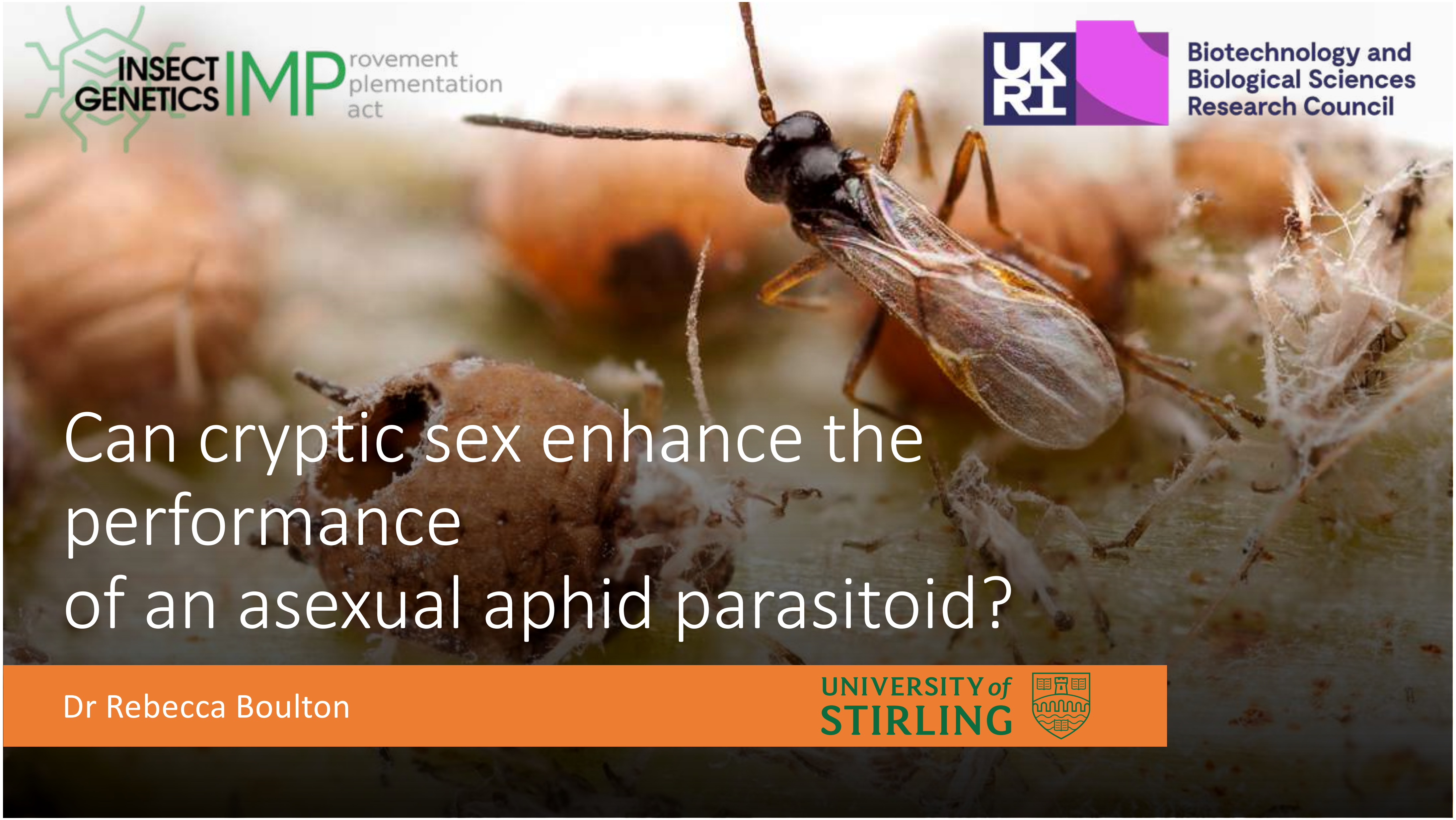


Can cryptic sex enhance the performance of an asexual aphid parasitoid?

