2010

Sexual conflict

- in a gonochorist a mated female may not want to engage in additional copulations
  - if she has enough received sperm to fertilise her eggs and if additional matings offer no advantage
- avoiding males avoids (at least some) sexual conflicts
Sexual conflict

- the female function of a mated hermaphrodite may not want to engage in additional copulations
  - if it has enough received sperm to fertilise its eggs and if additional matings offer no advantage
- thus the female function may want to avoid engaging in additional matings, but the male function of the same individual will want to continue to mate

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Sexual conflict

- thus if two mated simultaneous hermaphrodites meet they may have incompatible mating interests
  - both individuals may want to donate, but not receive, sperm
- mating should take place if the net benefit for mating is positive
  - this can occur even if there is a cost to one sex, as long as it is sufficiently beneficial for the other sex
- a possible solution is reciprocal mating where acceptance of sperm receipt is conditional on sperm donation
- this is expected to lead to sexually antagonistic coevolution (a sexual arms-race) between
  - adaptations in the recipient that allow to remove (or otherwise control) sperm received in such matings (a form of cryptic female choice)
  - counter-adaptations in the donor that prevent sperm removal by the recipient (a form of male persistence)
Sexual conflict

- sexual conflicts over the mating role

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**Sexual conflict**

- egg trading in the hamlets (*Hypoplectrus* spp.)
  - both individuals should prefer to fertilise the eggs of the partner
  - they solve this by alternately assuming the male and female role
Sexual conflict

how do they prevent cheating?

• check, and if necessary, punish your partner!
• checking the partner is easier with external fertilisation

(with reciprocation)  (with)
\[ \ldots X - Y - X - Y - X \ldots \]
\[ b \]

(without)
Sexual conflict

This video was created to accompany our 2007 article in Scuba Diving Magazine

Sexual conflict

- conditional sperm receipt
  - in order to donate sperm one also has to accept their receipt
  - ➔ simultaneously reciprocal mating behaviour
Sexual conflict

- simultaneously reciprocal mating behaviour:

- is sperm acceptance really conditional on donation?
  - available data do not allow to test this

- does this lead to fertilisation trading?
  - the little available data suggest that not

- what do you do with sperm you did not want?
  - cryptic female choice by control, rejection or digestion
Sexual conflict

- possible mechanisms for cryptic female choice
  - storage tubules for sperm of different sperm donors in the free-living flatworm *Paromalostomum dubium*

Sperm tubes in *Paromalostomum dubium*
Mating behaviour in *Macrostomum lignano*

Sexual conflict

- sperm digestion
  - connection between sperm-receiving organ and the gut in the free-living flatworm *Promacrostromum paradoxum* (Platyhelminthes: Macrostomidae)

*Fig. 3. Promacrostromum paradoxum nov. gen. nov. spec.; Organisations-schema des Genitalapparates.*

Schärer et al. 2004

An-der-Lan 1939
Sexual conflict

- conditional sperm donation
  - with efficient cryptic female choice sperm donation ≠ fertilisation
  - if most sperm is digested, mating in male role can become costly
  - sperm donation can become conditional on sperm receipt (only mate with partners that are also willing to invest a lot)
  - conditional sperm trading in a planarian flatworm

- an experimental test of the conditional sperm trading hypothesis in a sea slug
  - a ‘cauterised’ individual can not donate sperm, and is thus forced to cheat
  - the focal individual reciprocates fewer copulations to a cheater than to a control
  - the focal individual deserts cheaters more often than controls
  - but an alternative explanation is choice against a ‘sick’ partner
Sexual conflict

- hypodermic sperm donation
  - allows to avoid receiving sperm (and any costs required to control such received sperm)
  - allows to bypass cryptic female choice (even if hypodermic fertilisation is not very efficient, it may still be better)

\[\text{Pseudaphanostoma psammophilum} \quad \text{(Acoela)}\]

\[\text{Pseudoceros bifurcus} \quad \text{(Platyhelminthes: Polycladida)}\]

Michiels & Newman 1998

Penis fencing in \textit{Pseudobiceros} sp. (Polycladida)
Hypodermic sperm donation in *Macrostomum hystrix*
Sexual conflict

• manipulation of cryptic female choice
  • the function of the love dart in pulmonate snails

The love-dart (D) is produced and stored in the stylophore (S, often called dart sac) and shot by a forceful eversion of this organ. The mucus glands (MG) produce the mucus that is deposited on the dart before shooting. The penis (P) is intromitted to transfer the spermatophore. The sperm container is formed in the epiphallus (EP), while the spermatophore’s tail is formed by the flagellum (FL). When a bursa tract diverticulum (BTD) is present, the spermatophore is received in this organ. Together with the bursa tract (BT) and bursa copulatrix (BC) these form the spermatophore-receiving organ (SRO, indicated in grey), which digest sperm and spermatophores. Sperm swim out via the tail of the spermatophore to enter the female tract and reach the sperm storage organ (SP, spermathecae) within the fertilization pouch (FP)-spermathecal complex. Other abbreviations: AG, albumen gland; G, genital pore; HD, hermaphroditic duct; OT, ovotestis; PRM, penis retractor muscle; SO, spermoviduct; V, vaginal duct; VD, vas deferens.

Koene & Schulenburg 2005

Sexual conflict

• manipulation of cryptic female choice
  • the function of the love dart in pulmonate snails

Figure 2. Paternity assignments per egg clutch from an experiment in which needle injections replaced dart shooting. Future mothers were mated twice. In one mating, sperm transfer was accompanied by an injection of mucus from the dart gland and in the other mating sperm transfer was accompanied by an injection of saline. Mean ± s.e.m. is shown. First donor: $F_{1,35} = 5.086$, $p = 0.030$; second donor: $F_{1,35} = 10.652$, $p = 0.002$.

Koene & Chase 1998
Chase & Blanchard 2006
Sexual conflict

- manipulation of cryptic female choice
  - morphological diversity of the love dart

Koene & Schulenburg 2005
Sexual conflict

- manipulation of cryptic female choice
  - coevolution between male and female traits

- preventing the partner from mating again
  - can target the male or female function
  - e.g. penis biting in banana slugs, *Ariolimax* (has only rarely been observed)

Koene & Schulenburg 2005
Sexual conflict

- ways of manipulating the partner via seminal fluid

Schärer 2014

Sexual conflict

(a) (b) (c)

Lange et al. 2014
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  - cryptic female choice
  - rejection or digestion of received sperm
  - sperm trading
  - bypassing female control (hypodermic impregnation)
  - manipulation of cryptic female choice
  - preventing the partner from mating again
Literature

• **Mandatory Reading**
  - none

• **Suggested Reading**

• **Books**