Bruidsschatten, liefdespijlen & sekuele selectie

Joris M. Koene
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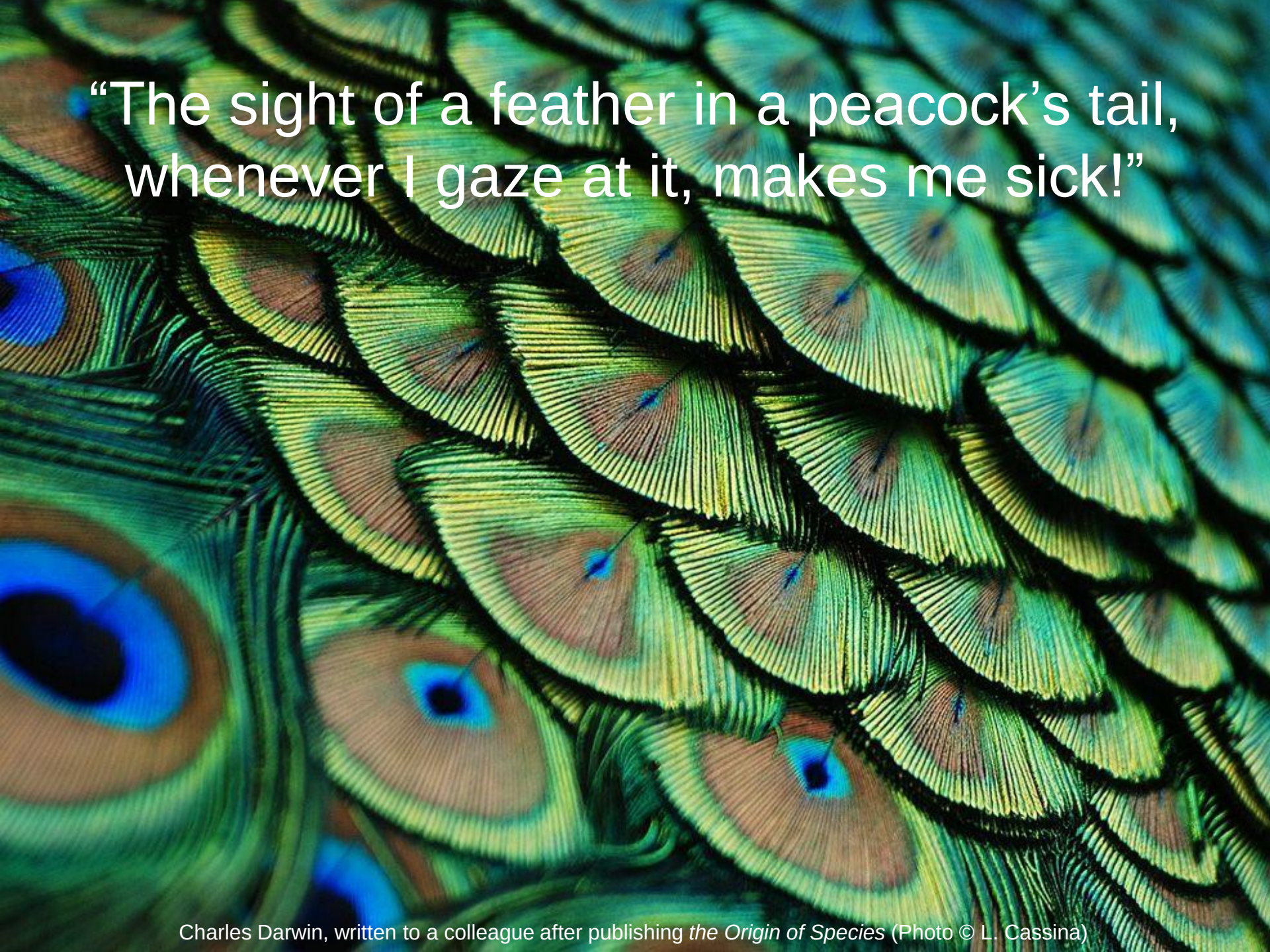
Bruidsschatten, liefdespijlen & sekuele selectie

(introduction to the) Mating Game

Sexual selection

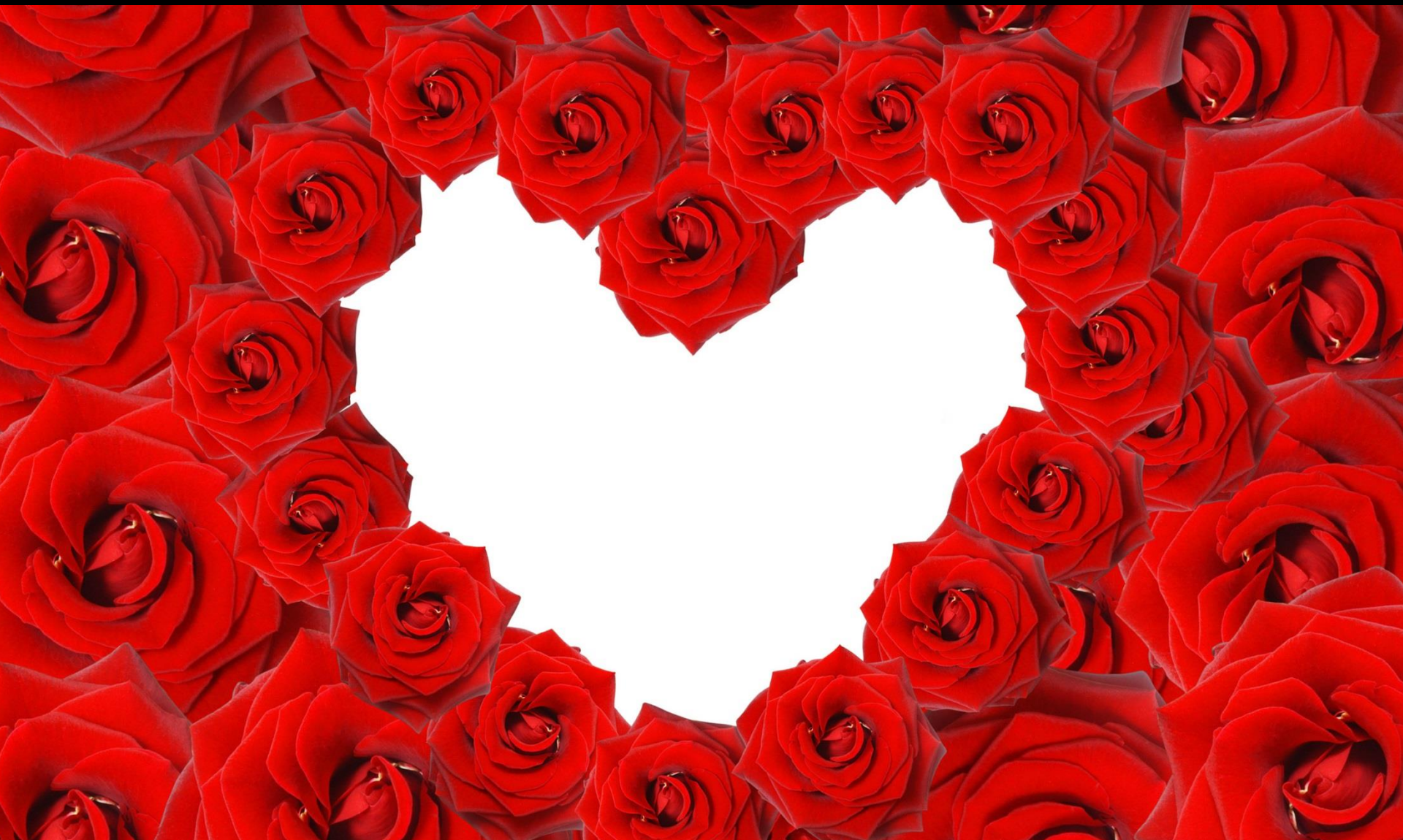
Sex is *ambiguous*

Love darts and semnal fluids



Charles Darwin, written to a colleague after publishing *the Origin of Species* (Photo © L. Cassina)

Males and females reproduce in harmony



Males and females reproduce in harmony

Males give 'gifts' to females

Males give 'gifts' to females

Kingfisher *Alcedo azurea* © National Geographic

Nursery-web spider *Pisaura mirablis* © Premaphotos

Dance Fly *Empis snoddyi* © M.A. Brittain

Tropical house cricket *Gryllodes sigillatus* © D. Funk

Males and females reproduce in harmony… ***or do they*?**

The Mating Game

Banksy “Sperm Alarm”

The Mating Game

Moore et al. 2012

Quality	Score	# Males	Male ID	# Females	Female ID
High	7	1	A	1	P
	6	2	B,BB	2	Q,QQ
	5	4	C,CC,D,DD	4	R,RR,S,SS
	4	6	E,EE,F,FF,G,GG	6	T,TT,U,UU,V,VV
	3	4	H,HH,I,II,	4	W,WW,X,XX
	2	2	J,JJ	2	Y,YY
Low	1	1	K	1	Z

The players

Egg layers (♀) and Sperm donors (♂)

Each player gets:
- 4 ♀ or many ♂ gametes
- Unique letter (A-K or P-Z)
- Quality score from high (7) to low (1)

The rules

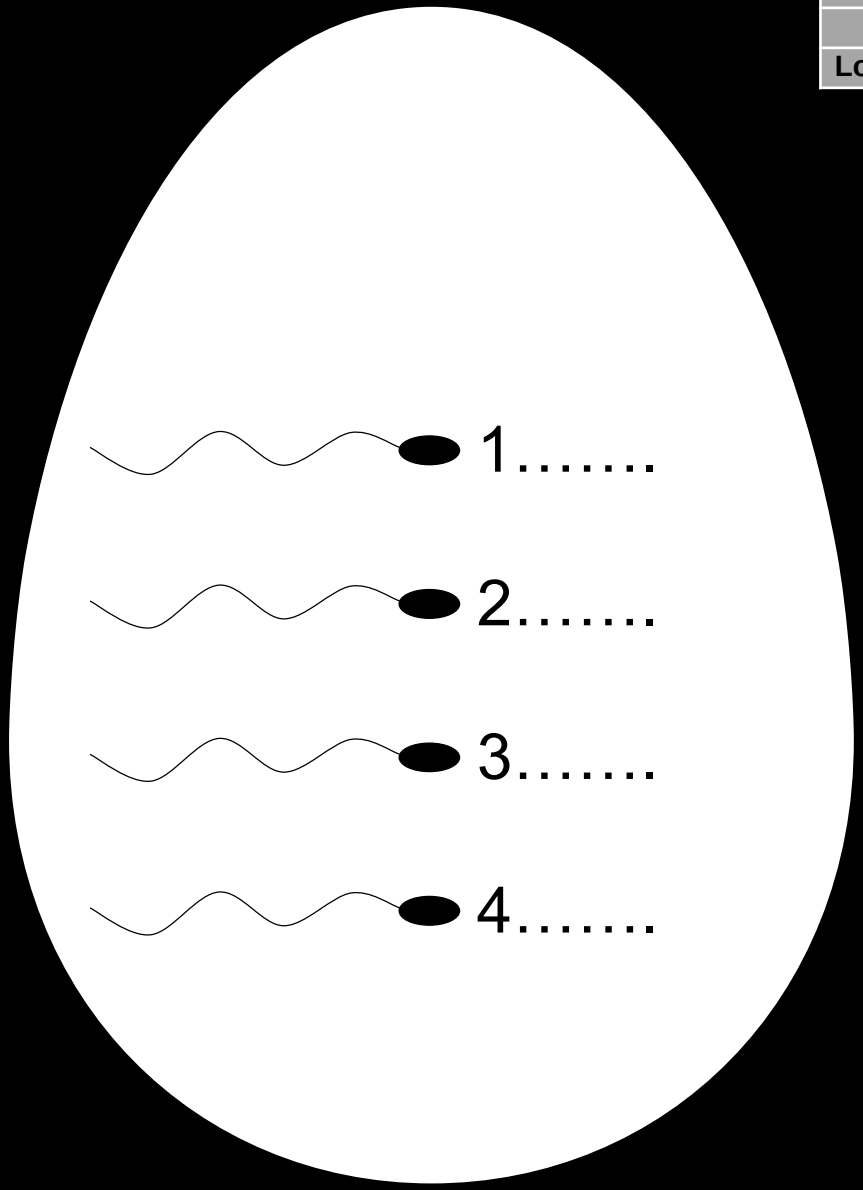
♂♂ donate to ♀♀ if both partners agree

One sperm is donated at a time to fertilise an egg

♀♀ will note down the letters of the sperm donors they accept

After the ‘mating season’, outcomes are entered into Excel for interpretation.

The egg layer



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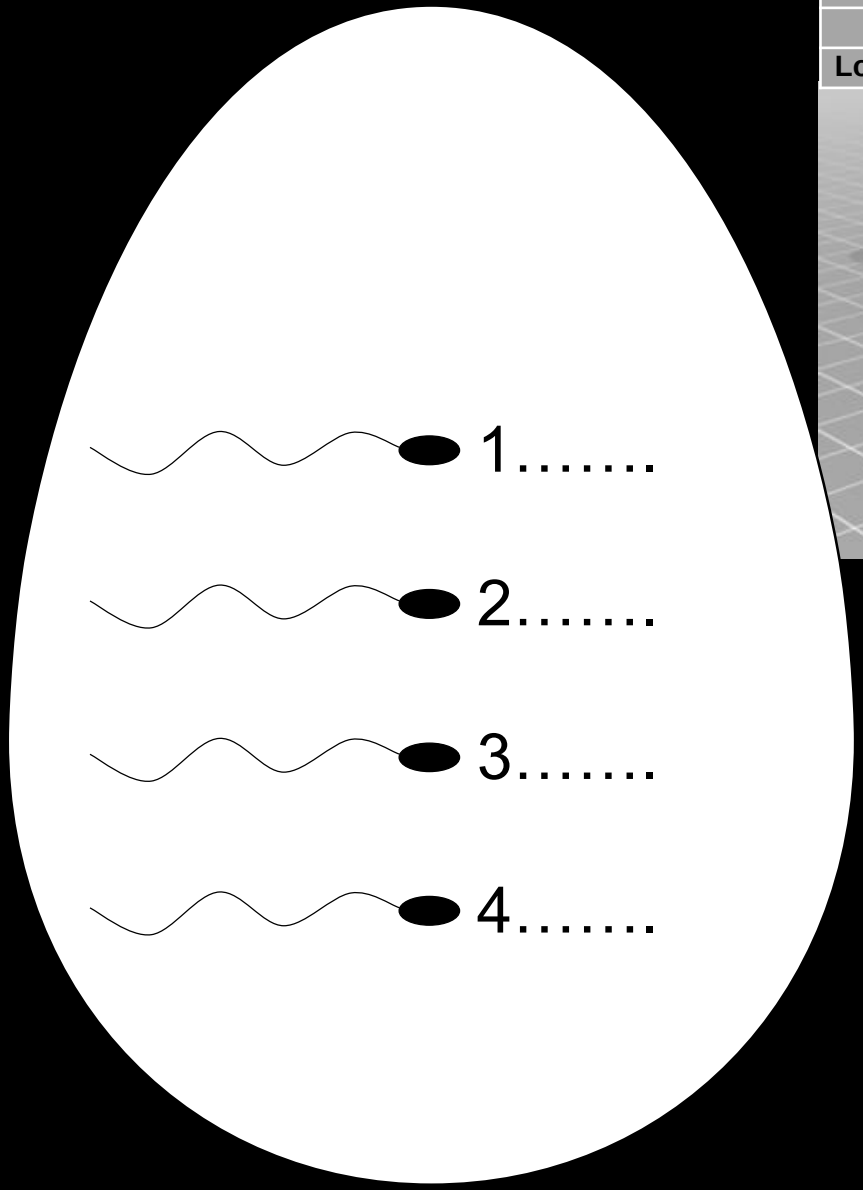
The egg layer



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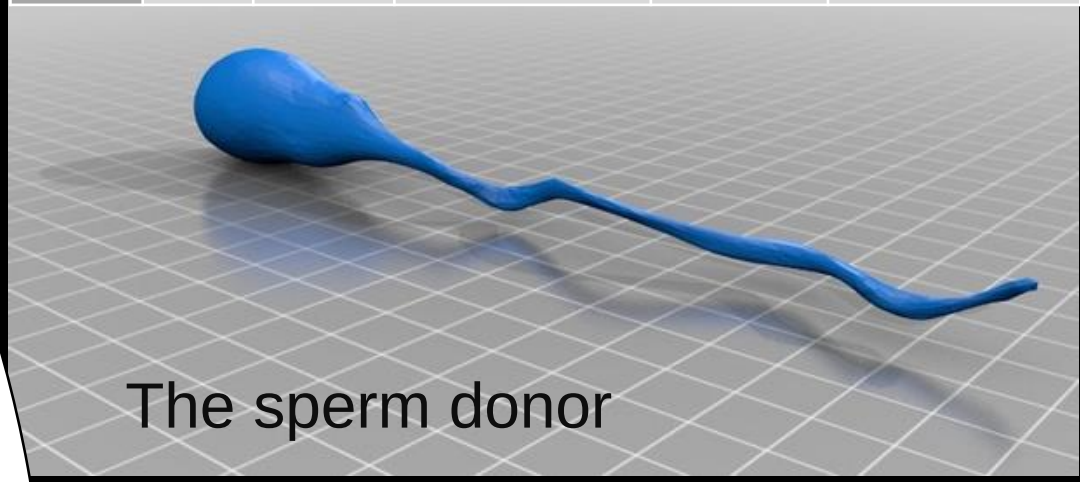
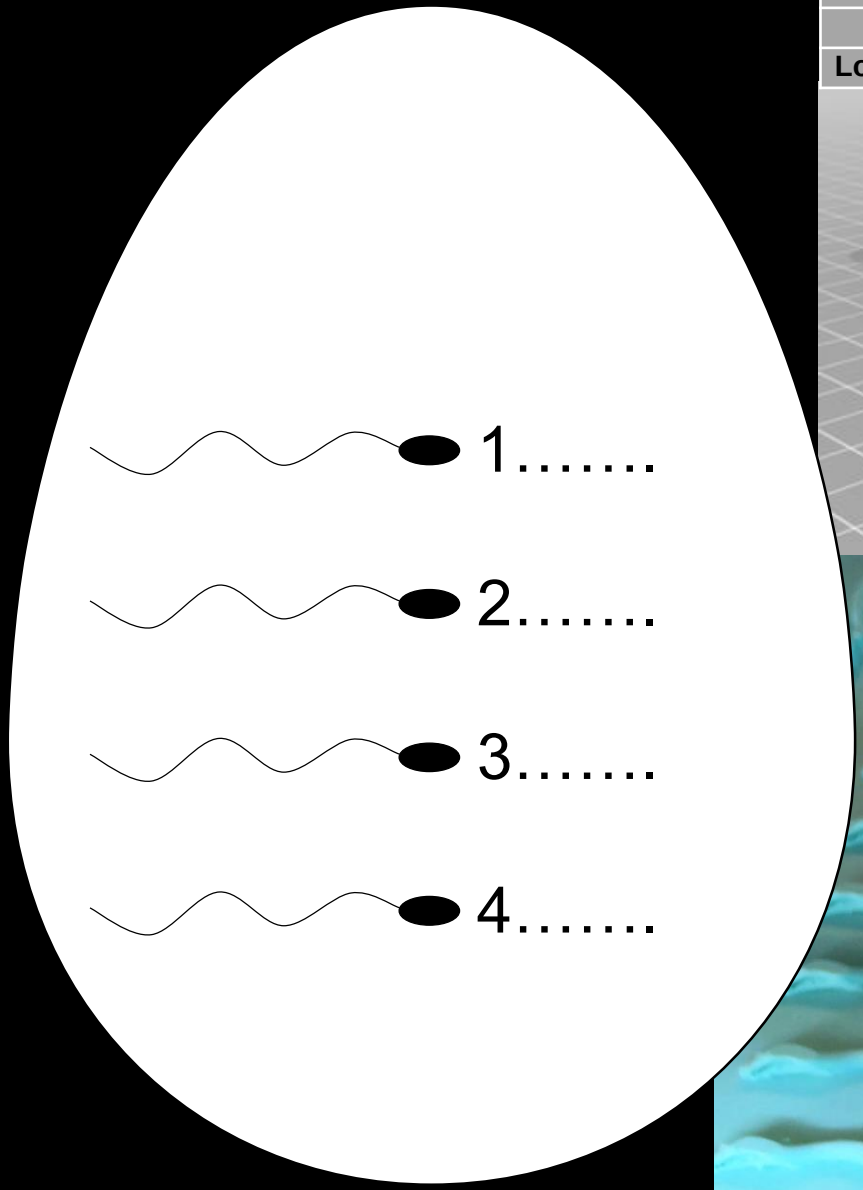


The egg layer



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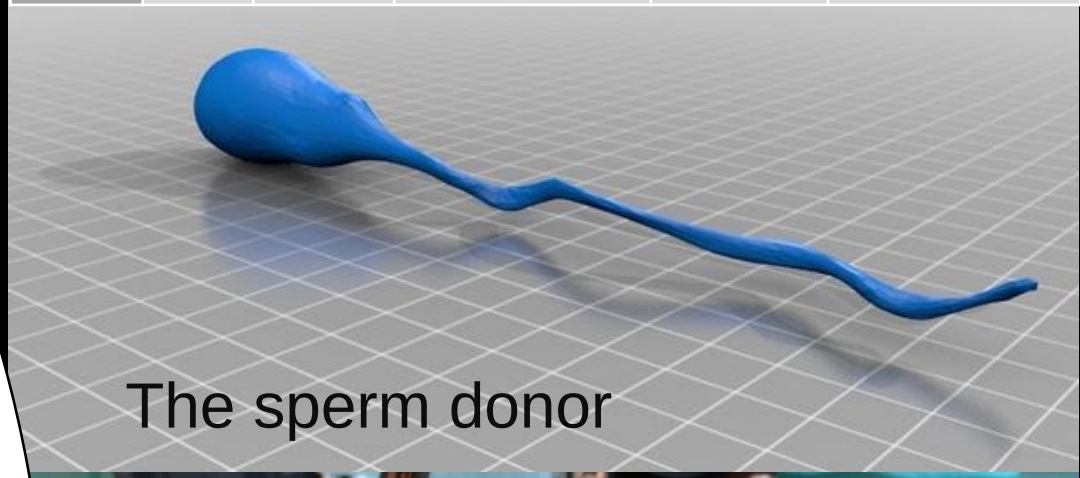

The sperm donor

It’s mating season!