Dr Rebecca Boulton

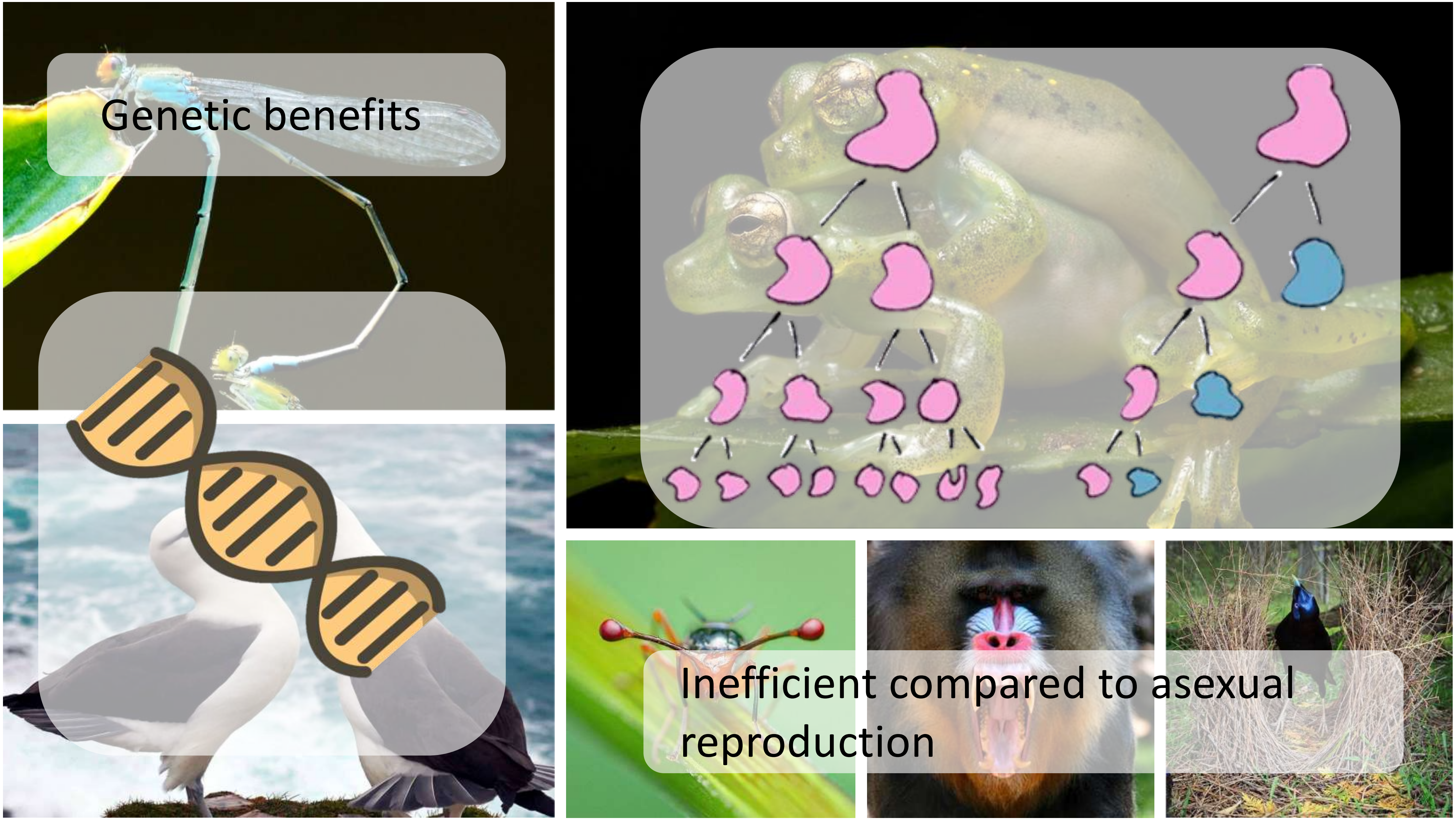
UNIVERSITY of STIRLING

INSECT GENETICS IMProvement IMPlementation IMPact

UKRI Biotechnology and Biological Sciences Research Council







Genetic benefits
Inefficient compared to asexual reproduction

Lysiphlebus fabarum

Cosmopolitan distribution

Sexual and asexual populations

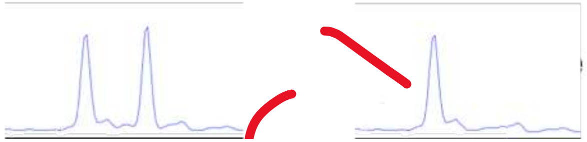
Asexuality is inherited as a single locus recessive trait

Asexual females still mate

Does mating = sex?

