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
  - cross-sex selection effects
- sexual conflict
  - conditional egg trading in 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 24 of the 34 animal phyla (about 70%)
- it is frequent or dominant in 14 phyla
- the 10 purely gonochoristic phyla contain relatively few species
- only 5-6% of species 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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modified from Jarne & Auld 2006
Advantages

- reproductive assurance (Darwin 1876)
  - if one does not find a partner, one can still choose to 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
  - but many hermaphrodites actually do not occur at low density!
- “local mate competition” (Charnov 1979, Charnov 1982)
  - favoured under limited male-male competition
- local sperm competition (Schärer 2009)
  - competition between related sperm leads to diminishing returns on male reproductive investment

➙ all of these factors will generally tend to favour a female-biased sex allocation
Advantages

- simultaneous hermaphrodites probably often have a higher female than male investment (i.e. a female-biased sex allocation)
  - this means that the fitness returns per unit of male investment are higher

![Histological section through the ovotestis of a Barred Hamlet](image)

Sexual selection

- Darwin (1874) 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 is little evidence for traits involved in pre-copulatory sexual selection (but in gonochorists we often identify pre-copulatory secondary sexual traits based on their sex-limited expression!)
  - in simultaneous hermaphrodites a lot of sexual selection occurs at the post-copulatory stage (i.e. sperm competition and cryptic female choice)
  - Parker’s (1970) recognition of sperm competition therefore paved the way to a better understanding of sexual selection in simultaneous hermaphrodites
Sexual selection

- Reminder: 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 available
  - 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
    - this leads to eager males and choosy females and results in 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
    - if true, then simultaneous hermaphrodites may often mate to give, rather than to receive, sperm
    - sexual conflict between the sperm donor and the sperm recipient could therefore be very intense
Sexual selection

• two recent studies have confirmed that Bateman’s principle also applies to copulating simultaneous hermaphrodites
  • namely Anthes et al. (2010) and Pélissié et al. (2012) in the freshwater snails Biomphalaria glabrata and Physa acuta, respectively

Sexual selection

• mating chains and mating rings in sea slugs provide some evidence for a high eagerness to mate

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from http://www.seaslugforum.net/find/7061

from http://www.seaslugforum.net/find/16512
Sexual selection

- An individual’s male mating success may often not be independent of its female mating success
  - So optimizing one without affecting the other can be difficult or even impossible

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 in contrasting ways
  - So this can lead to unique cross-sex effects on the Bateman gradients

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 (β_{ms} > 0 and β_{fn} < 0) that are reduced by some costs of matings via the other sex function (β_{ms} and β_{fn} < 0). The overall Bateman gradient is steeper for the male function (β_{ms} > β_{fn}), but male RS is depressed more strongly through female matings than vice versa (β_{ms} < β_{fn}).

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 available eggs and if additional matings offer little advantage
- avoiding males may permit the females to avoid (at least some) costs linked to sexual conflict

- similarly, the female function of a mated hermaphrodite may not want to engage in additional copulations
  - if it has received enough sperm to fertilise its available eggs and if additional matings offer little advantage
- thus the female function may want to avoid engaging in additional matings, but the male function of the same individual may often want to continue to mate

- 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 benefits for mating are positive
  - this can occur even if there are costs to one sex function, as long as it is sufficiently beneficial for the other sex function (Michiels & Koene 2006)
- 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 female resistance or cryptic female choice)
  - counter-adaptations in the donor that prevent sperm removal by the recipient (a form of male persistence)

Charnov 1979; Michiels 1998
Sexual conflict

- sexual conflicts over the mating role

![Compatibility Chart](image)

Michiels 1998

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Sexual conflict

- egg trading in hamlets (*Hypoplectrus* spp.)
  - this species has a highly female-biased sex allocation
  - both individuals should prefer to fertilise the eggs of the partner
  - they solve this by alternately assuming the male and female role

![Color Morphs](image)

![Ovotestis](image)

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colour morphs of the genus *Hypoplectrus*

ovotestis of *Hypoplectrus puella*
Sexual conflict

- how do they prevent cheating?
  - check on, and if necessary, punish your partner!
  - checking the partner is easier with external fertilisation
Sexual conflict

- conditional sperm receipt
  - in order to donate sperm one also has to accept receipt
  -ynchronously reciprocal mating behaviour

Archaphanostoma agile (Acoela)
Deroceras sp. (Pulmonata)
Monocelis fusca (Proseriata)
Lumbricus terrestris (Oligochaeta)
when we observe simultaneously reciprocal mating behaviour we can ask:

- is sperm acceptance really conditional on donation?
  - the available data currently does not allow to test this
- does this lead to fertilisation trading?
  - the little available data suggest that it does not, or at least not very well
- what do you do with sperm you did not want?
  - cryptic female choice by control, rejection or digestion
Sexual conflict

- sperm digestion may also occur in other ways
  - connection between sperm-receiving organ and the gut in the free-living flatworm *Macrostomum paradoxum* (Platyhelminthes: Macrostomidae)

*Fig. 3. Premacrostromum paradoxum* nov. gen. nov. spec.; Organisations-schema des Genitalapparates.
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 give back a lot)
  - ➔ conditional sperm trading was proposed in a planarian flatworm

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

- hypodermic sperm donation
  - may allow an individual to avoid receiving sperm (and any costs required to control such received sperm)
  - may allow to bypass cryptic female choice (even if hypodermic fertilisation is not very efficient, it may still be better)
  - but when approaching others there is also a risk of getting stabbed oneself

Pseudophanostoma psammophilum
(Acoela)

Pseudoceros bifurcus
(Platyhelminthes: Polycladida)

Penis fencing in Pseudobiceros bedfordi (Polycladida)

from the BBC nature documentary 'The Mating Game'
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

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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: $F_{1,95} = 5.086, p = 0.030$; second donor: $F_{1,95} = 10.652, p = 0.002$.

Koene & Chase 1998

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Chase & Blanchard 2006
Sexual conflict

- manipulation of cryptic female choice
  - tremendous morphological diversity of the love dart
Sexual conflict

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

Sexual conflict

* preventing the partner from mating again
  * this could target both the male or the female function of the partner
  * e.g. penis biting in banana slugs (*Ariolimax*), but this has only rarely been observed
Sexual conflict

(d) (i)

(ii) (iii)

Siphopteron sp. 1 - Intertwining
Summary: Sex in Simultaneous Hermaphrodites

- distribution of hermaphroditism
- advantages of hermaphroditism
- sexual selection
  - Bateman's principle
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- sexual conflict
  - conditional egg trading in 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

Literature

- Mandatory Reading
  - none
- Suggested Reading
- Online Resources
  - A short PBS 'Deep Look' episode on love darts in garden snails
    https://www.youtube.com/watch?v=UOcLa44TXA