Two-fold cost of sex?

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Summary

- sex allocation theory
- the sea urchin (a gonochoristic broadcast spawner)
- the human (a gonochoristic mammal with biparental care)
- the stickleback (a gonochoristic fish with paternal care)
- the fig wasp (a gonochoristic insect with local mate competition)
- the hamlet (an outcrossing simultaneous hermaphrodite)
- the cladoceran (a cyclical parthenogen)

- an excellent 25’ movie on fig wasp pollination biology for those who are interested

Sex allocation theory

- predicts the optimal investment to male and female reproduction in sexually reproducing organisms
  - sex ratio in gonochorists (species with separate sexes, dioecious species)
  - sex order and timing of (or size at) sex change in sequential hermaphrodites
  - allocation to male and female function in simultaneous hermaphrodites

- predicts the optimal sexual system
  - gonochorism, sequential hermaphroditism, simultaneous hermaphroditism or a mixture of these sexual systems
    - e.g. androdioecy, gynodioecy, or protandrous simultaneous hermaphroditism
    - what about cyclical parthenogenesis?

- predicts the existence and extent of plasticity in sex allocation
  - plastic sex allocation in response to the environment (environmental sex determination) may be advantageous under some conditions
Sex allocation theory

- in a sexually reproducing organism each individual has exactly one father and one mother
- therefore the fitness that can be obtained via male and female reproduction is exactly equal
- so frequency-dependent selection should lead to an equal investment in male and female reproduction
  - i.e., a 50:50 sex ratio in species with separate sexes if males and females are equally costly
- the two-fold cost of sexual vs. parthenogenetic reproduction is a direct consequence of this ‘Fisherian’ sex ratio theory
- but this theory makes a number of restrictive assumptions
  - e.g., random mating and large population size

The sea urchin (Strongylocentrotus purpuratus)

- sea urchins release their eggs and sperm into the water (mass broadcast spawning)
- after gamete release there is intense (numerical) competition between the sperm for the fertilisation of the eggs
  - in some cases there can also be sperm limitation
- there is no parental care (no postzygotic investment)
- males and females are expected to invest equally into gamete production and sex ratios should be equal
- a parthenogenetic mutant would therefore be expected to have the full two-fold advantage
The sea urchin (*Strongylocentrotus purpuratus*)

- male and female purple sea urchins indeed appear to invest about equally into gamete production
- but parthenogenesis does not seem to occur in nature
  - although it can be induced artificially in the laboratory

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The human (*Homo sapiens*)

- females have a prolonged pre- and postnatal investment in the child
- males contribute paternal care to varying degrees, but generally less than the female
- the sex ratio at birth is approximately even, but significantly biased towards males
  - approx. 105 boys per 100 girls
- due to higher male infant mortality the sex ratio is approximately even at sexual maturity
- a parthenogenetic human female would be expected to have a high advantage
  - although the social fathers could become suspicious if the offspring do not resemble him at all
The human (*Homo sapiens*)

- this reasoning may apply to many mammals
- but there are no natural examples of parthenogenetic mammals
  - although parthenogenesis has recently been produced experimentally in mice
- a possible reason is genomic imprinting (a difference in gene expression depending on the origin of an allele)
  - for some genes only the paternally inherited allele is expressed
  - for other genes only the maternally inherited allele is expressed
  - a parthenogenetic offspring would therefore miss the paternally imprinted genes, and would not develop properly
- a parthenogenetic mutant may thus not be able to reproduce
- genomic imprinting therefore probably constrains mammals to reproduce sexually

The stickleback (*Gasterosteus aculaetus*)

- in sticklebacks males build nests and care for the developing eggs and the young
  - eggs that are not cared for do not survive
- a parthenogenetic female could lay her eggs in the nest of a male
  - but will the male be willing to care for such eggs?
- male sticklebacks are known to cannibalise eggs in their nest
  - can they recognise eggs not fertilised by them?
- the success of a parthenogenetic mutant will depend on whether the males recognise eggs they did not fertilise
  - in any case parthenogens will be unable to replace sexuals completely as they also depend on receiving paternal care
The stickleback (*Gasterosteus aculaetus*)

- a recent study compared the rate of egg cannibalism in control (own) vs. experimental (mixed) broods
- they found a higher rate of total cannibalism in mixed broods
- so a parthenogenetic mutant may not have a two-fold advantage