7 x asexual lines

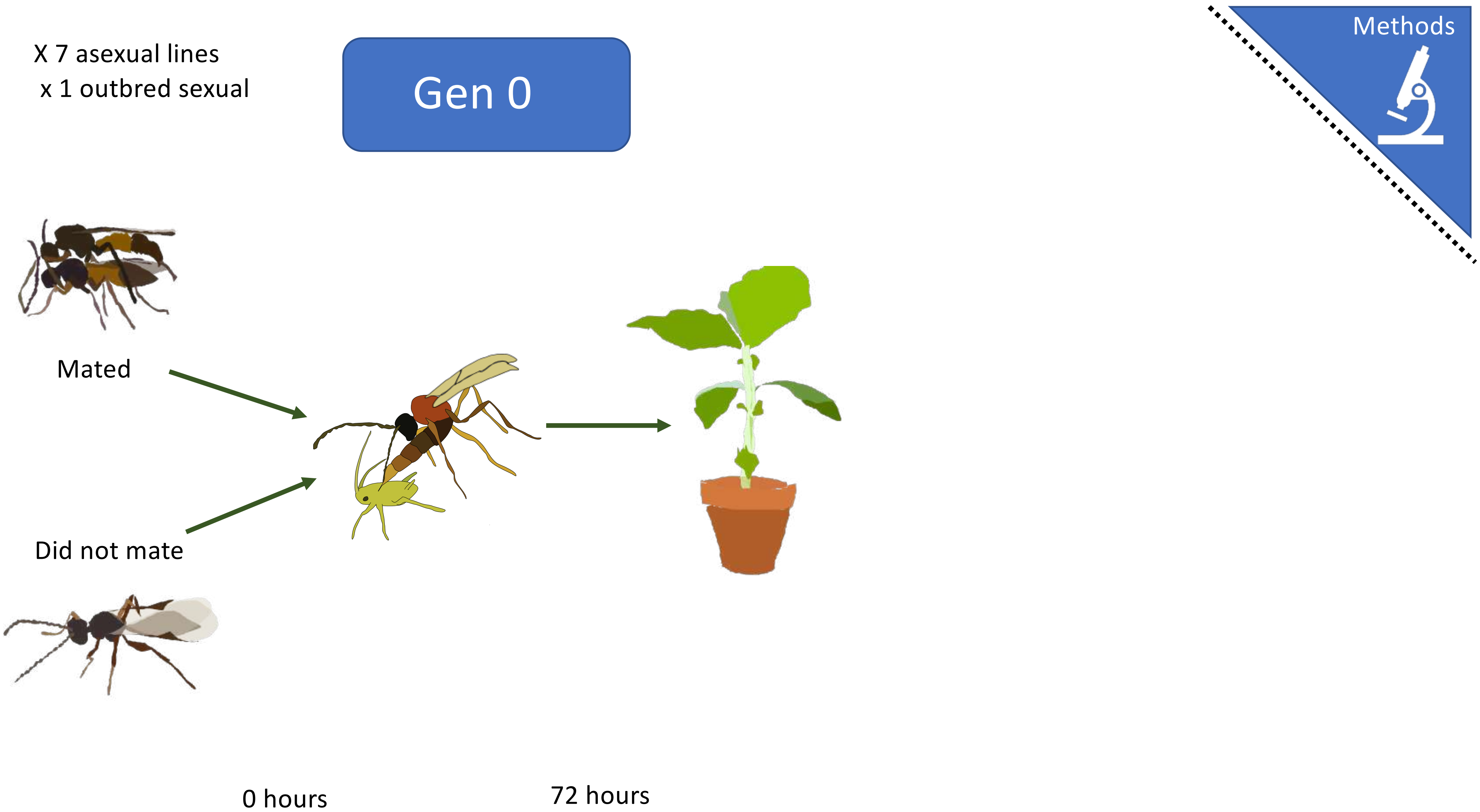
Does mating = sex?