Quality	Score	# Males	Male ID	# Females	Female ID
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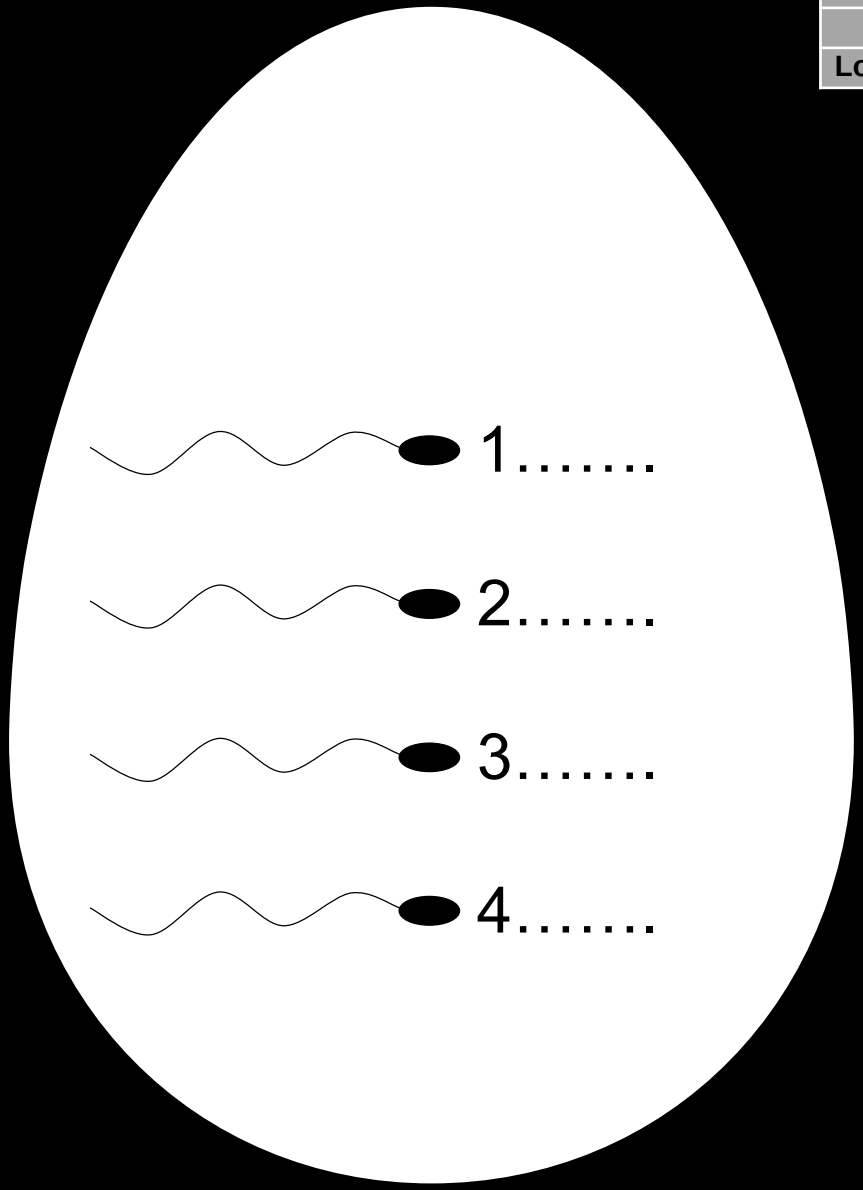


The rules

♂♂ donate to ♀♀ if both partners agree

One sperm is donated at a time to fertilise an egg

♀♀ will note down the letters of the sperm donors they accept (max. 4 donors)

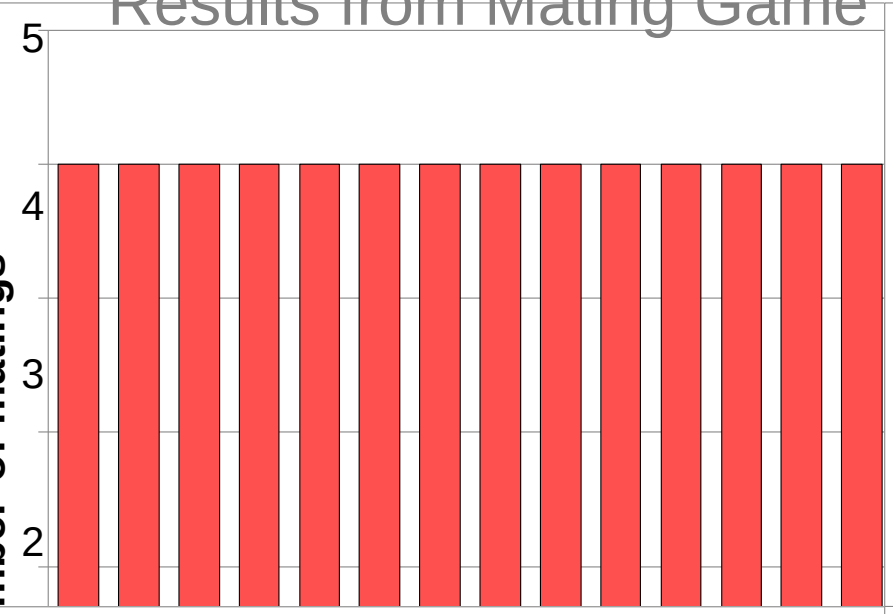
After the ‘mating season’, outcomes are entered into Excel for interpretation.

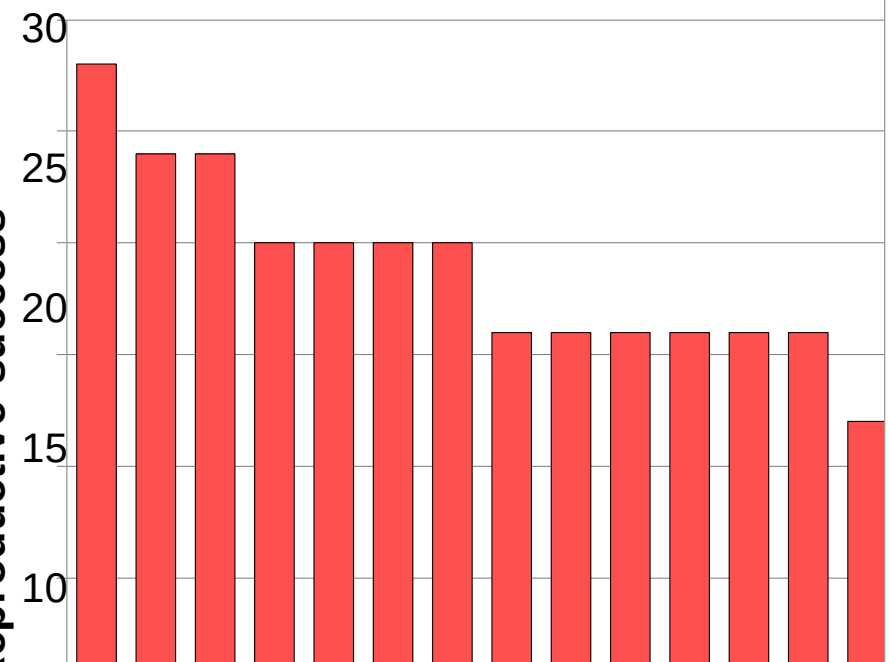
The Mating Game (entering the results)

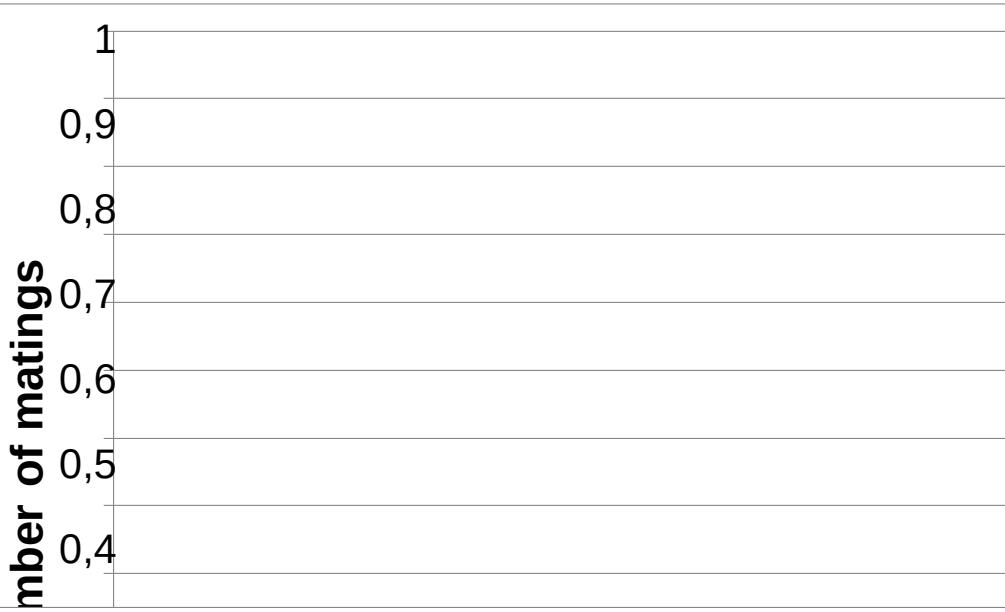
Scene from Monty Python's 'The Meaning of Life'
Video: https://youtu.be/fUspLVStPbk
Lyrics: https://youtu.be/k4mGrNGuJTM

♀ ♂

Results from Mating Game







Origin of sexual selection: Anisogamy
(sexual reproduction involving 2 gametes that differ in size/form**)**

Females

Produce few expensive gametes: *eggs*

Males

Produce many cheap gametes: *sperm*

Origin of sexual selection
Bateman's principle: eggs are expensive, sperm are cheap

Females

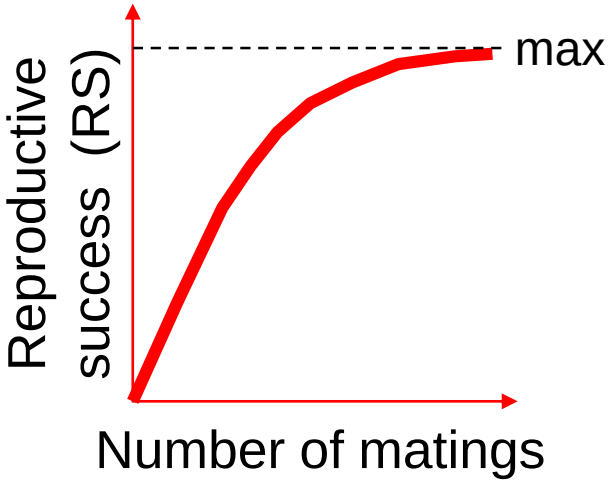
Produce few expensive gametes: *eggs*

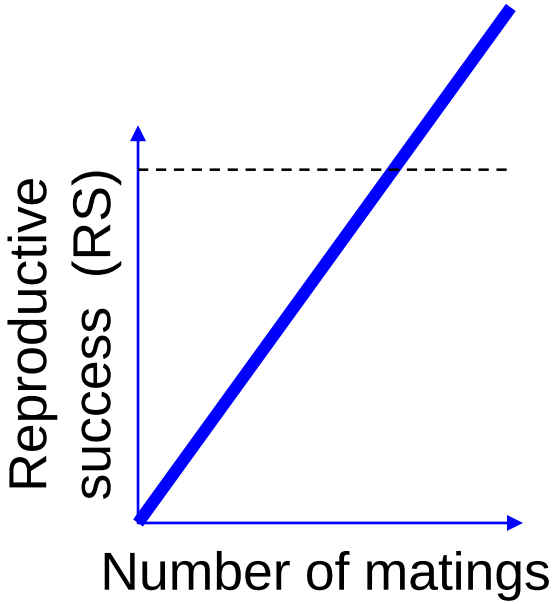
Reproductive success (RS) depends on resources, not mates

Males

Produce many cheap gametes: *sperm*

Reproductive success (RS) depends on number of mates, not resources





Bateman 1948

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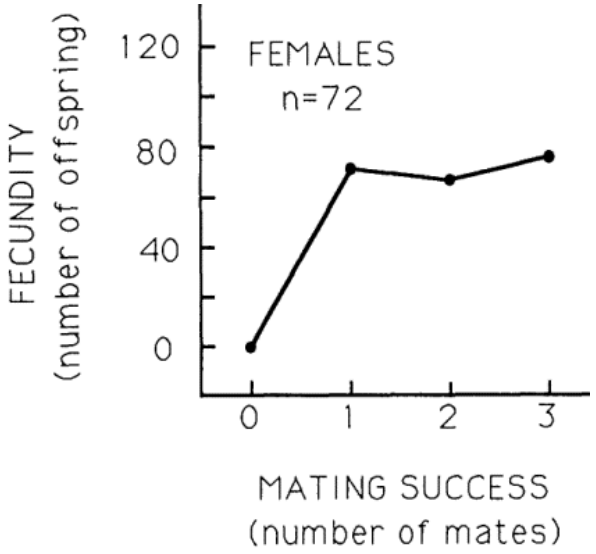

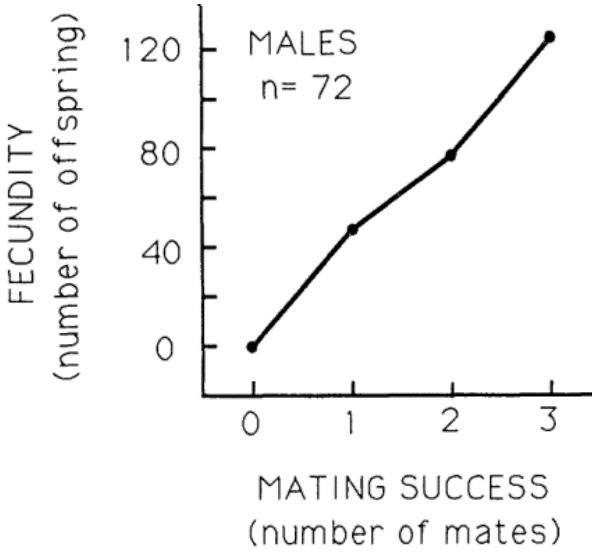

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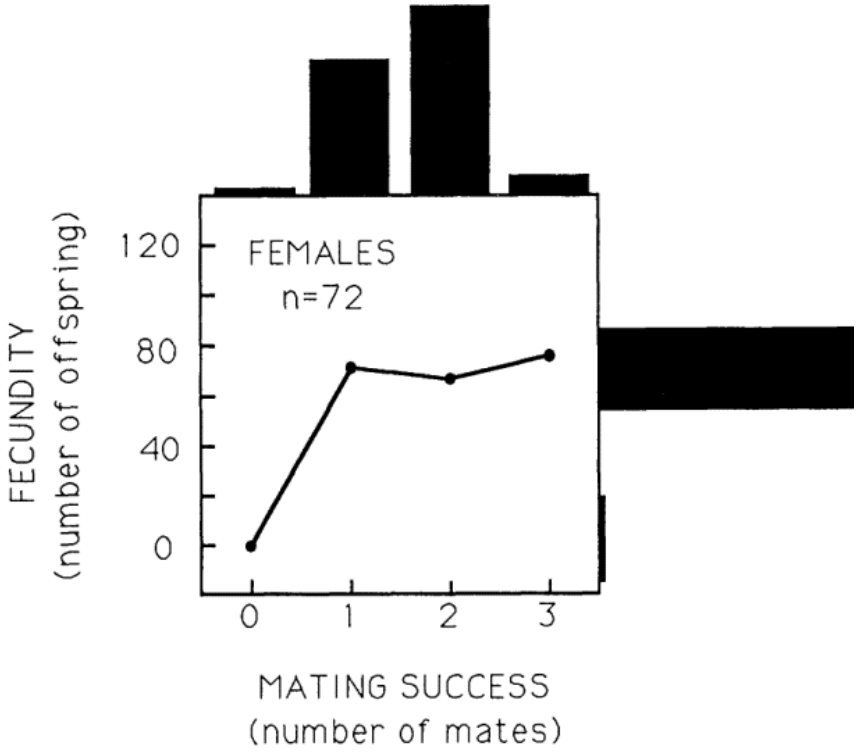
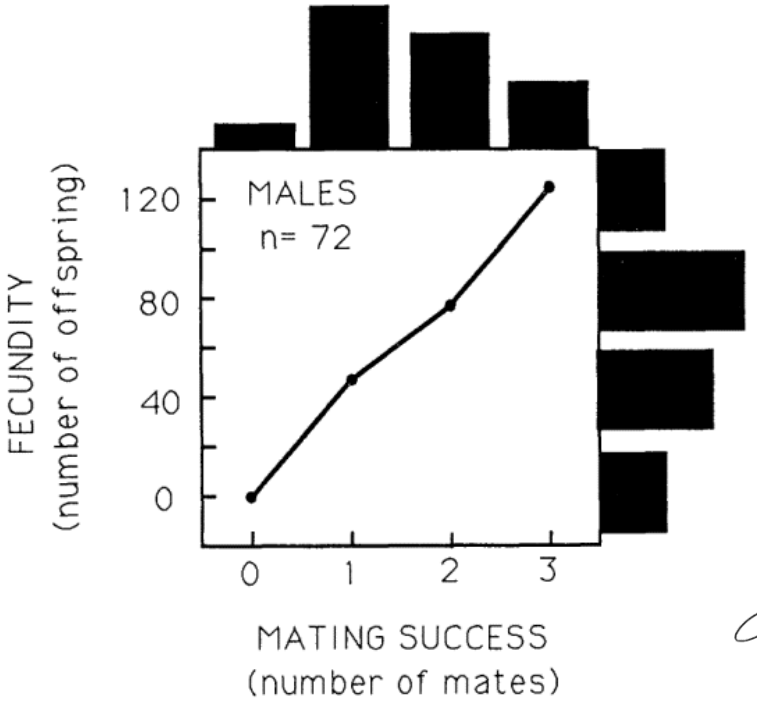