![Bar graph showing the comparison between experimental and control broods](image)

**Fig. 1.** Number of totally cannibalised and partly cannibalised clutches in the exchange experiment and control treatment. Males totally cannibalised significantly more clutches when they contained foreign eggs (*G*. *aculeatus*). *P* < 0.05. From *Frommen et al. 2007*

The fig wasp

- a female enters a fig and lays her eggs into some of the flowers
- the then fig quickly closes the ostiole and thereby prevents additional females from entering it
- the larvae develop inside galls
- males and females emerge
- the males (usually brothers) fertilise the females (usually their sisters)
- fertilised females leave the fig carrying the pollen and lay eggs in other figs and pollinate them
The fig wasp

- **local mate competition in fig wasps**
  - a female should maximise the number of grand-children she produces
  - if she is the only foundress laying eggs in a fig an equal sex ratio will lead to competition between her sons

- so it is advantageous for her to make a maternal sex-ratio adjustment
The fig wasp

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- **under these conditions a parthenogenetic female has only a small advantage**

The hamlet (*Hypoplectrus sp.*)

- **hamlets perform an intriguing mating behaviour called egg trading**
  - the fish alternate between the male and the female sexual role and exchange parcels of eggs that are fertilised by the partner
- **sperm competition is never observed**
- **this leads to a situation that is equivalent to local mate competition (local sperm competition)**
  - high sperm production leads to competition between the own sperm
  - so it is advantageous to produce a female-biased sex allocation

*mating in Hypoplectrus puella*
The hamlet (Hypoplectrus sp.)

- the ovotestis of the hamlet has more ovarian than testicular tissue
- a parthenogenetic mutant therefore has a relatively small advantage over the sexuals
  - but this may depend on whether the mutant still produces viable sperm

![ovotestis of Hypoplectrus puella](Image)

The cladoceran (Daphnia magna)

- *Daphnia magna* regularly alternates between parthenogenesis and sexual reproduction
  - while conditions are favourable females reproduce parthenogenetically with ameiotic eggs
  - if conditions deteriorate females produce males and meiotic eggs, and reproduce sexually, yielding resting eggs
- a completely parthenogenetic mutant only has a small advantage and it will no longer be able to produce resting eggs
  - and resting eggs are important for over-wintering and dispersal
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Reading

chapter 13
the evolution of genetic systems
II. Some consequences of sex

- The sex ratio
- Sibling and outcrossing
- Hermaphroditism
- Sexual selection
- Further reading
- Problems
- Computer projects

chapter 13
the evolution of genetic systems
II. Some consequences of sex

In this chapter, I assume sexual reproduction, and discuss some consequences.

The sex ratio

It is a familiar fact that, in most dioecious species, there are approximately equal numbers of males and females. Why should this be so? The answer would be that, in most species, sex is determined by the segregation of X and Y chromosomes in the males of the heterogametic sex (usually the male), and that males generate a 1:1 ratio. This is true enough as far as it goes. If it were selectively advantageous to do so, however, organisms would readily have evolved some mechanism that produced a sex ratio different from 1:1. We therefore want a selective explanation for this ratio.

For the present, assume that the sex ratio is determined by genes acting in the parents, for example, genes could act in the heterogametic sex by altering the ratio of male- and female-determining genes produced, or, in the heterogametic sex, by altering the success of the two types of gametes in fertilization. However, I assume that a gene in a parent cannot alter its own likelihood of being transmitted to a gamete.

Pure, consider a simple explanation of the 1:1 ratio. Suppose that there were more females in the population than males. Then males would have, on average, more children than females. Therefore, a gene acting in a parent would be transmitted to more descendants if it could cause that parent to produce the rare sex—that is, males. Similarly, if there were more males in the population than females, a gene causing parents to produce females would spread. Hence the only evolutionarily stable sex ratio would be 1:1, because only then is the reproductive value of a sex equal to that of a sibling. This argument, originally due to R. A. Fisher, is made more precise in Box 15.1. In fact, it is shown that if the number of males and females that are equal at equilibrium, but the potential reproductive cost of males and females if the costs of a son and a daughter are equal, equal expenditure implies a 1:1 ratio.

from Maynard Smith 1998