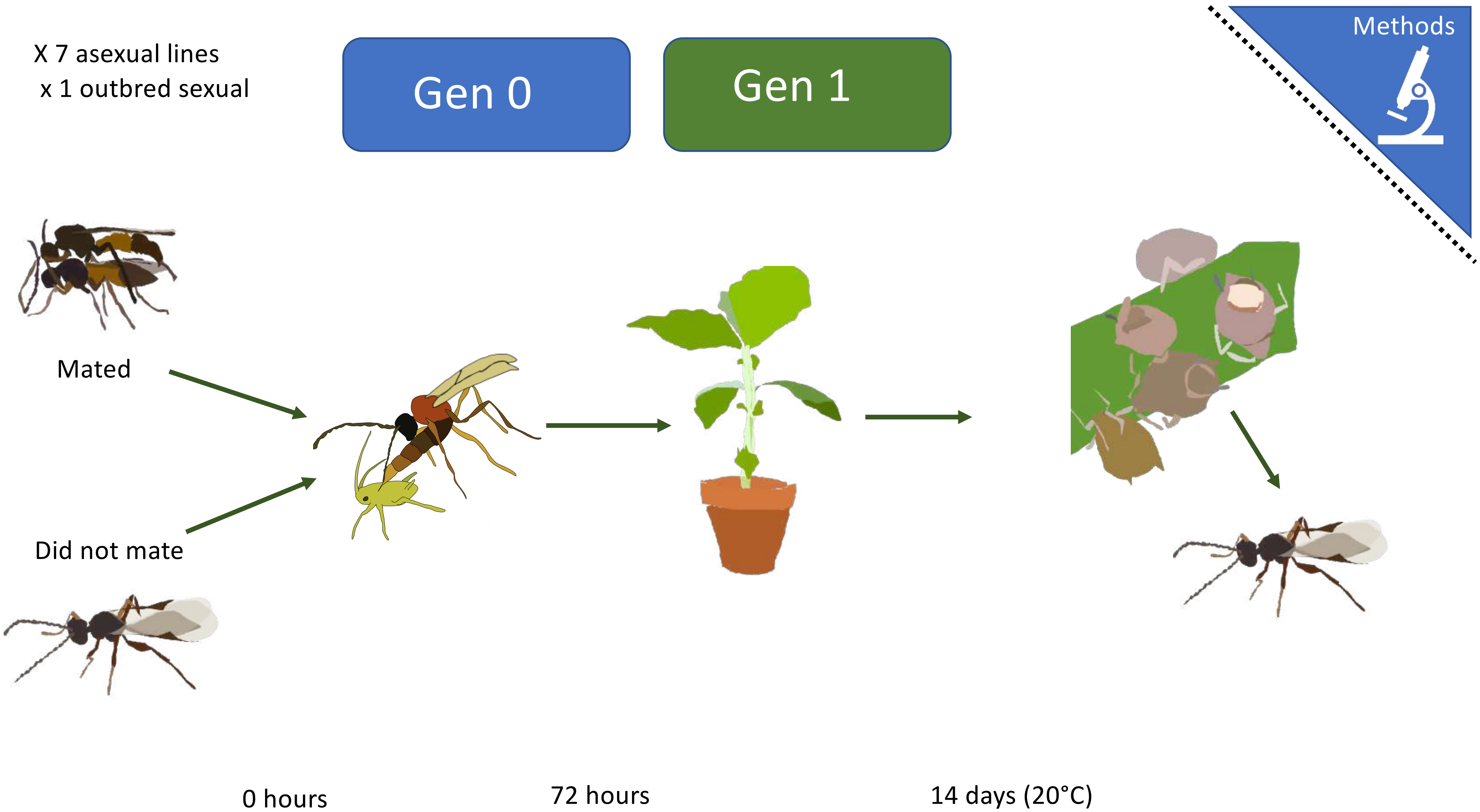


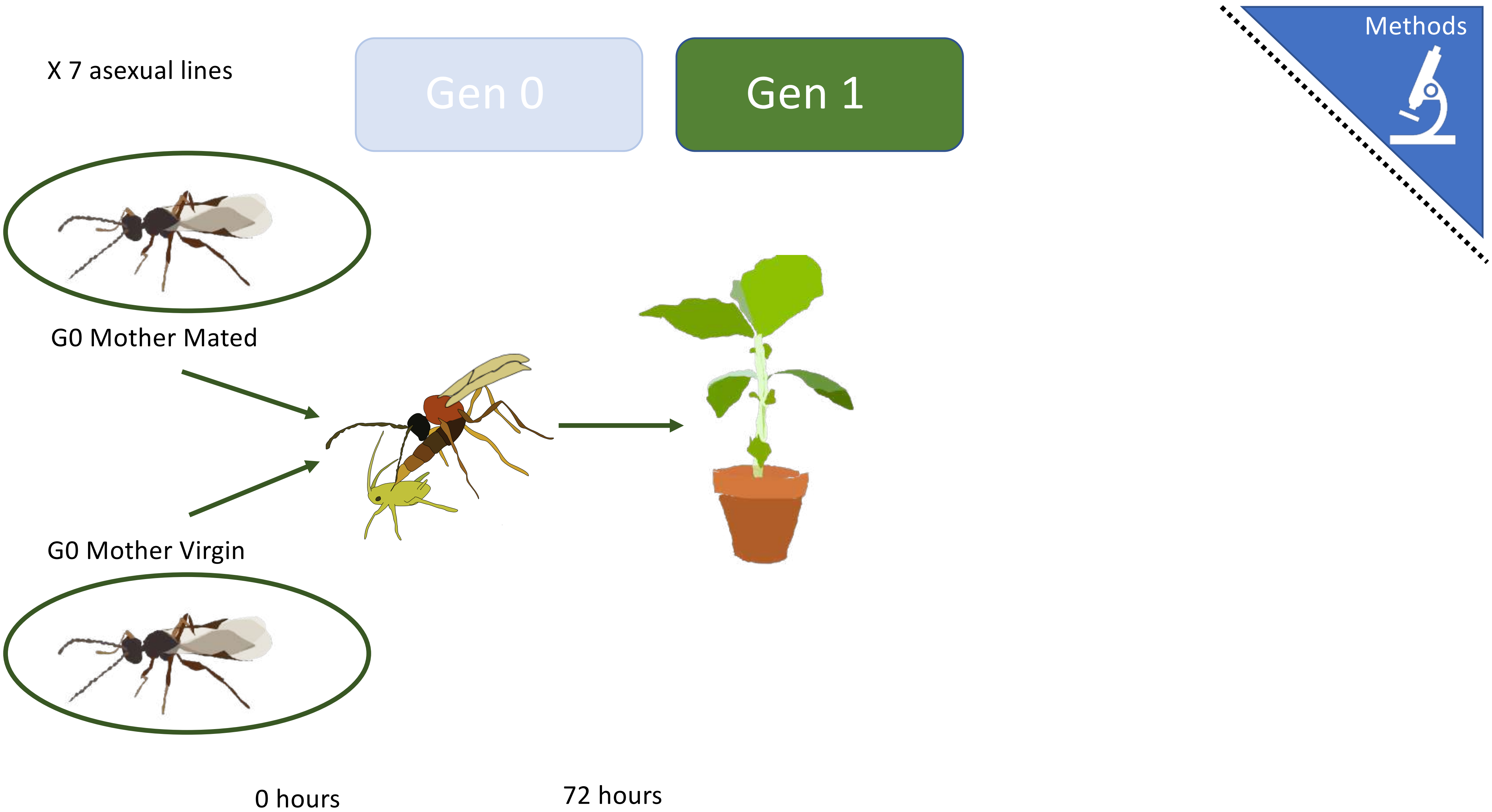
Line	Proportion used sperm
348	
402	
554	
64	
658	
66	
84	