Arnold 1994

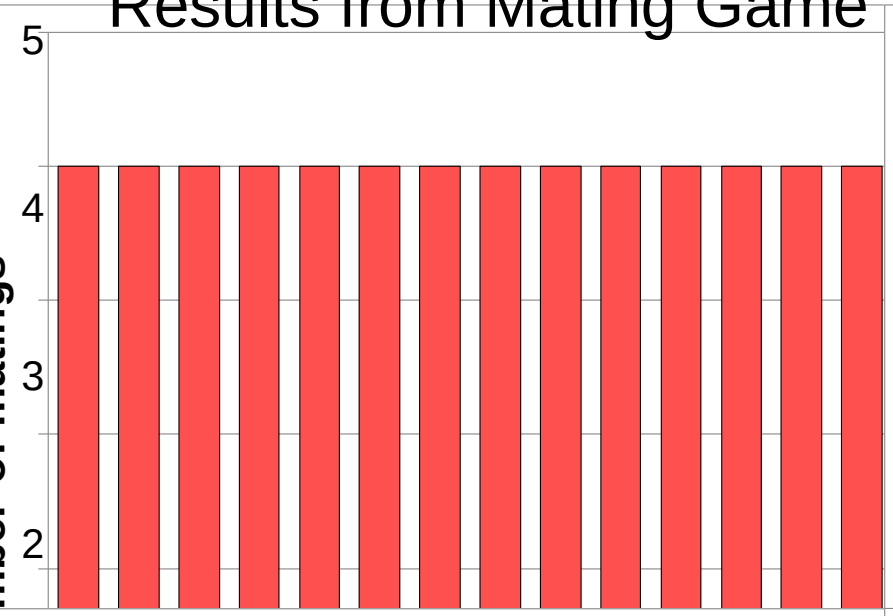
Origin of sexual selection
Bateman's principle: consequences

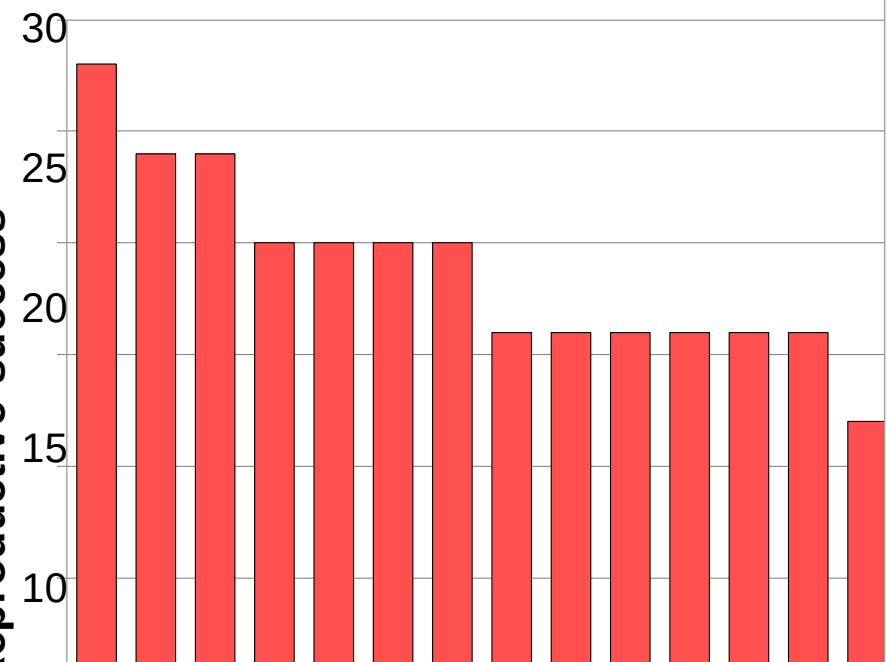
Females	**Males**
Produce few expensive gametes: *eggs*	Produce many cheap gametes: *sperm*
Reproductive success (RS) depends on resources, not mates	Reproductive success (RS) depends on number of mates, not resources
RS less variable Weak sexual selection	RS more variable Strong sexual selection
Invest in offspring and expect resources from mate	Invest in mate attraction and do not expect resources from mate
Less eager to mate and more choosy	More eager to mate and less choosy

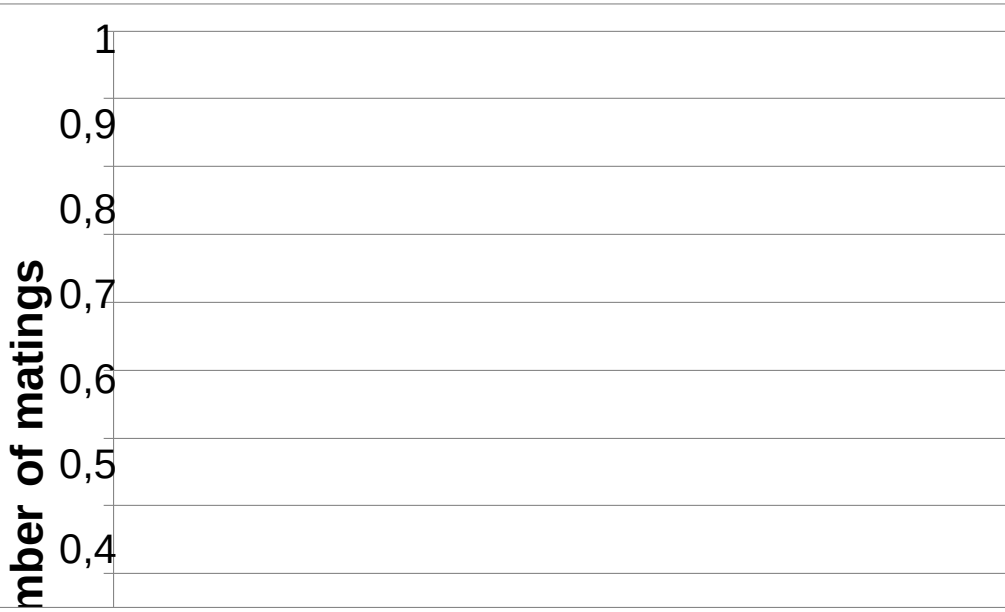
Bateman 1948

♀ ♂

Results from Mating Game







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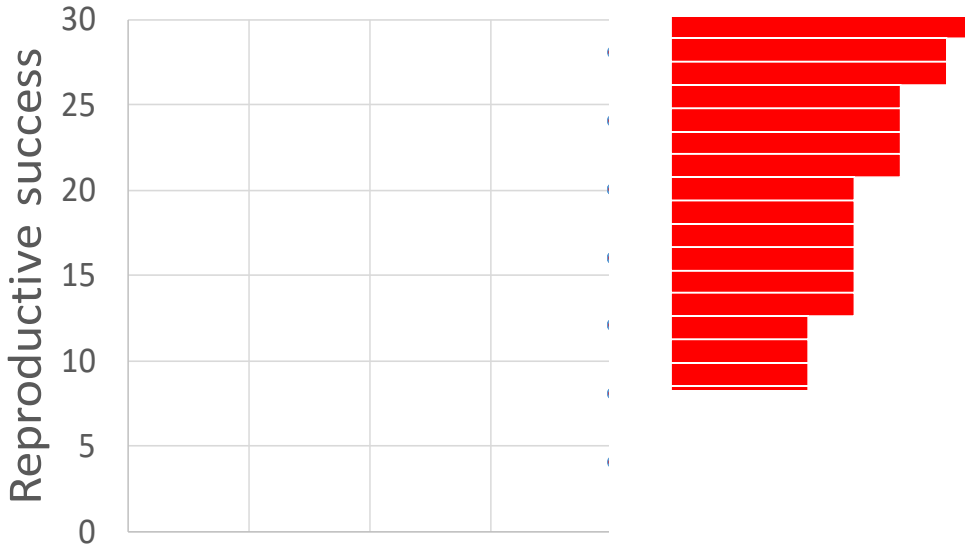
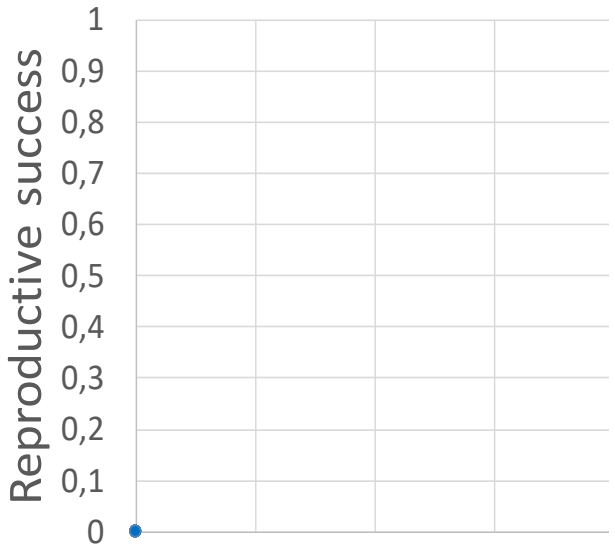
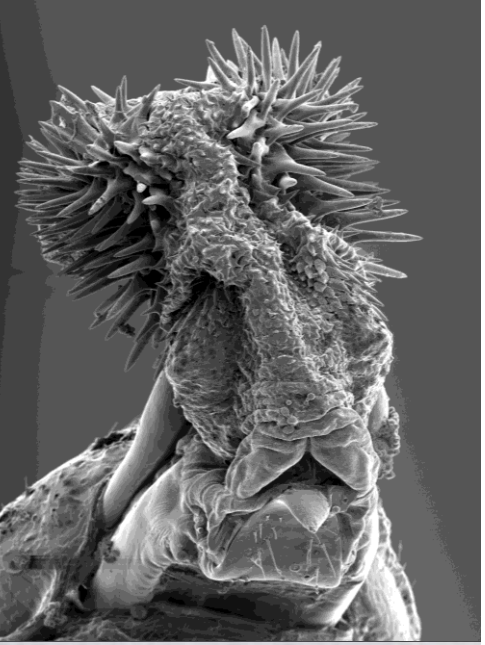
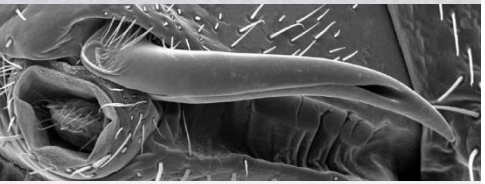








Competition for fertilisation (Sexual selection)

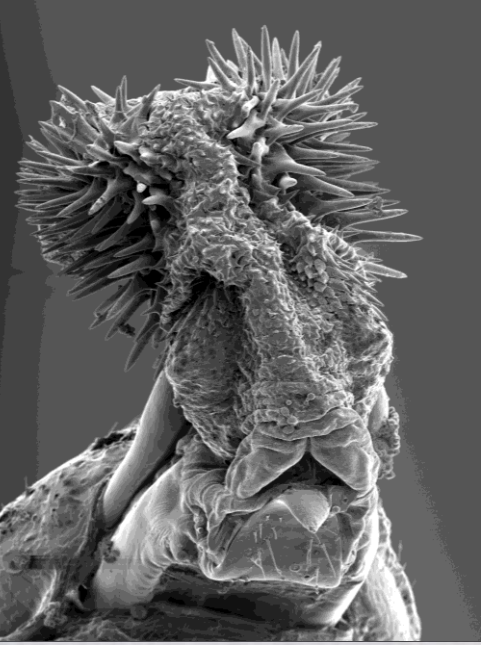
Male

Costly ejaculates,
sperm digestion,
sperm storage

Adaptations to increase fertilisation chances

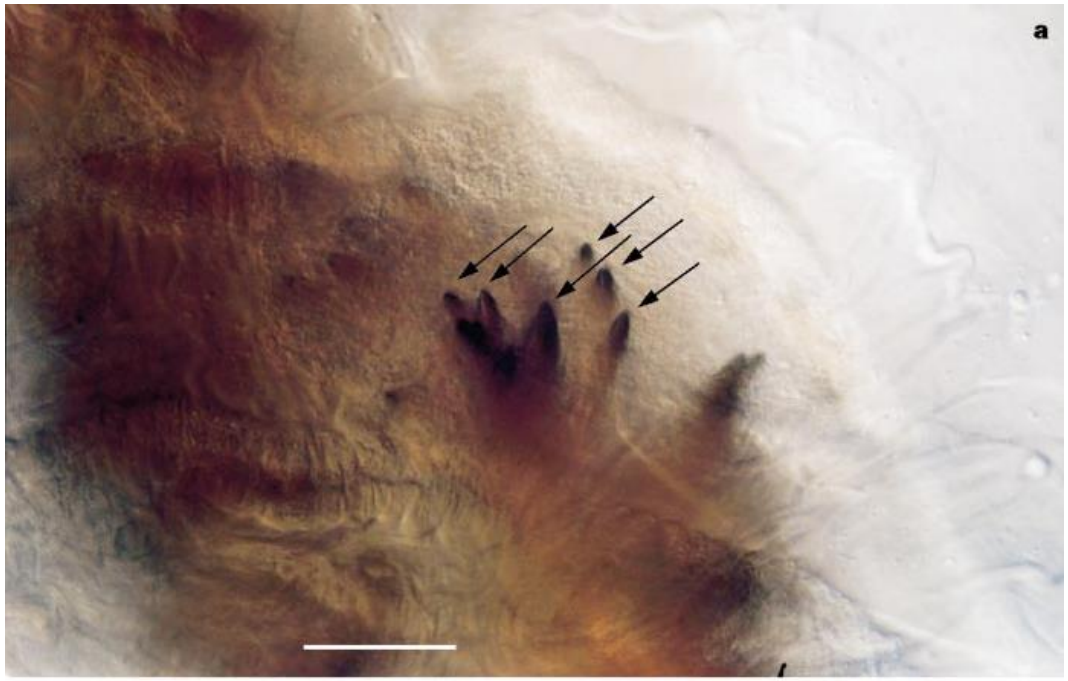
Inhibit remating
Influence egg laying
Increase sperm storage

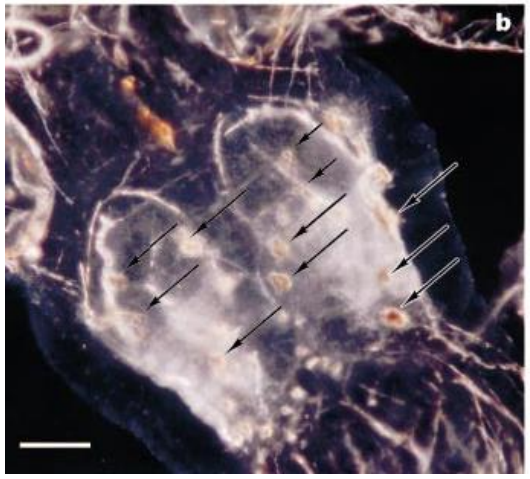
* Reviewed in Koene 2012; Photos: Rönn, Siva-Jothy, Jaenike, Arnqvist, Han



Seed beetle/Bean weevil
Callosobruchus maculatus

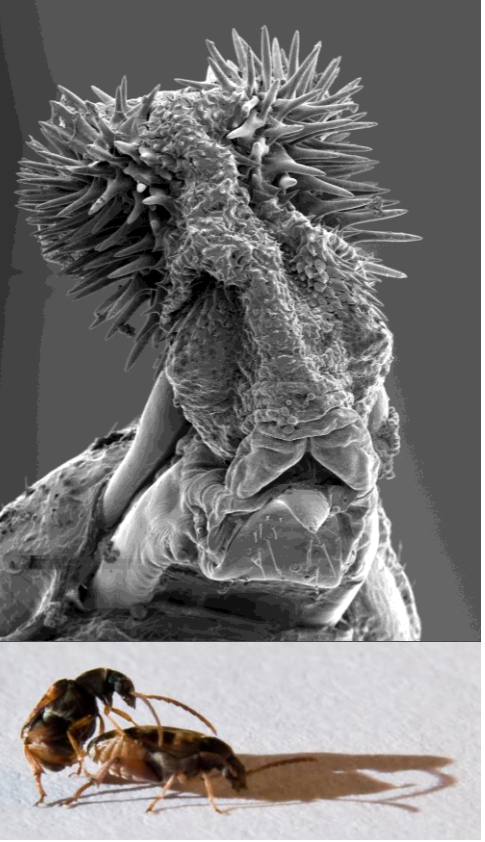
Damage caused to female by male seed beetle



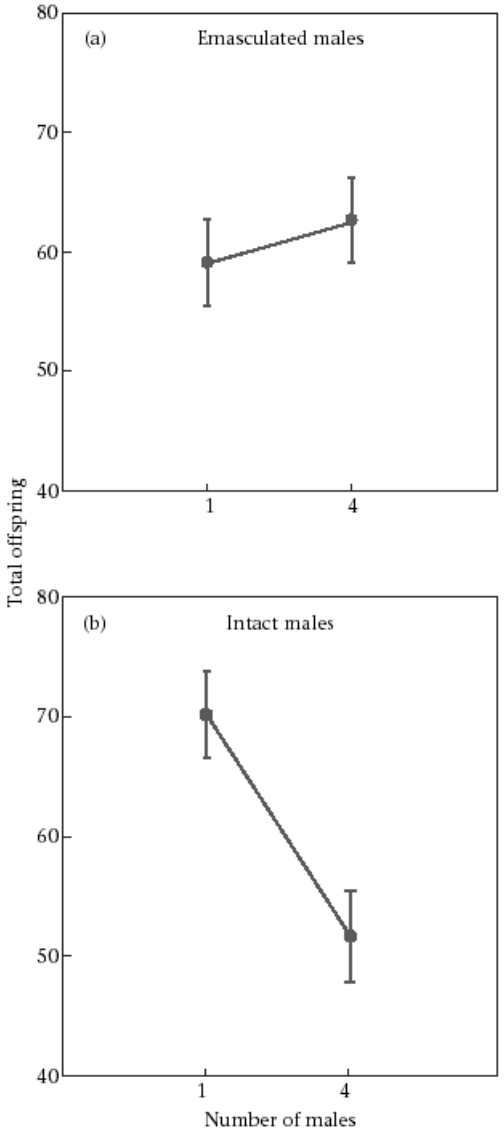


Crudgington & Siva-Jothy 2000

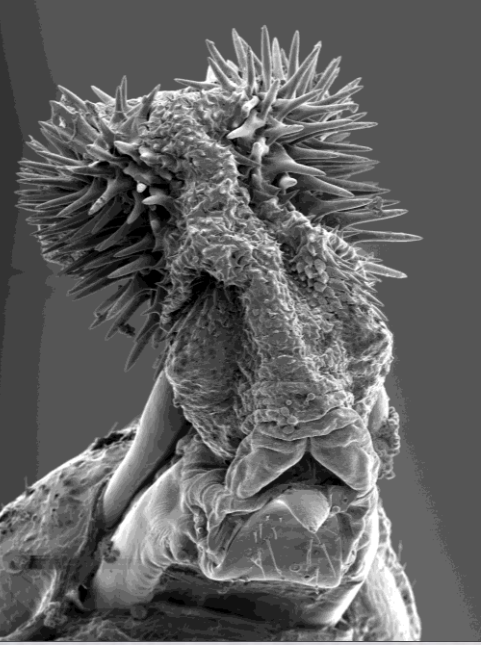
Damage caused by male reduces female fitness