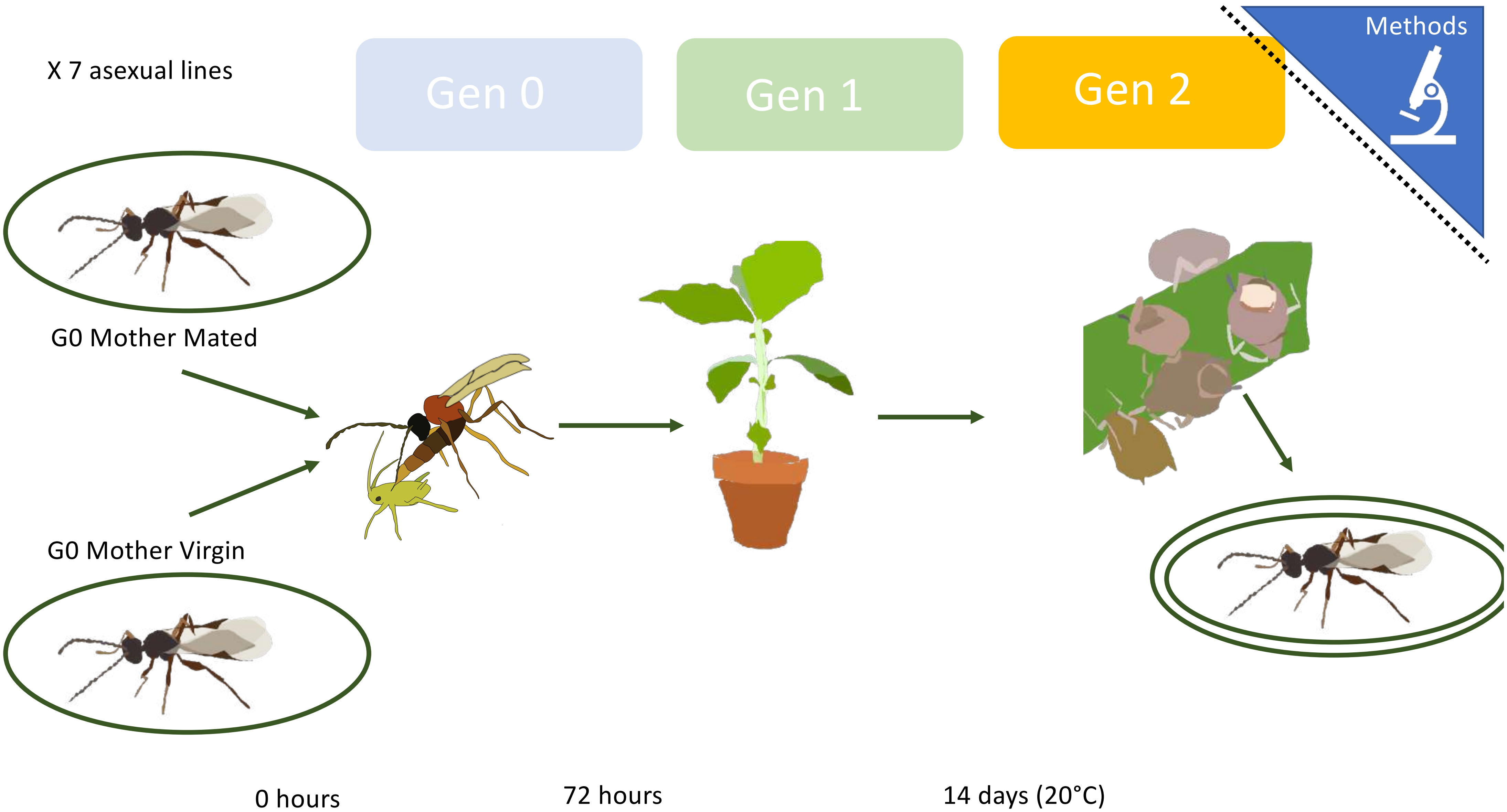
Does mating = sex?

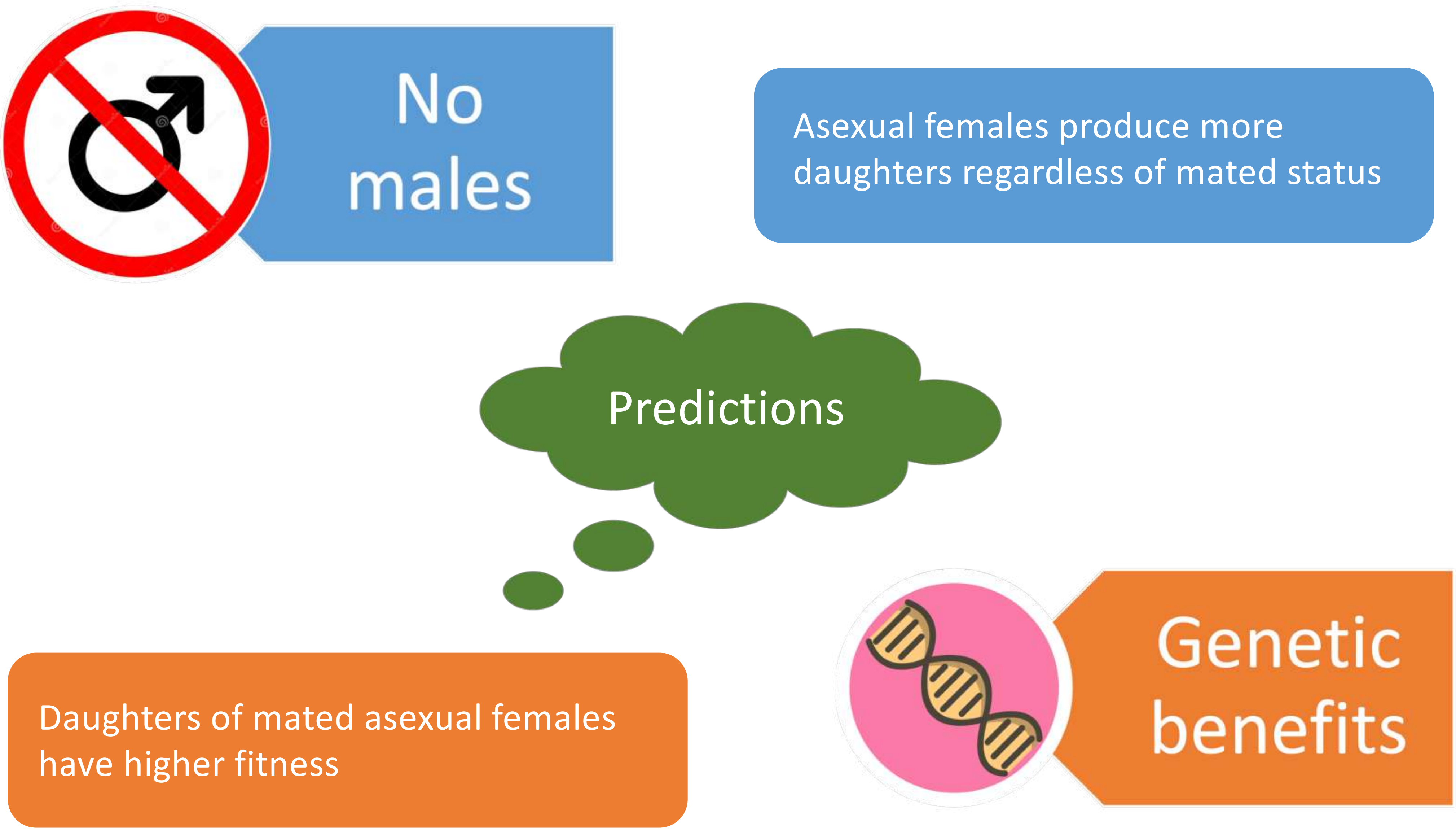
Facultative sex = the best of both worlds