Seed beetle/Bean weevil
Callosobruchus maculatus

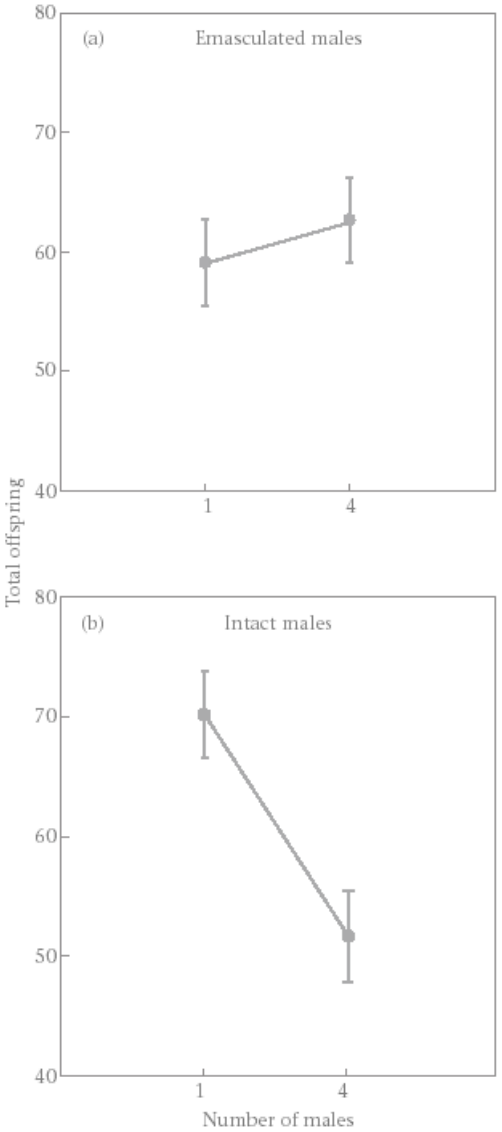


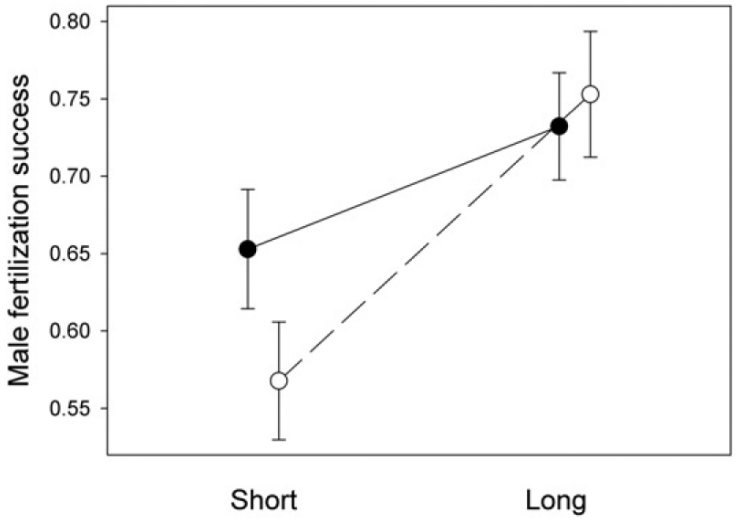
Den Hollander & Gwynne 2010

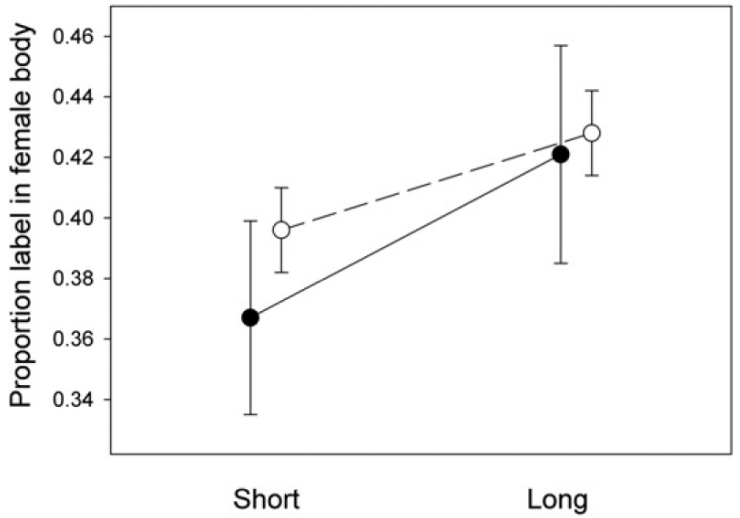


Seed beetle/Bean weevil
Callosobruchus maculatus

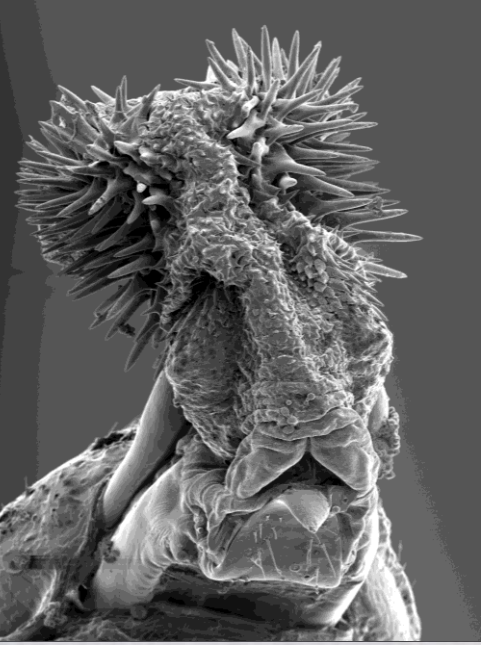
Damage caused by male
reduces female fitness & increases male fitness







Hotzy et al. 2012
Den Hollander & Gwynne 2010



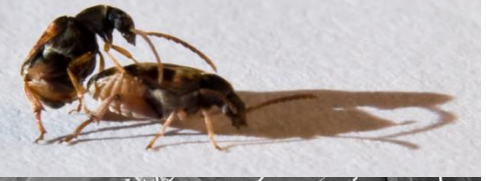
Competition for fertilisation

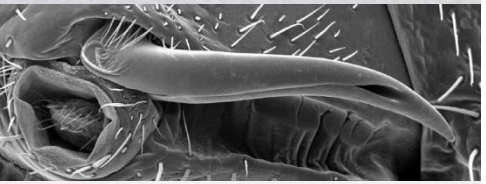
Male
Costly ejaculates,
sperm digestion,
sperm storage

Adaptations to increase
fertilisation chances

Sexual conflict with
Female

Counter-
adaptations





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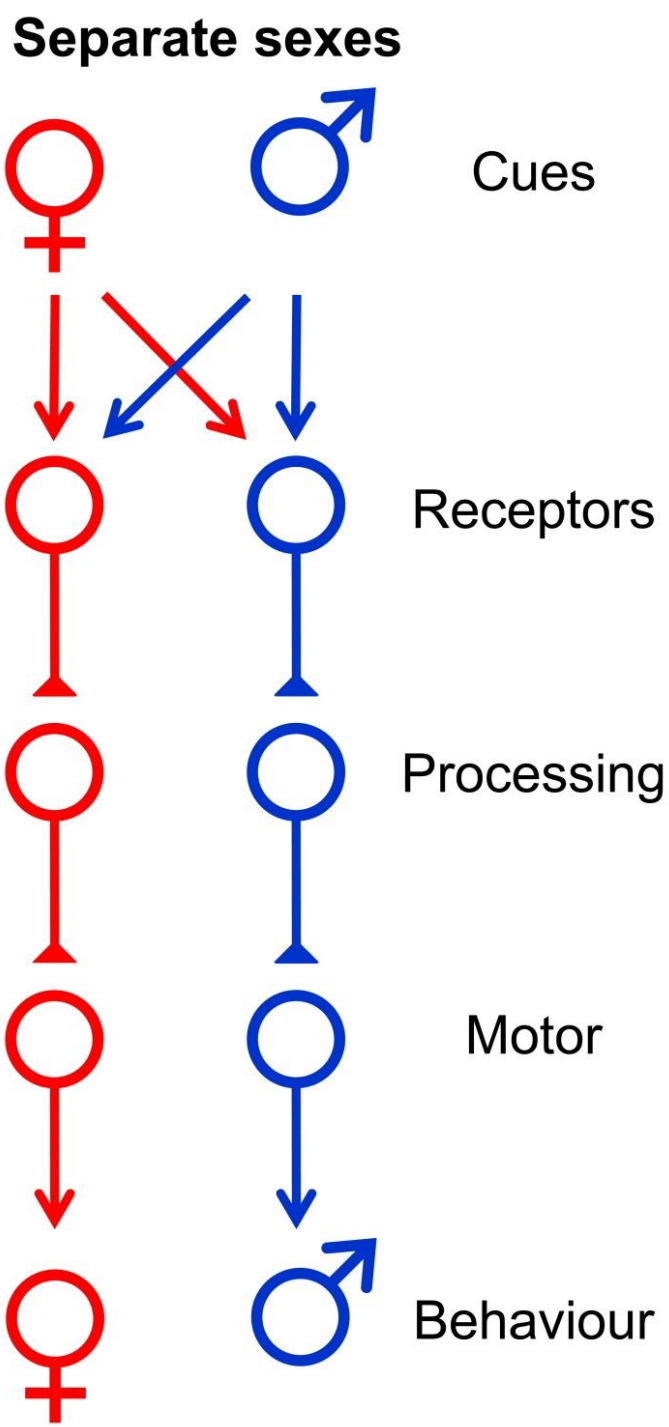
Rönn, Siva-Jothy, Jaenike, Arnqvist, Han

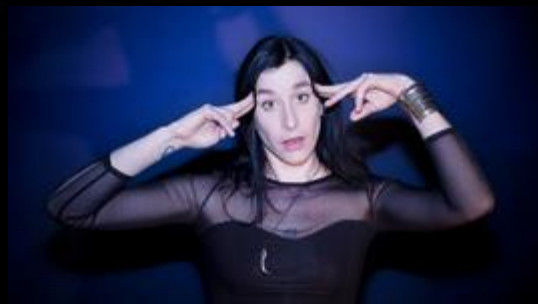

Separate sexes
Cues
Receptors
Processing
Motor
Behaviour

Sex
is
ambiguous

VERANDER
SEX

Sex
is
ambiguous

GESLACHT!



A maned lioness in Botswana’s Okavango Delta
© Deon De Villiers

Panthera leo © Jamie Thom

Reversed sex roles

Hippocampus erectus
© George Grall

Gulf pipefish
Syngnathus scovelli
© Kimberly Paczolt

Sex change

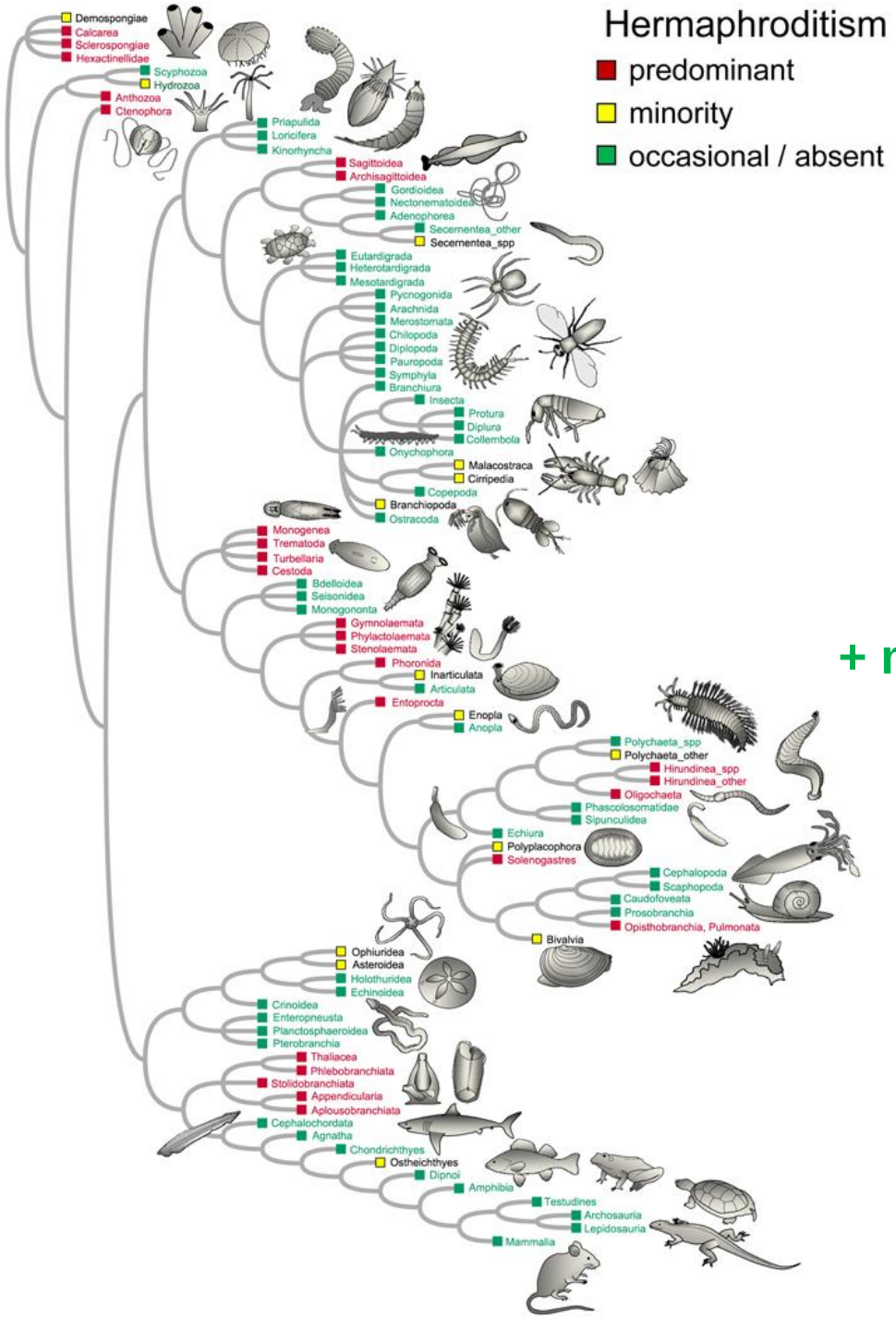
Kobudai
Semicossyphus reticulatus
© Tony Wu

Amphiprion ocellaris
© Tim Lafferty

Gamete exchange

Black hamlet
Hypoplectrus nigricans

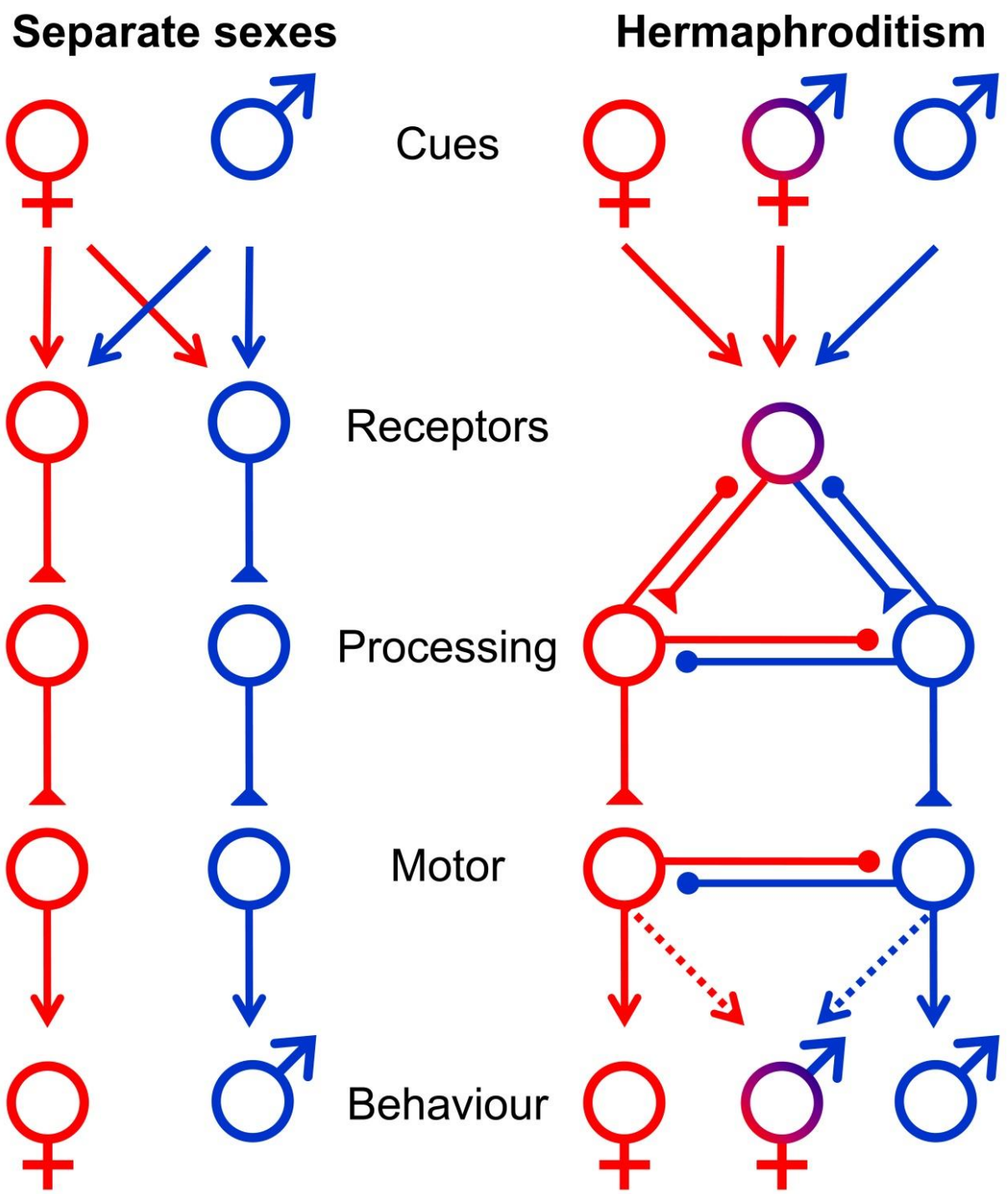
Hermaphrodites are everywhere!



+ most plants

Hermaphrodites are everywhere

…and have control issues



DiCristo & Koene 2017 + in prep.

"No sexual selection 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".

Darwin 1871

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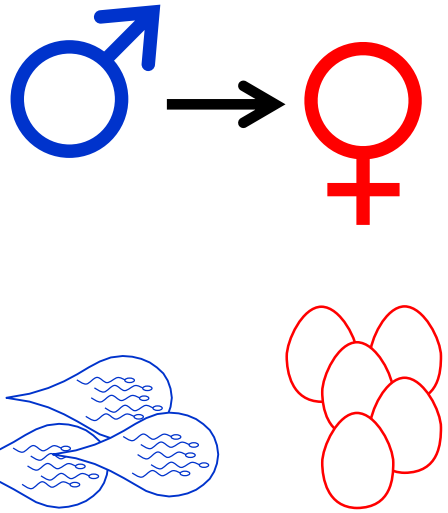
Darwin 1871

Sexual selection, also in simultaneous hermaphrodites

Sexual selection	**Pre-copulatory**	**Post-copulatory**
Intrasexual selection	Male-male competition	Sperm competition
Intersexual selection	Mate choice	Cryptic female choice

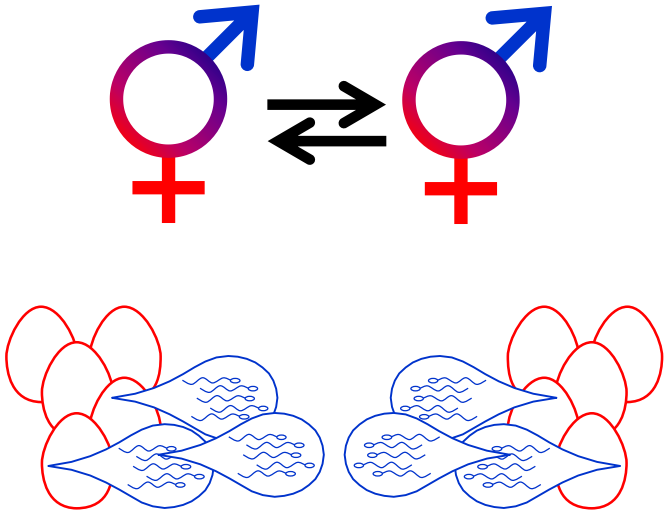
Darwin 1871, Parker 1970

Separate sexes



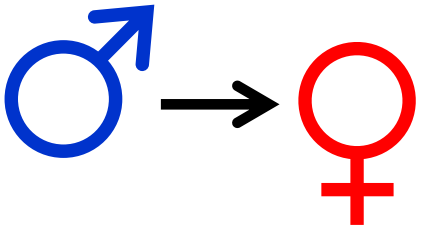
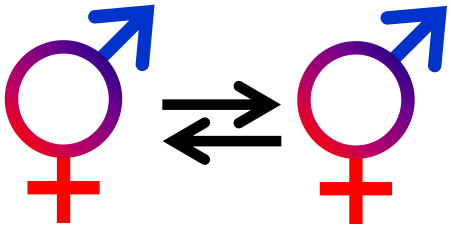
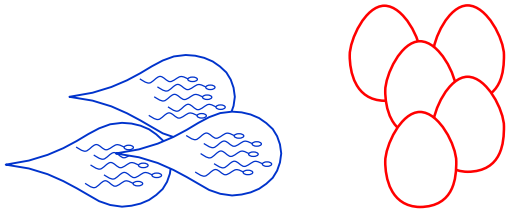
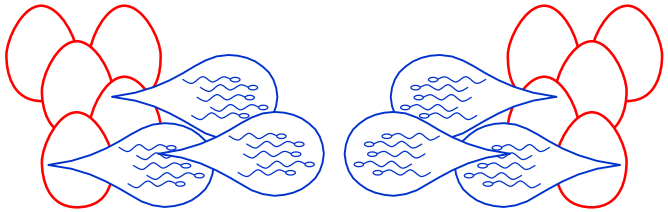
Sperm or eggs produced

Hermaphroditism



Sperm and eggs produced

Does this cause fundamental differences in sexual selection?