X 7 asexual lines
x 1 outbred sexual
Gen 0
Methods
Mated
Did not mate
0 hours
72 hours


X 7 asexual lines
x 1 outbred sexual
Gen 0
Gen 1
Methods
Mated
Did not mate
0 hours
72 hours
14 days (20°C)


X 7 asexual lines
Gen 0
Gen 1
Methods
G0 Mother Mated
G0 Mother Virgin
0 hours
72 hours


X 7 asexual lines
Gen 0
Gen 1
Gen 2
Methods
G0 Mother Mated
G0 Mother Virgin
0 hours
72 hours
14 days (20°C)


No males
Asexual females produce more daughters regardless of mated status
Predictions
Daughters of mated asexual females have higher fitness
Genetic benefits

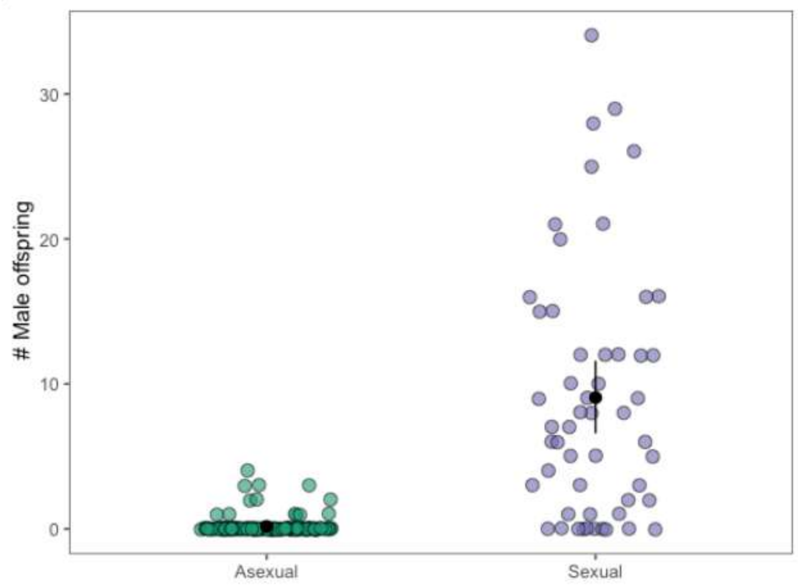
Gen 0

Gen 1

Gen 2

Results

Asexual females rarely produce males regardless of whether or not they mated



Gen 0