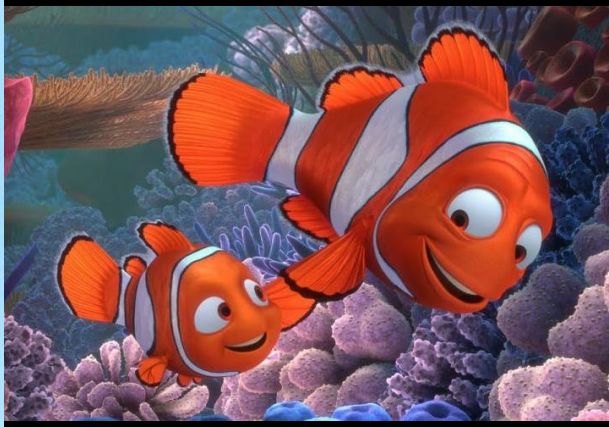
Separate sexes	fundamental differences	Hermaphroditism
		
		
Sperm <u>or</u> eggs produced	1	Sperm <u>and</u> eggs produced
Unidirectional (male donates, female receives)	2	Bidirectional (sperm donor is also recipient)
Female physiology affected	3	Both sexes' physiology affected

Imagine…

Imagine…

Jabba the Hutt (Star Wars)

Gynandromorph, G1 (Zhao et al. 2010)



Marlin (Finding Nemo)

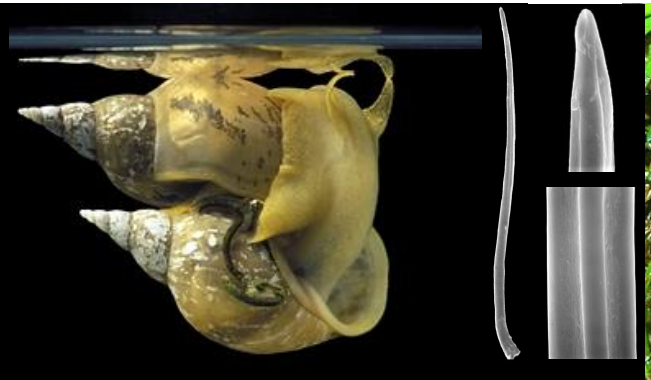
Hermaphroditus (Greek god)

Competition for fertilisation in simultaneous hermaphrodites

Sperm donor
Costly ejaculates,
sperm digestion,
sperm storage

Adaptations to increase
fertilisation chances

Inhibit remating
Influence egg laying
Increase sperm storage
Decrease sperm digestion



Baur 1998
Koene & Chase 1998a,b
Koene et al. 2013
Koene & Ter Maat 2005
Koene et al. 2002, 2005

Bedhomme et al. 2009
Koene 2012

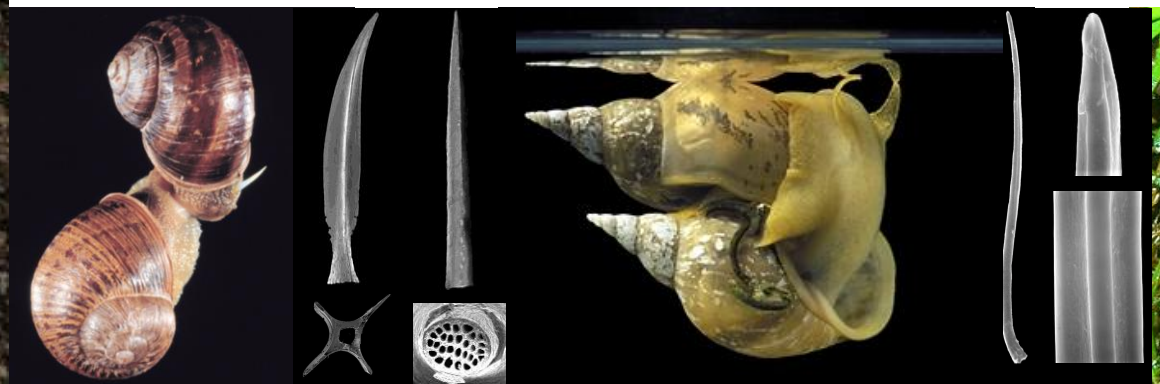
Competition for fertilisation in simultaneous hermaphrodites

Sperm donor
Costly ejaculates,
sperm digestion,
sperm storage

Adaptations to increase
fertilisation chances

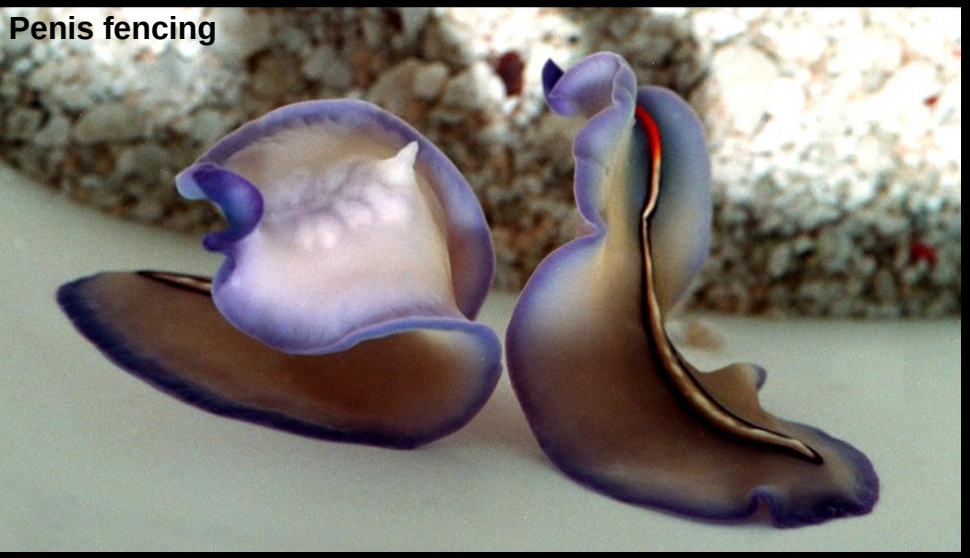
Sexual conflict with
Sperm recipient

Counter-adaptations



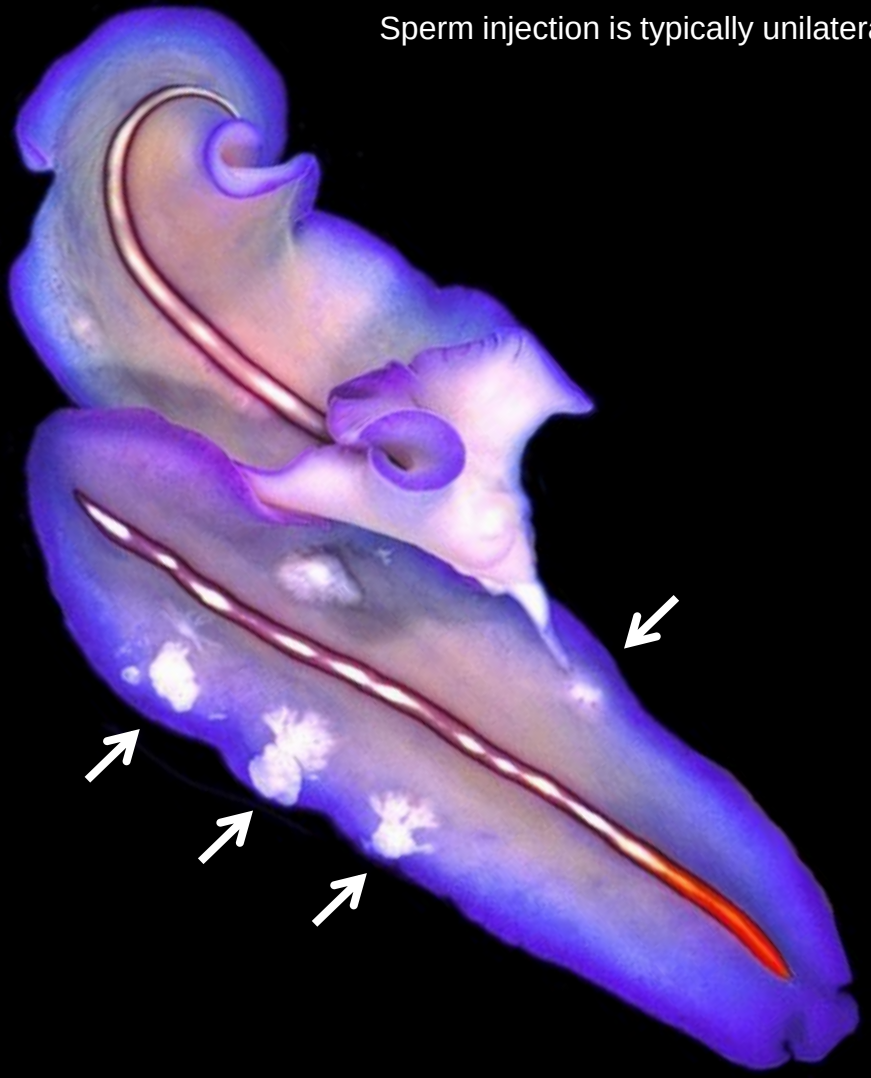
Bedhomme et al. 2009
Koene 2012

Tropical hermaphroditic flatworm (*Pseudoceros bifurcus*)



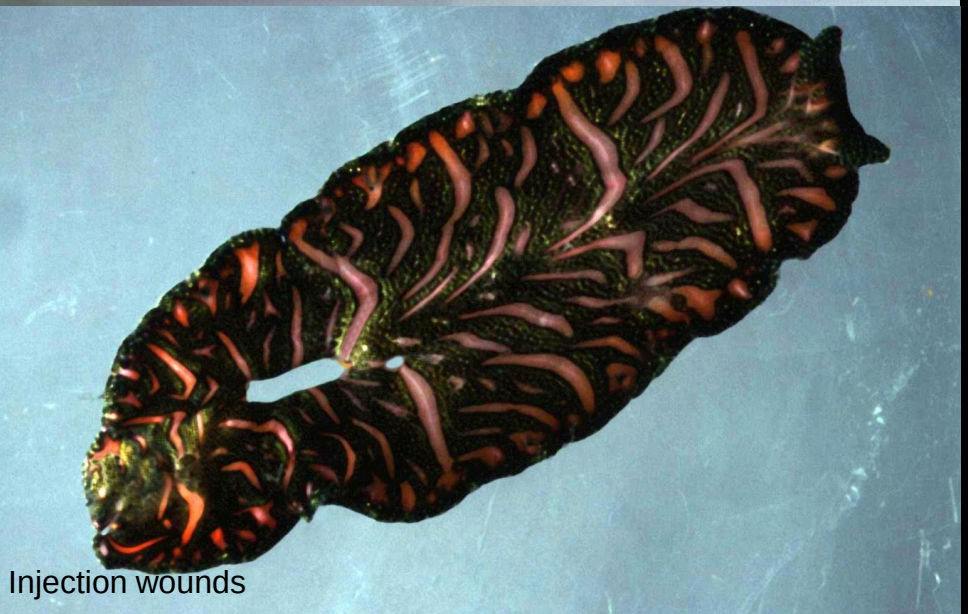
Injection wounds

Sperm injection is typically unilateral



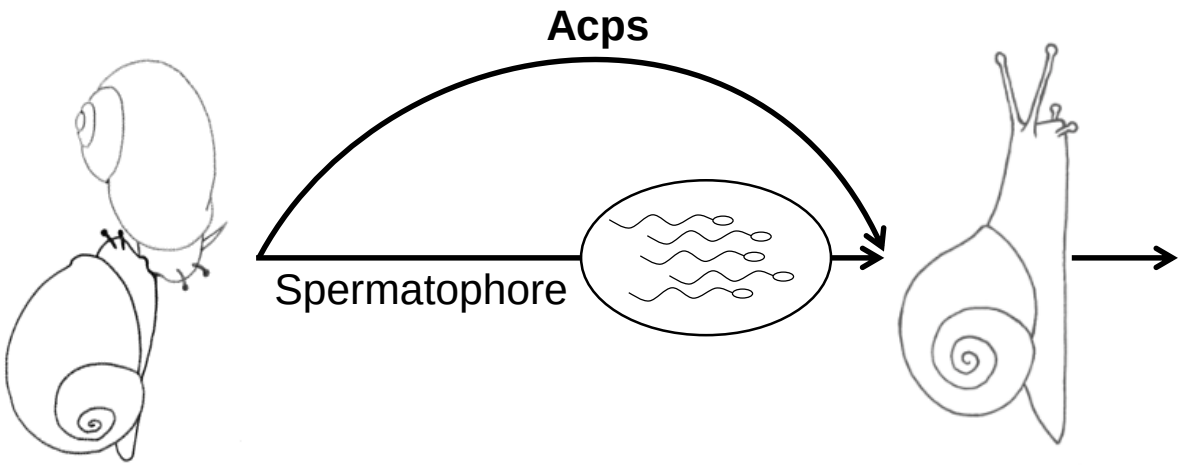
Michiels & Newman 1998

Tropical hermaphroditic flatworm (*Pseudobiceros bedfordi*)

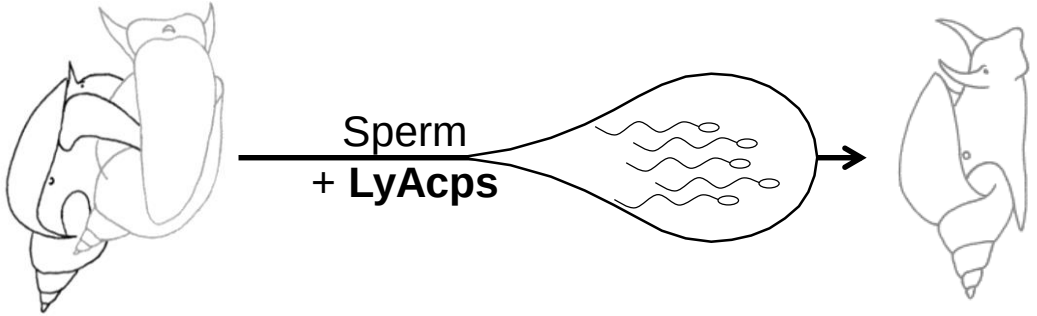


Michiels et al. unpubl., Whitfield 2004

Sperm transfer is accompanied by *accessory gland proteins*



More sperm storage
More paternity
Less remating
Less sperm digestion: **LDA**
(Love Dart Allohormone)



Less sperm transfer: **LyAcp5/8b**
Less paternity
Less egg laying: **LyAcp10**/ovipostatin
(Acp = Accessory gland protein)

Koene et al. 2010, Nakadera et al. 2014, Stewart et al. 2016, Zizzari et al. 2014, Jékely et al. 2018

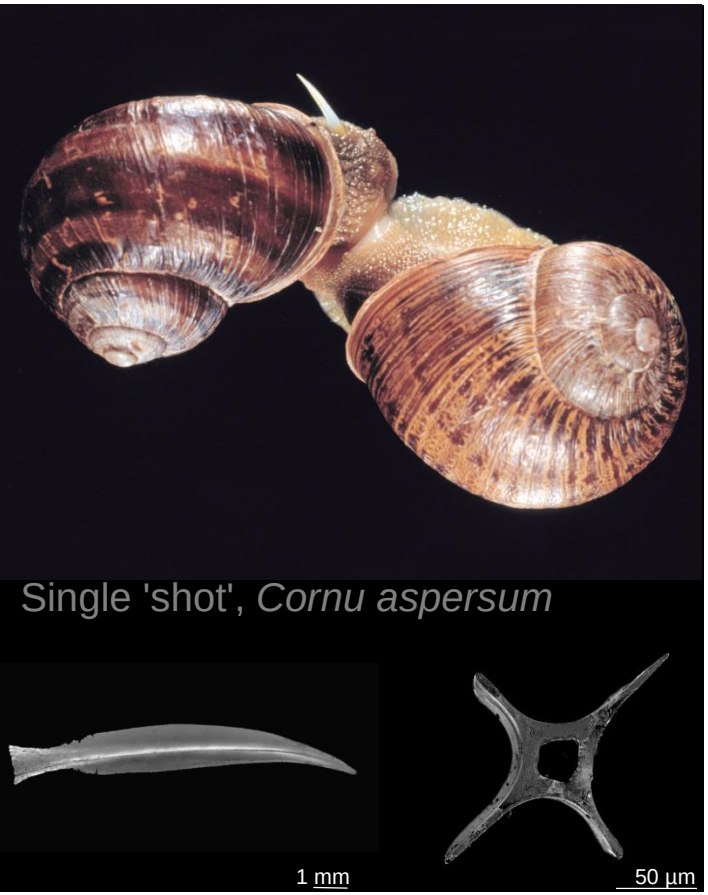
'Shooting' of love darts in land snails

Gilbert White "The Natural History of Selborne" 1981

'Shooting' of love darts in land snails

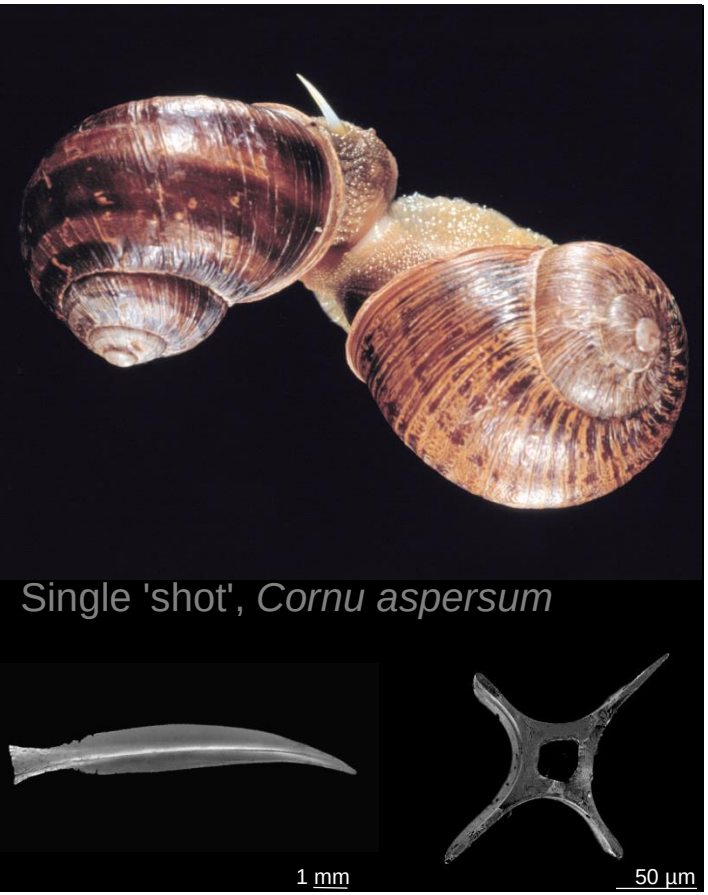
Isabella Rossellini “Green Porn”

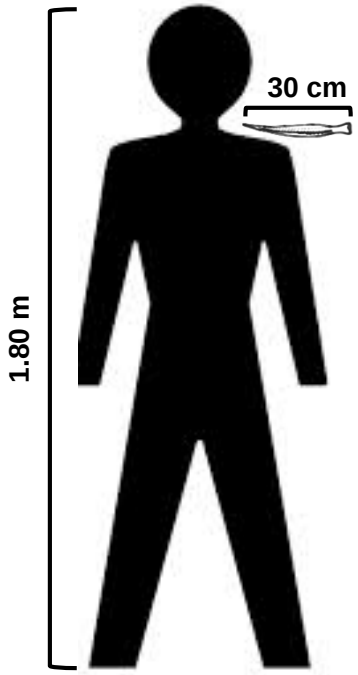
Injection of accessory gland products with a love dart in land snails



Koene & Chase 1998a,b

Injection of accessory gland products with a love dart in land snails

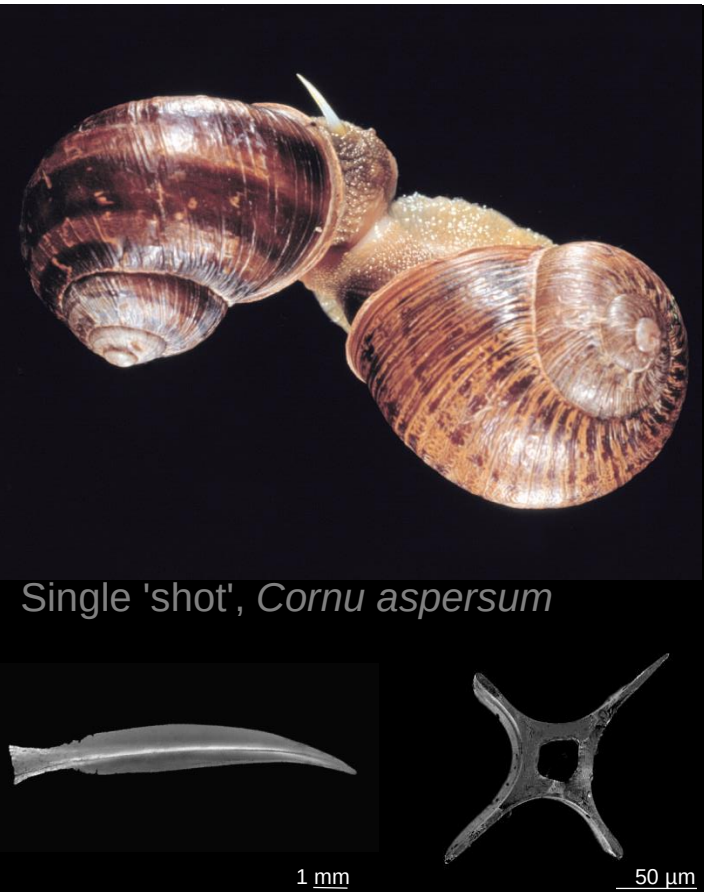




Koene & Chase 1998a,b

Koene & Chiba 2006

Injection of accessory gland products with a love dart in land snails



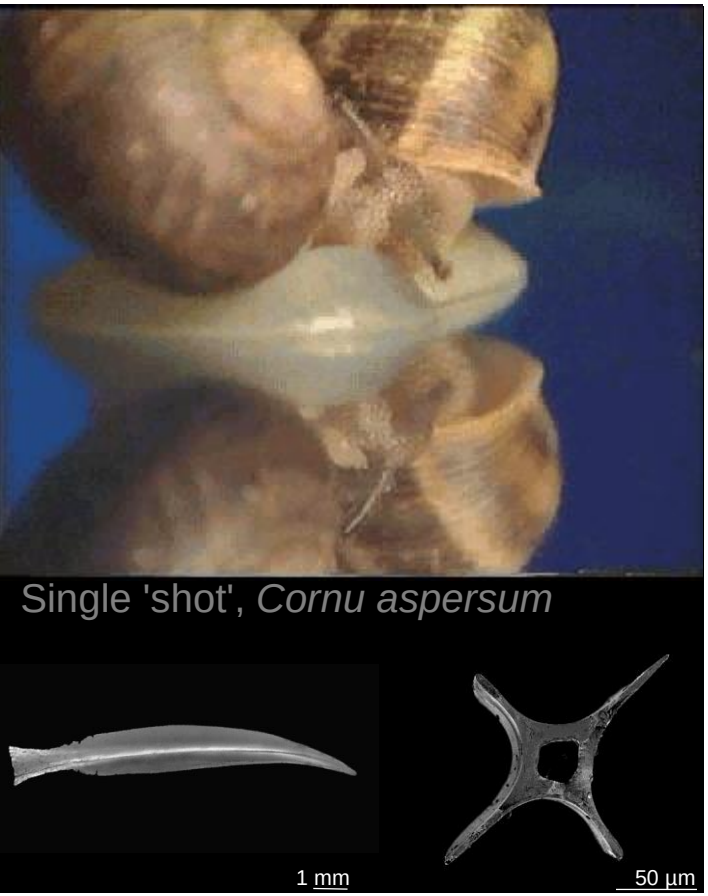
Both individuals shoot a dart into their partner

Dart shooting occurs before exchange of spermatophores

Koene & Chase 1998a,b

Koene & Chiba 2006

Injection of accessory gland products with a love dart in land snails



Both individuals shoot a dart into their partner

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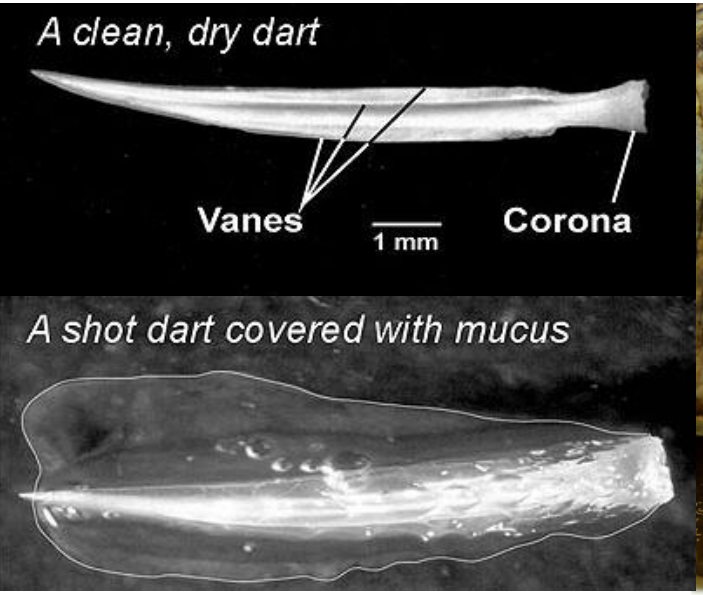
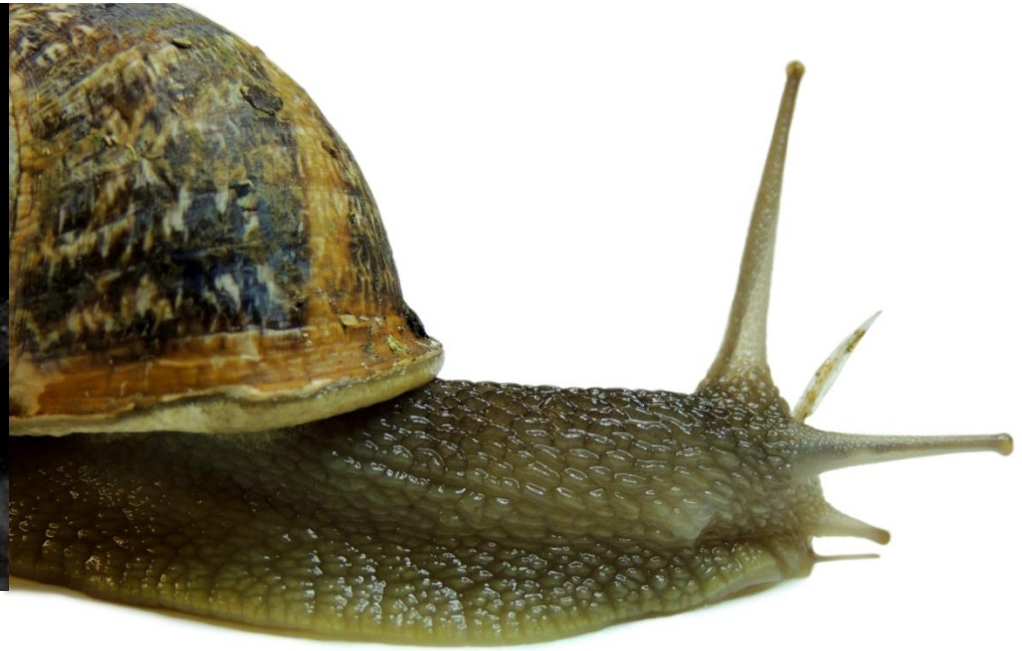
Koene & Chase 1998a,b

Koene & Chiba 2006

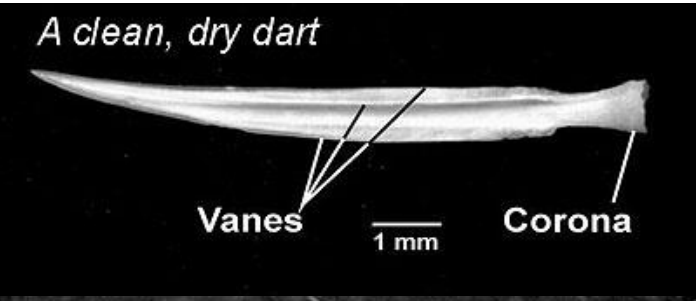
Love dart injection reduces sperm digestion and increases paternity

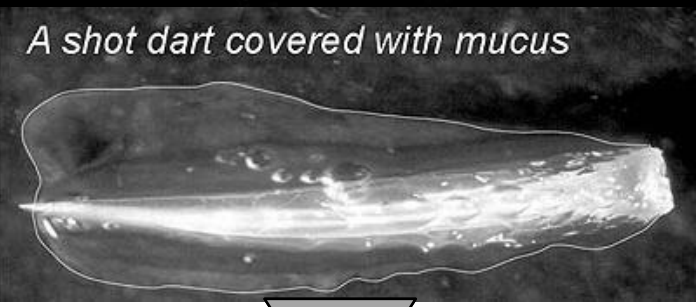


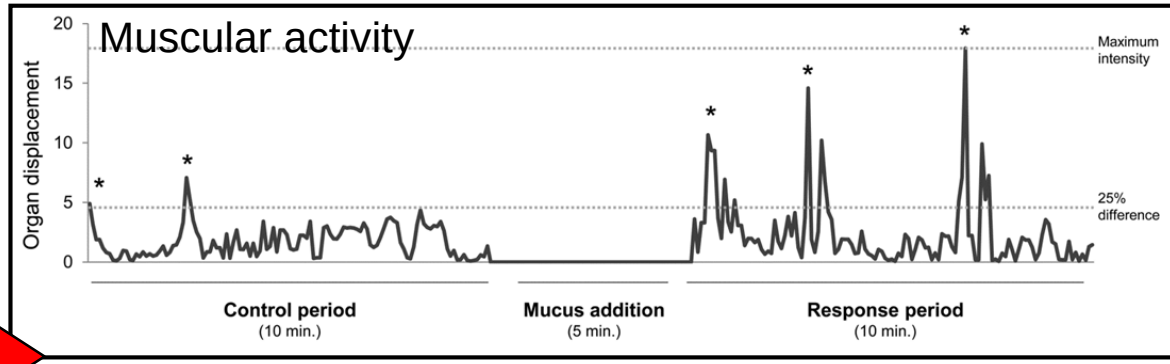


Reviewed in Lodi & Koene 2016a
Photos: R. Chase, M. Lodi

Love dart injection reduces sperm digestion and increases paternity

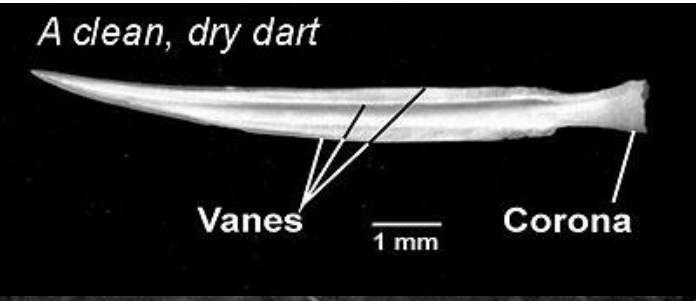


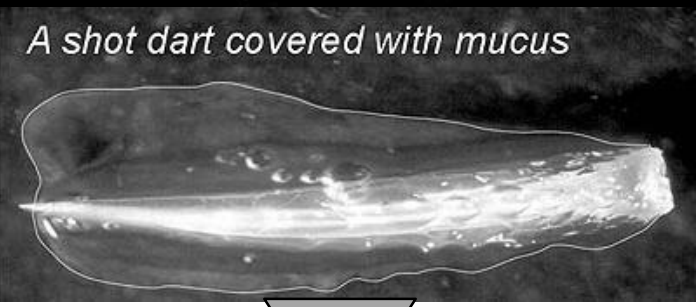




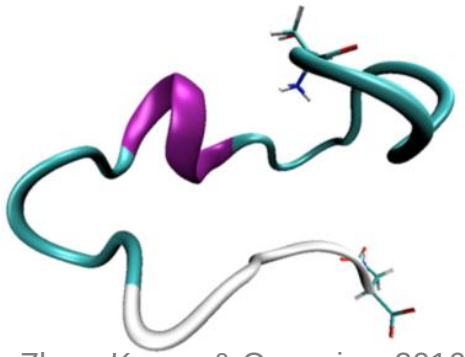
Koene & Chase 1998, Lodi & Koene 2016b, 2017

Love dart injection reduces sperm digestion and increases paternity

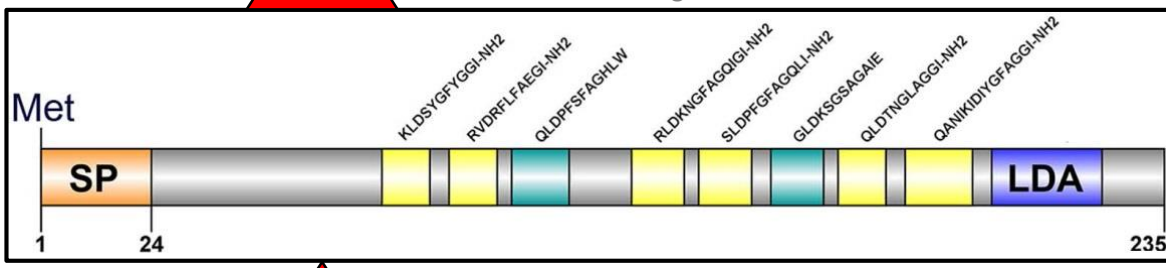


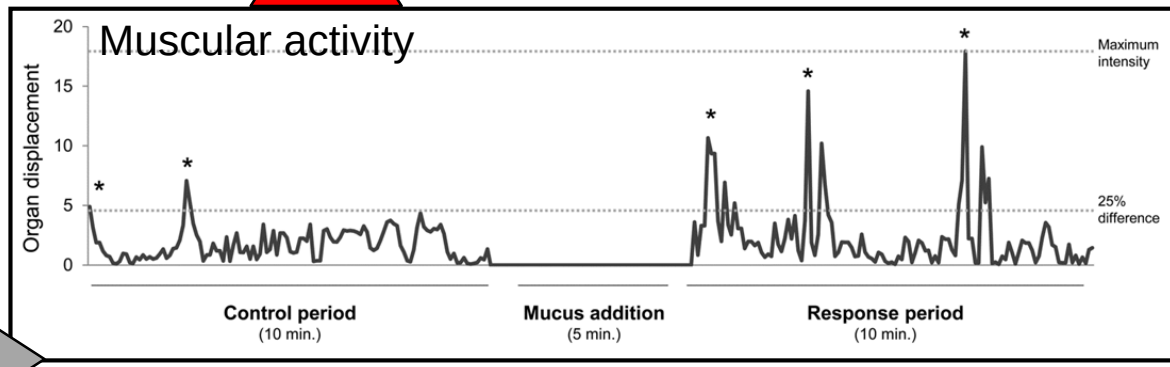


Love dart allohormone (LDA)
=
Buccalin-like peptide
(molluscan neuromodulator)

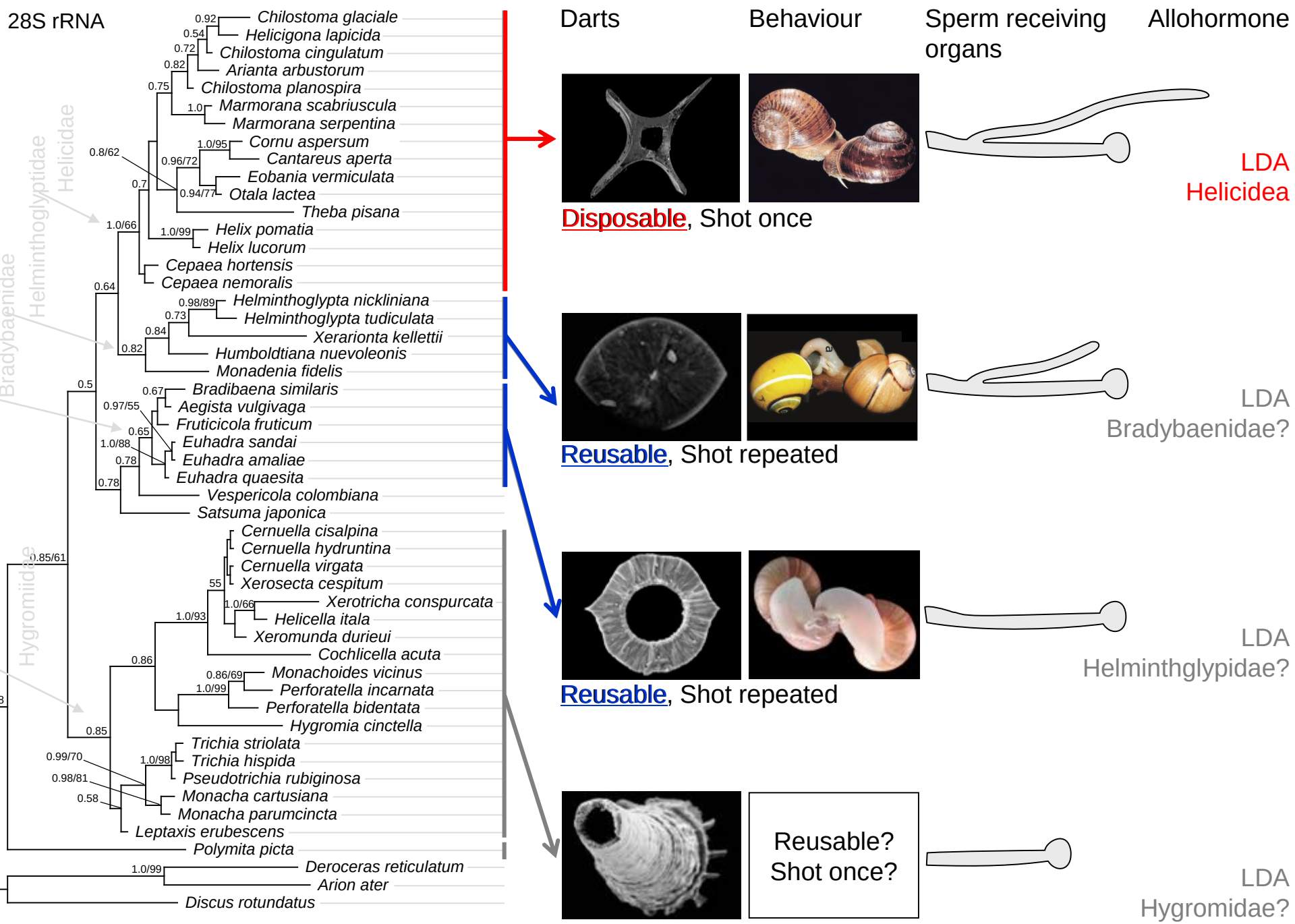


Stewart, Wang, Zhao, Koene & Cummins, 2016





Koene & Chase 1998, Lodi & Koene 2016b, 2017



Koene & Schulenburg 2005, Koene & Chiba 2006, Reyes Tur & Koene 2007, Reyes Tur et al. 2015, Lodi & Koene, 2016a

Conclusions, so far

Love dart allohormone is Buccalin-like neuromodulator

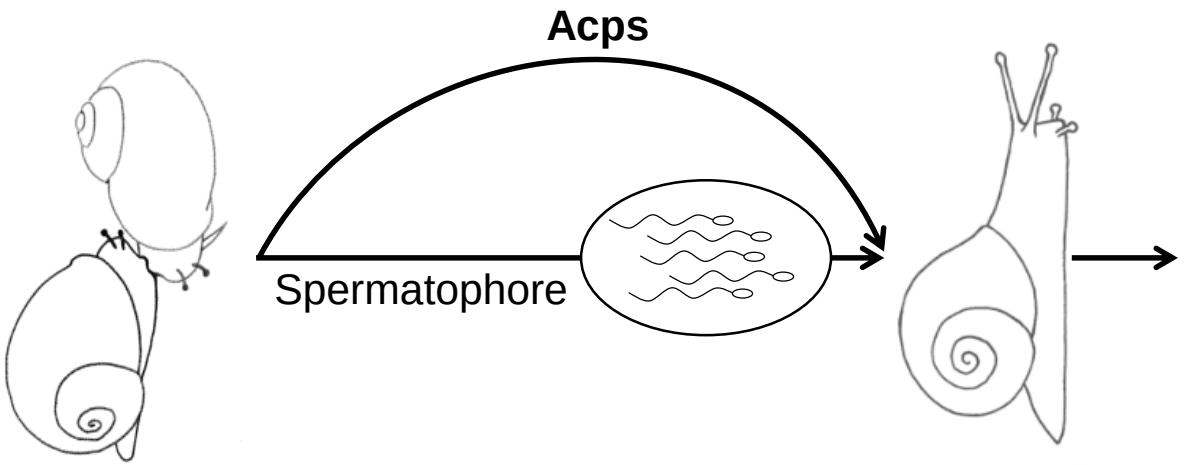
Counter-adaptive co-evolution between male and female within hermaphrodite

To do list: Comparative physiology and paternity effects in related species

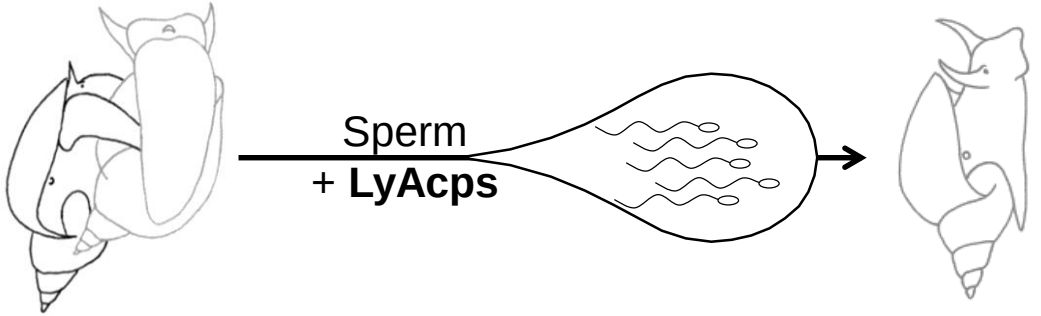
Are there fundamental differences in accessory gland protein function(s)?

Humboldtiana nuevoleonis
(Mollusca: Gastropoda: Humboldtianidae)
Koene & Schulenburg 2005

Sperm transfer is accompanied by *accessory gland proteins*



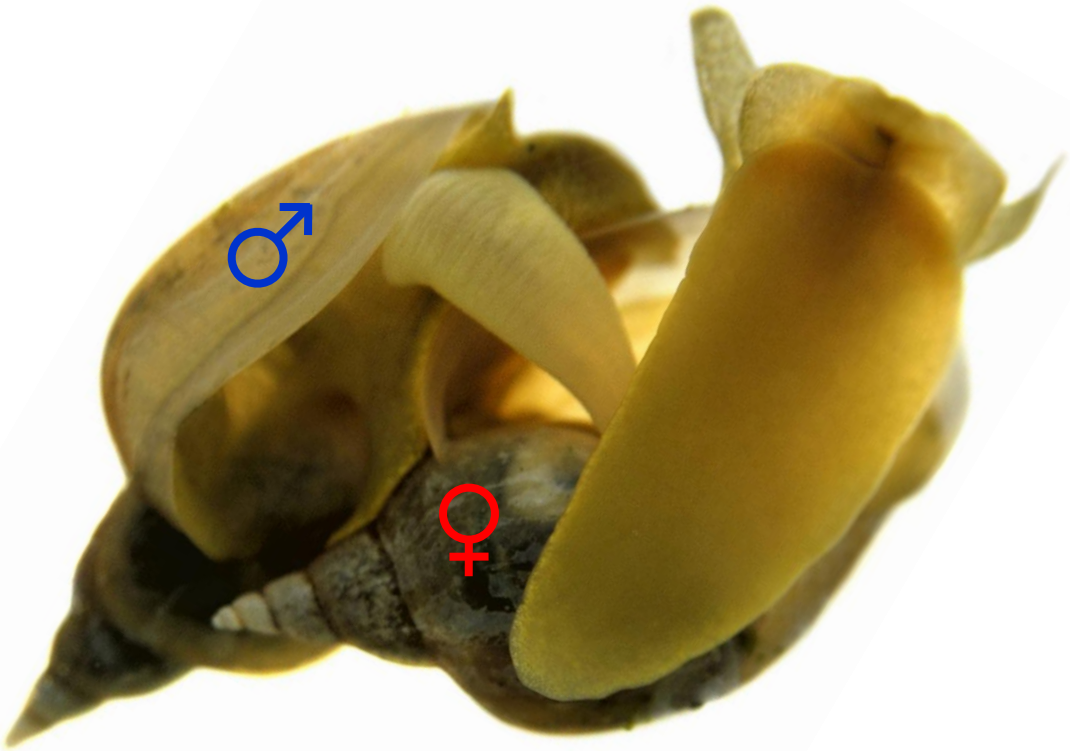
More sperm storage
More paternity
Less remating
Less sperm digestion: **LDA**
(Love Dart Allohormone)



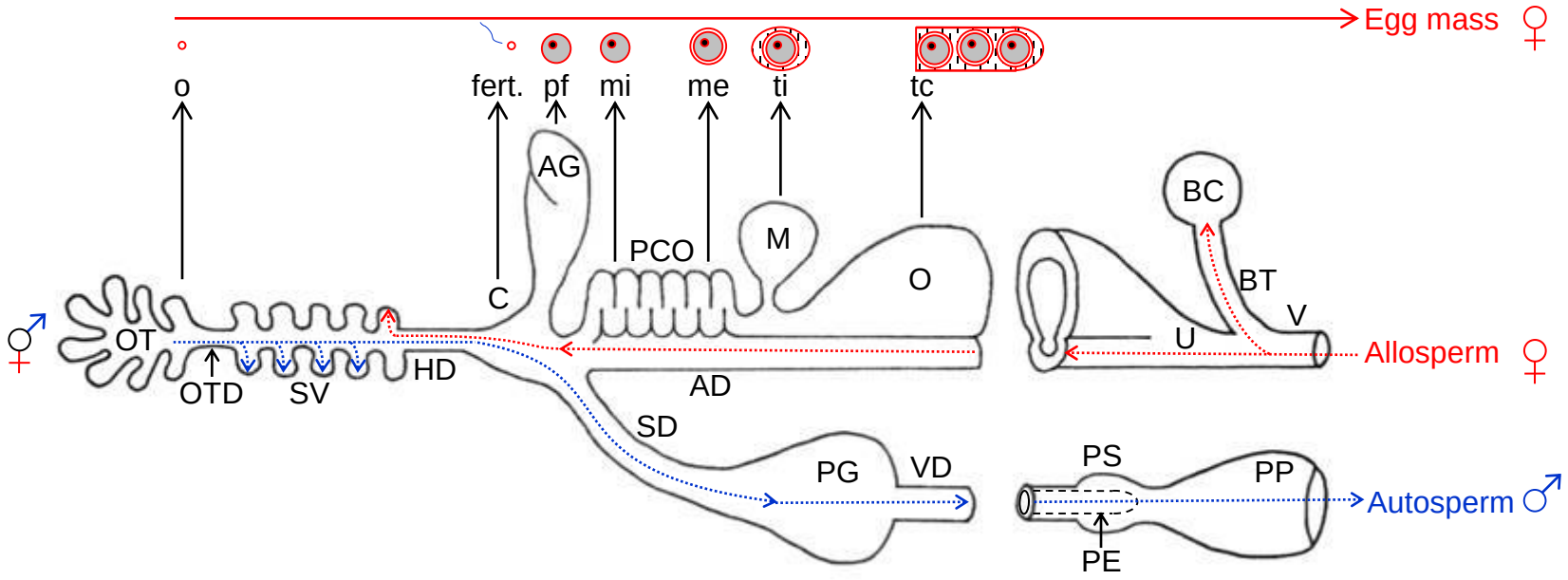
Less sperm transfer: **LyAcp5/8b**
Less paternity
Less egg laying: **LyAcp10**/ovipostatin
(Acp = Accessory gland protein)

Koene et al. 2010, Nakadera et al. 2014, Stewart et al. 2016, Zizzari et al. 2014, Jékely et al. 2018

Great pond snail *Lymnaea stagnalis*

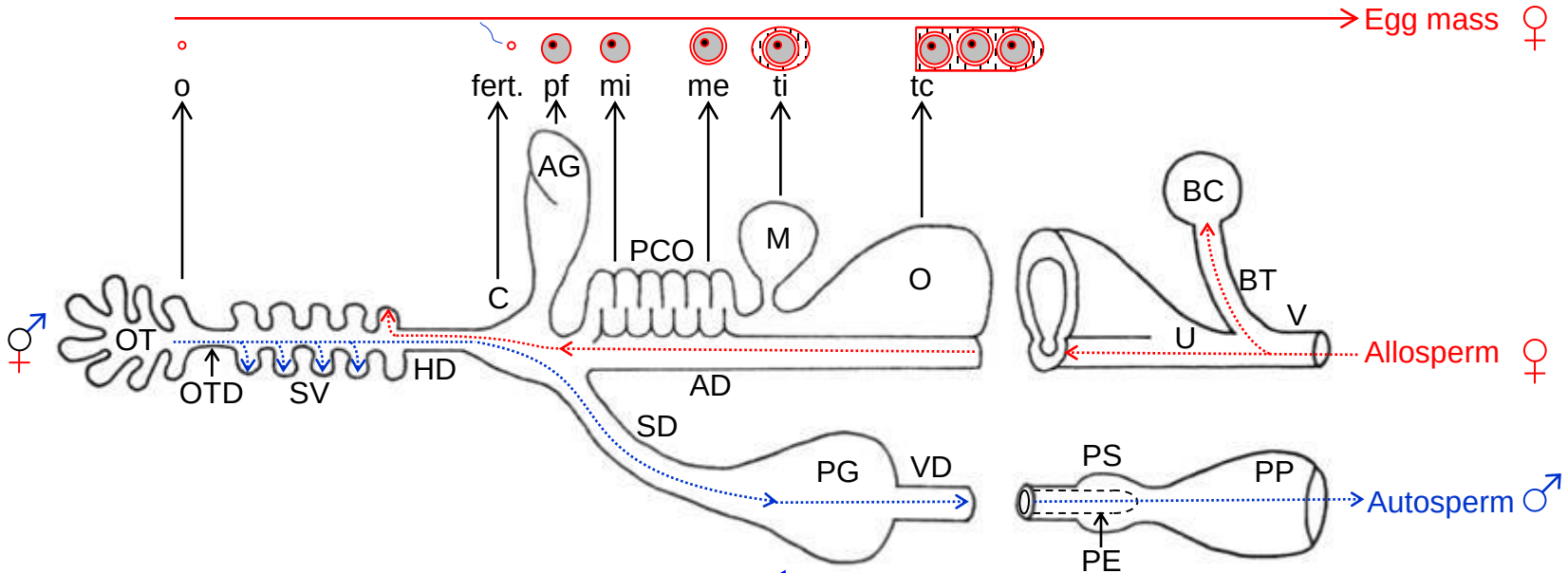


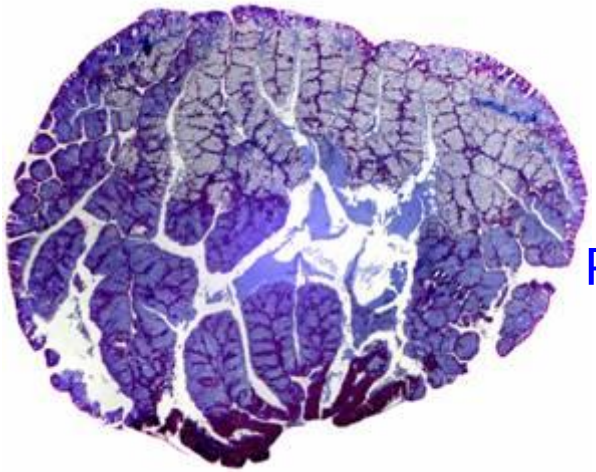
Reproductive system of the great pond snail *Lymnaea stagnalis*



reviewed in Jarne, David, Pointier & Koene 2010

Reproductive system of the great pond snail *Lymnaea stagnalis*

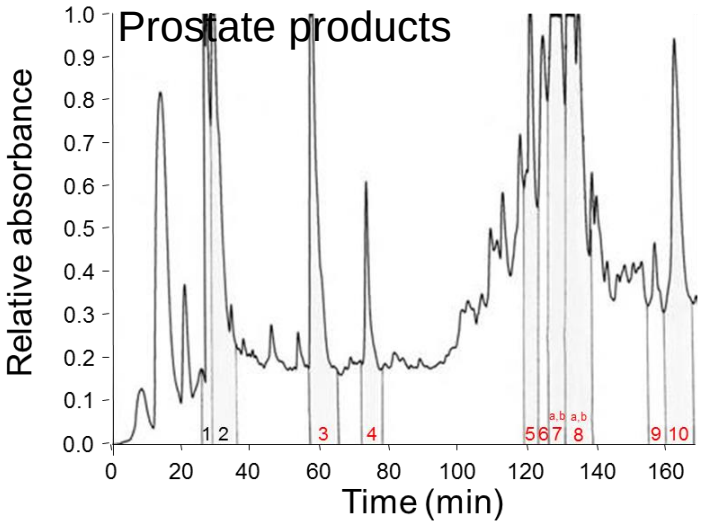


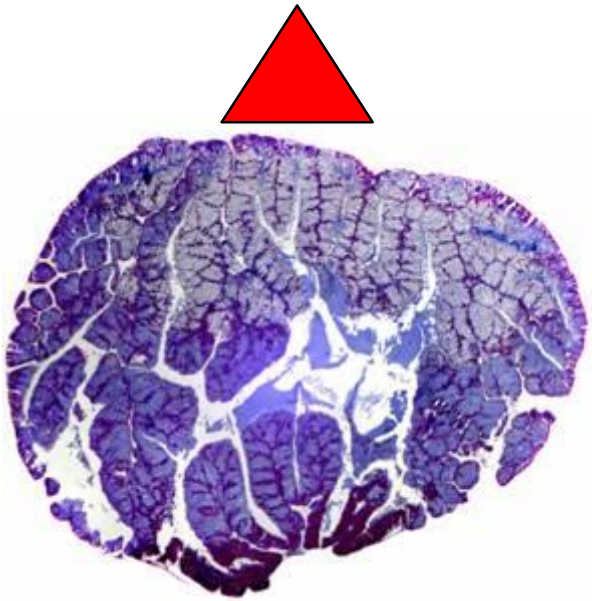


Prostate gland produces accessory gland proteins

reviewed in Jarne, David, Pointier & Koene 2010

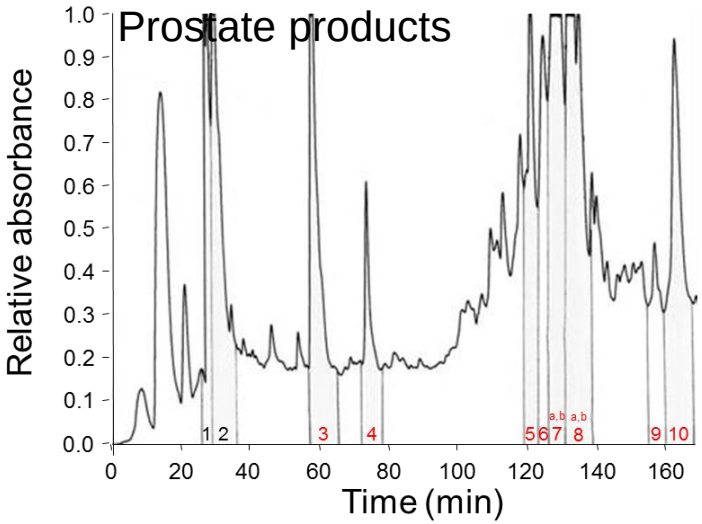
Testing the effects of accessory gland proteins on egg laying

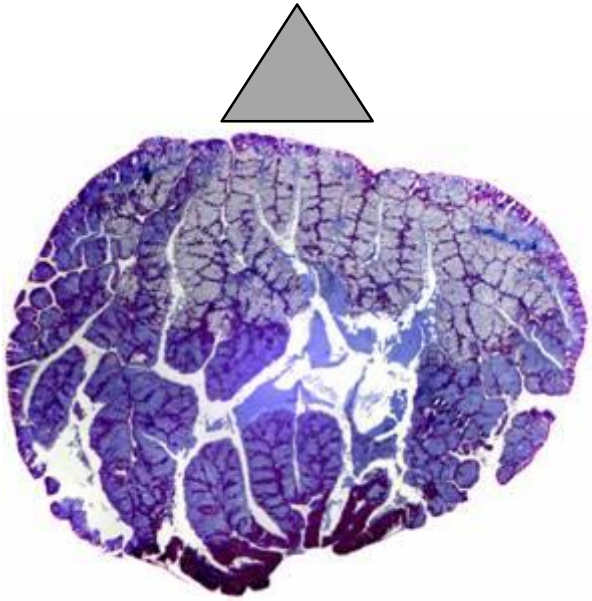




Koene et al. 2009, 2010

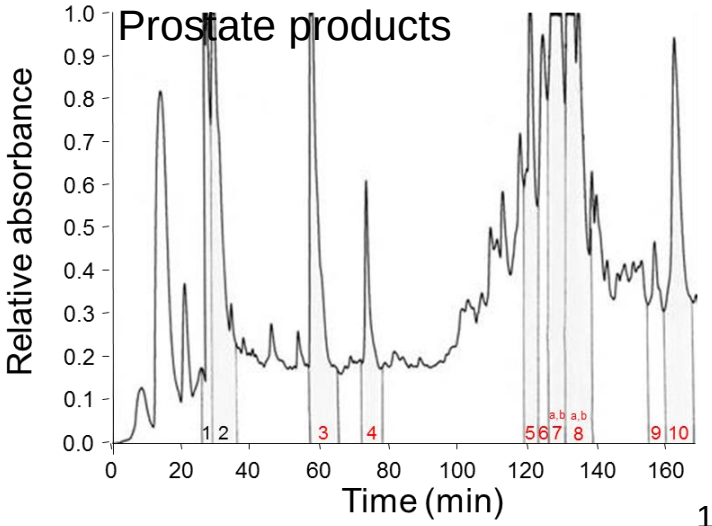
Testing the effects of accessory gland proteins on egg laying

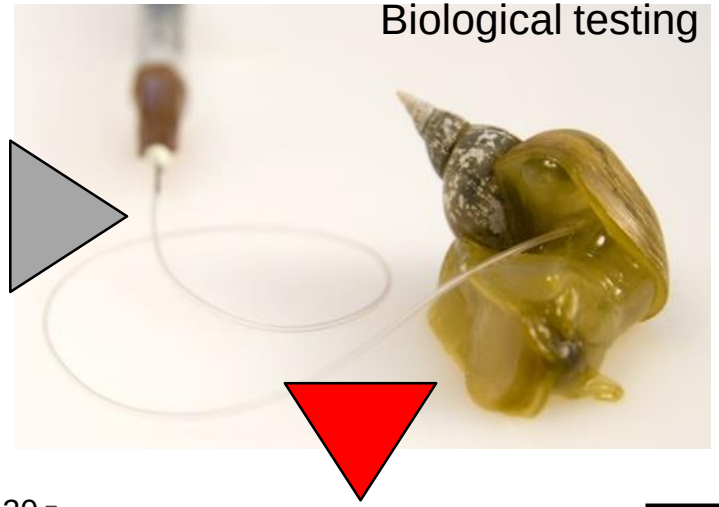


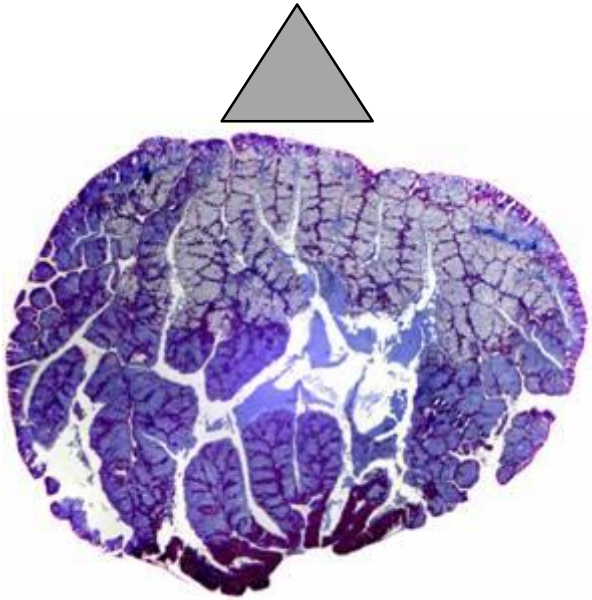


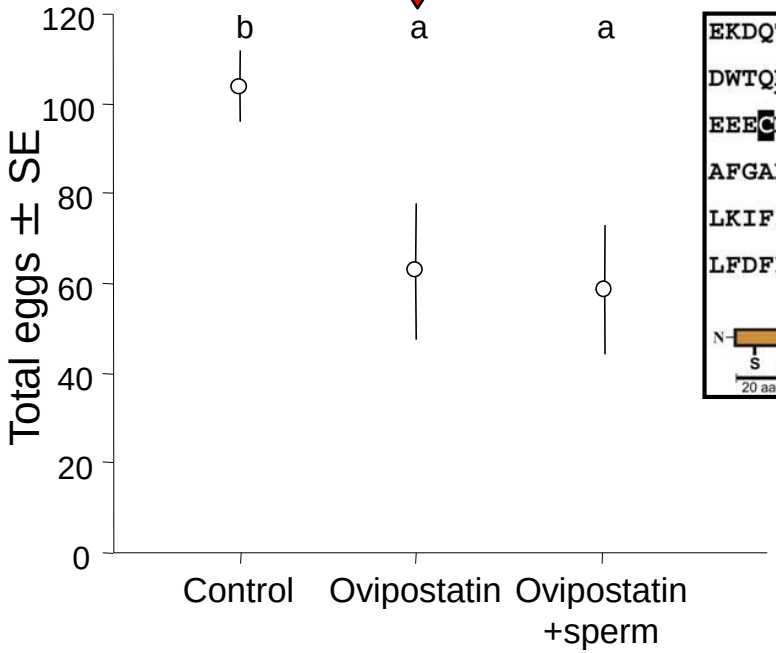
Koene et al. 2009, 2010
Van Iersel et al. 2014 (methods video)

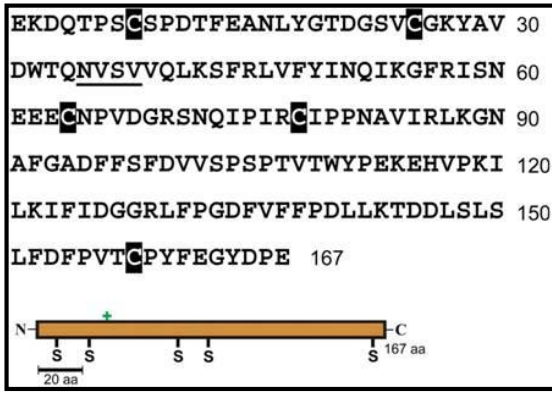
Testing the effects of accessory gland proteins on egg laying







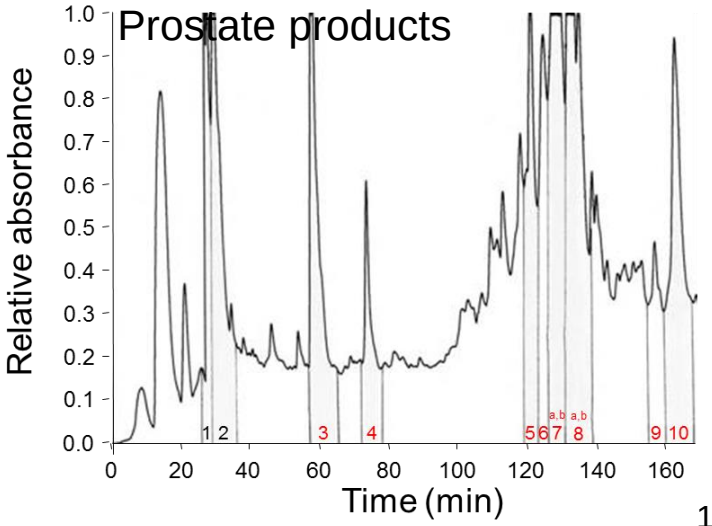


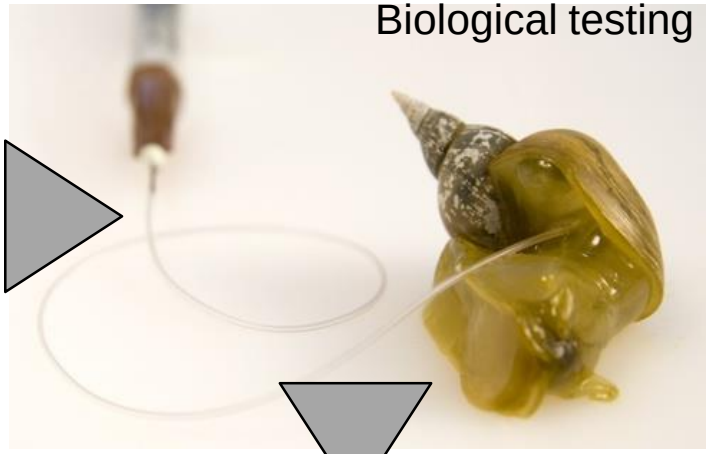


Ovipostatin/LyAcp10
(effect also found in other species)

Swart & Koene, unpubl.
Koene et al. 2009, 2010
Van Iersel et al. 2014

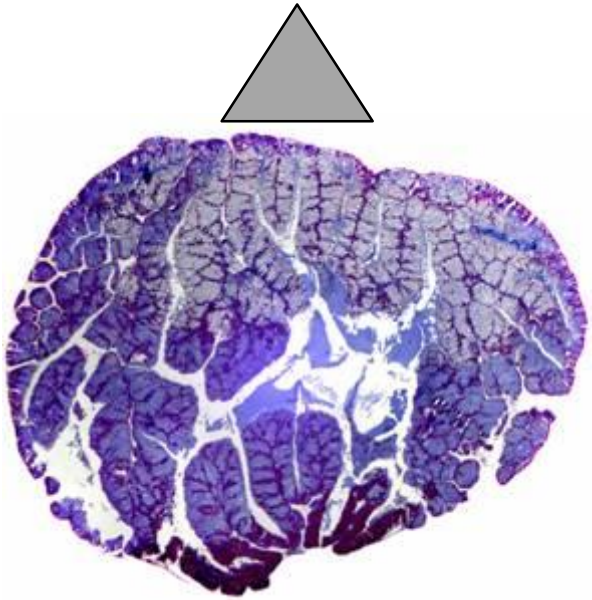
Testing the effects of accessory gland proteins on egg laying

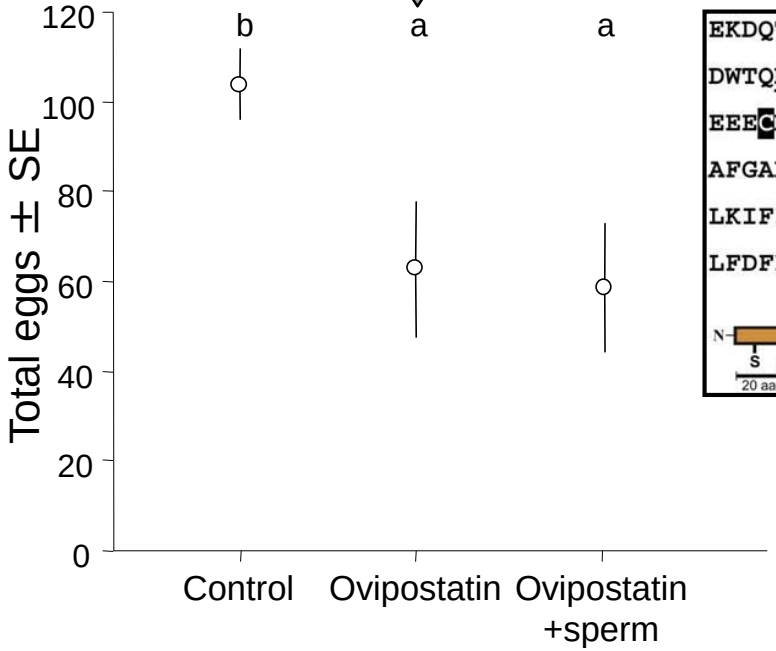


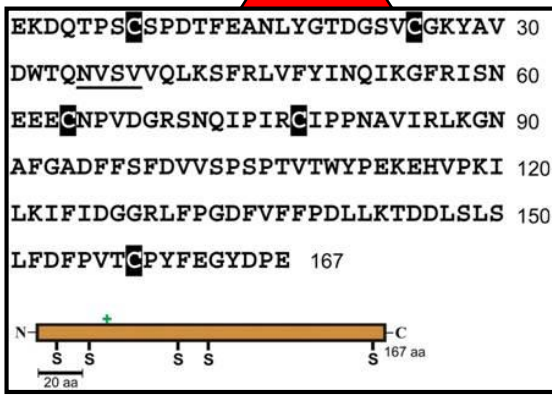


Ovipostatin/Acp10
in other genomes
Adema et al. 2017 + in prep.

ACPs affect egg
investment and
hatchling survival
Koene et al. in prep.

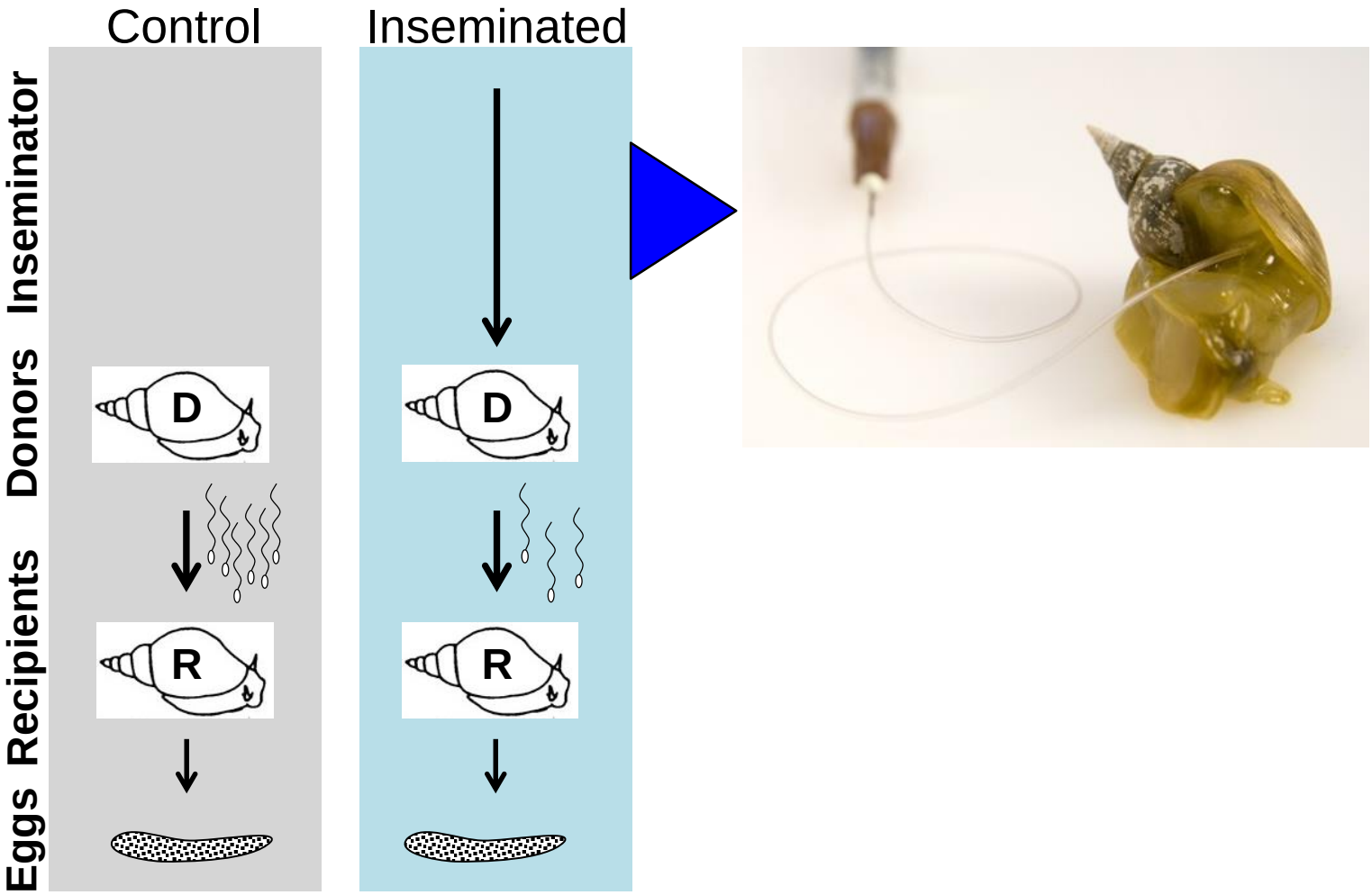






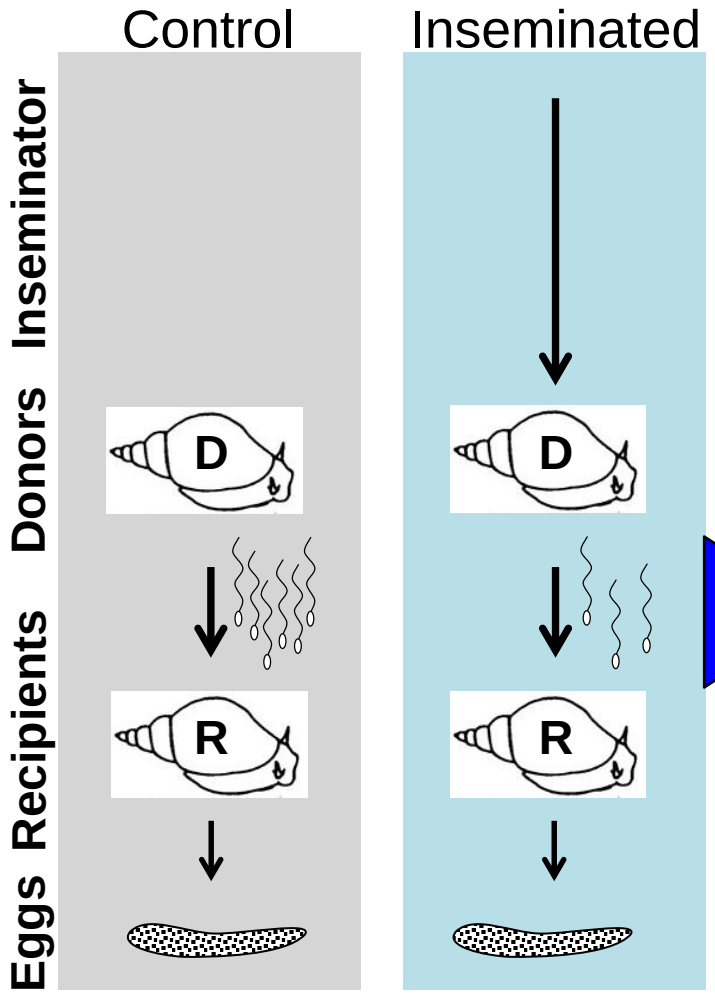
Ovipostatin/LyAcp10
(effect also found
in other species)
Swart & Koene, unpubl.
Koene et al. 2009, 2010
Van Iersel et al. 2014

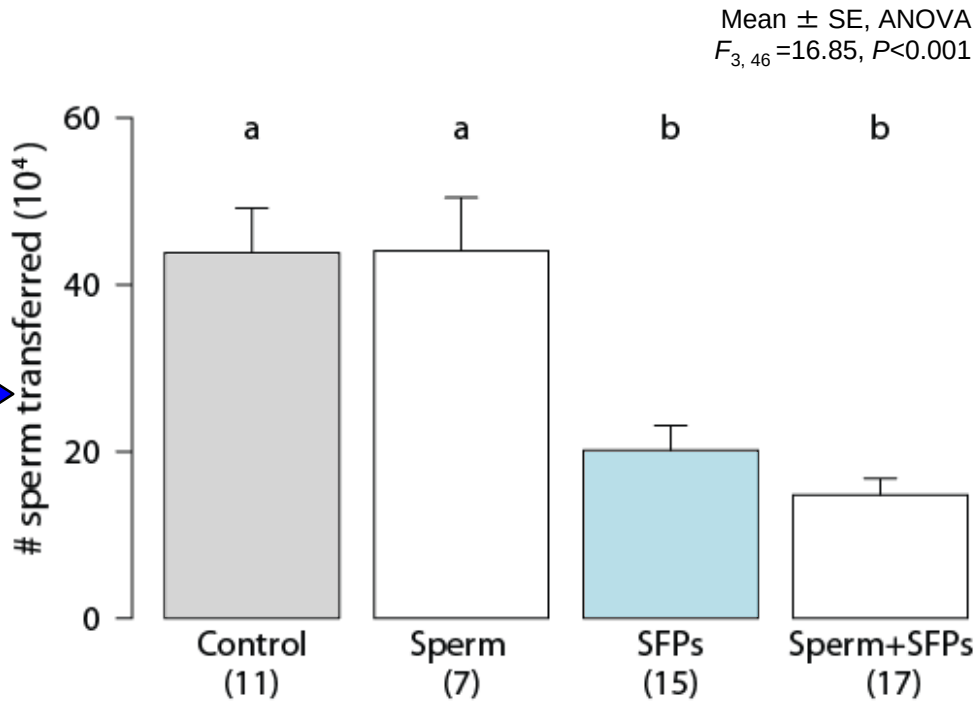
Testing the effects of accessory gland product on male reproduction



Nakadera et al. 2014

Testing the effects of accessory gland product on male reproduction





Recently inseminated snails (SFPs=ACPs) transfer **half** the amount of sperm

LyAcp5 (41aa) **SPADENDPSKEKLNAFGGADKLLEQIDALGPPMKVKPSGSE**

LyAcp8b (55aa) **DEGDDDNTETDDYGTGPITYNFPADDETDXFFVEWRMFXDAXWKRYNQAAGRXLD**...

Nakadera et al. 2014

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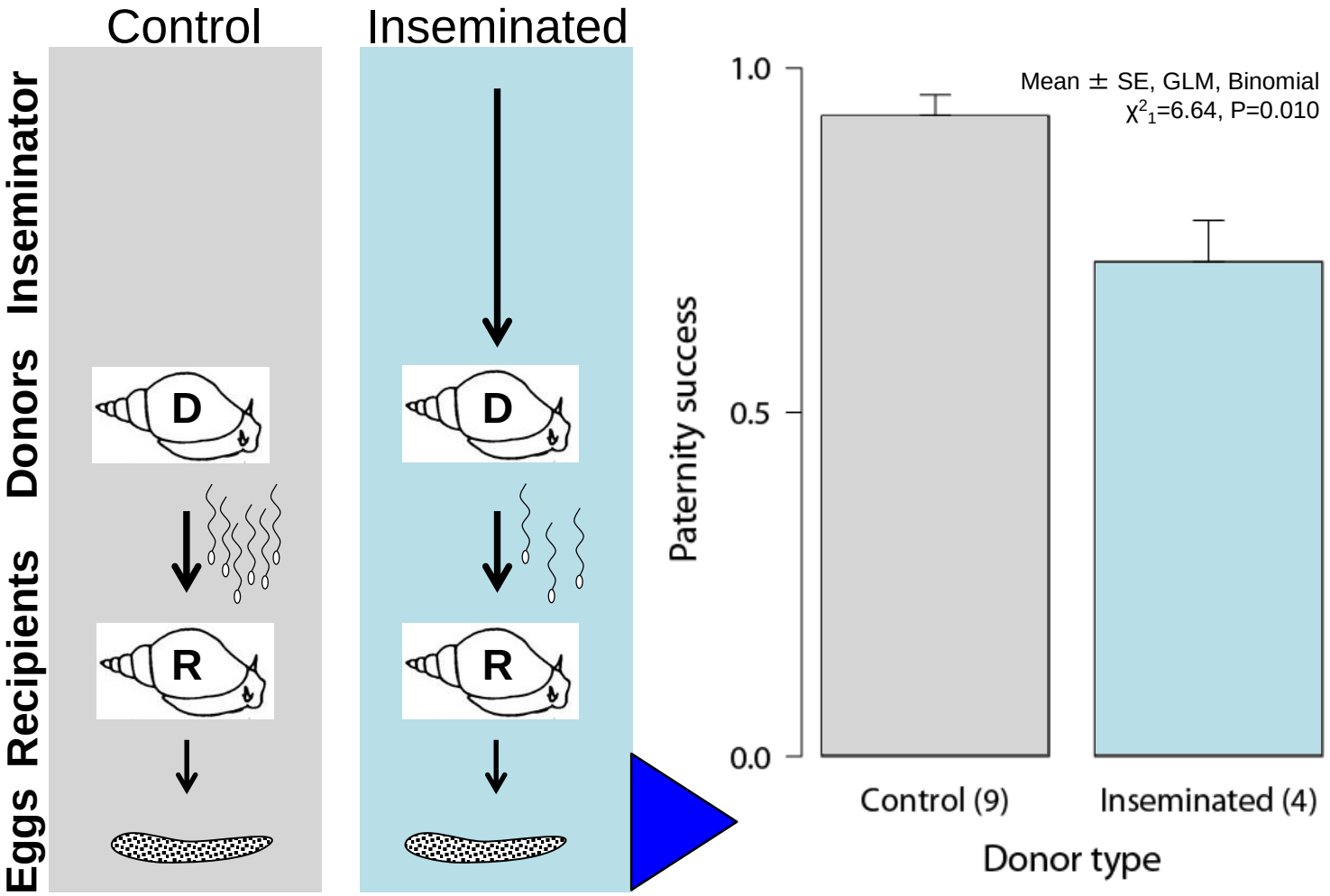

Recently inseminated snails get **less** paternity

Nakadera et al. 2014

In sum, (hermaphroditic) sex is complicated

Love dart allohormone is Buccalin-like neuromodulator

Counter-adaptive co-evolution between male and female within hermaphrodite

Accessory gland proteins influence female **and** male function of mating partner

Fundamental differences between separate sexes and hermaphroditism

KQED Science DeepLook: 'Everything You Never Wanted to Know About Snail Sex

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