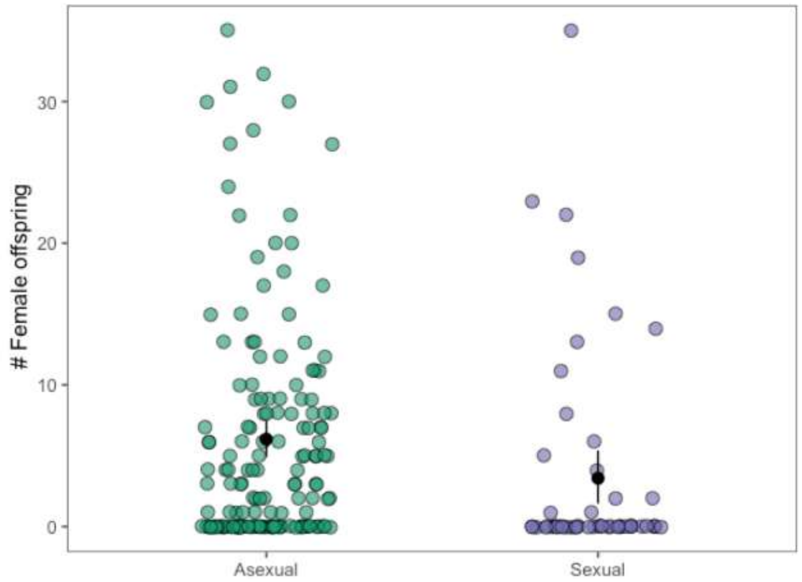
Gen 1

Gen 2

Results

Asexual females rarely produce males regardless of whether or not they mated

But this doesn't translate to more daughters



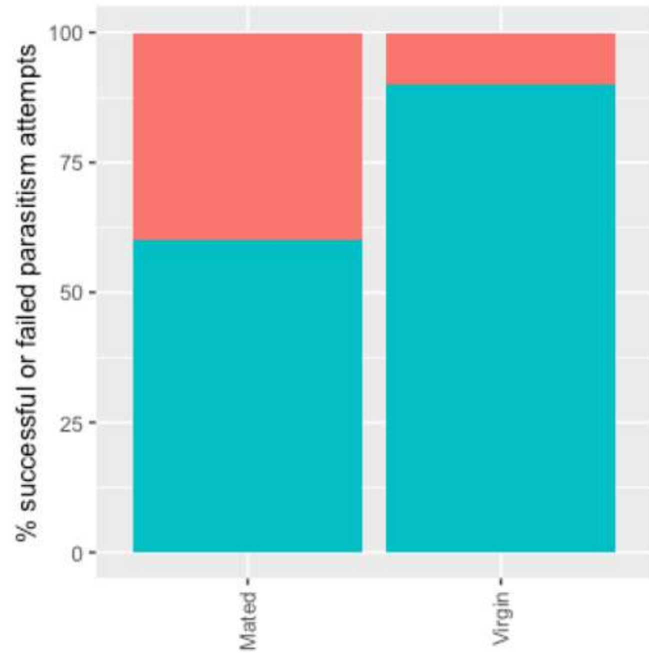
Gen 0

Gen 1

Gen 2

Results

Asexual females rarely produce males regardless of whether or not they mated



But this doesn’t translate to more daughters

G1 Daughters of mated (G0) asexual females have high rates of reproductive failure

Gen 0

Gen 1

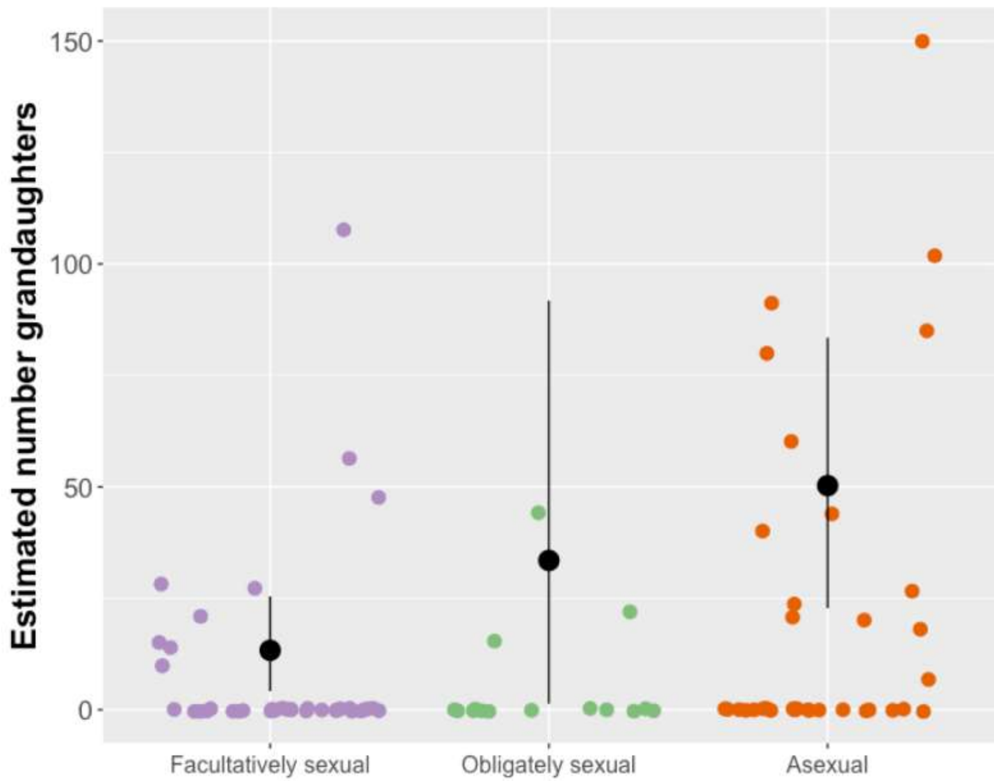
Gen 2

Results

Fitness outcome

Estimated granddaughter production *lowest* under facultative sex (mated asexual G0)

Obligately sexual and asexual G0 females statistically equivalent



$X^2 = 6.63$, df = 2, 90, $p = 0.04$

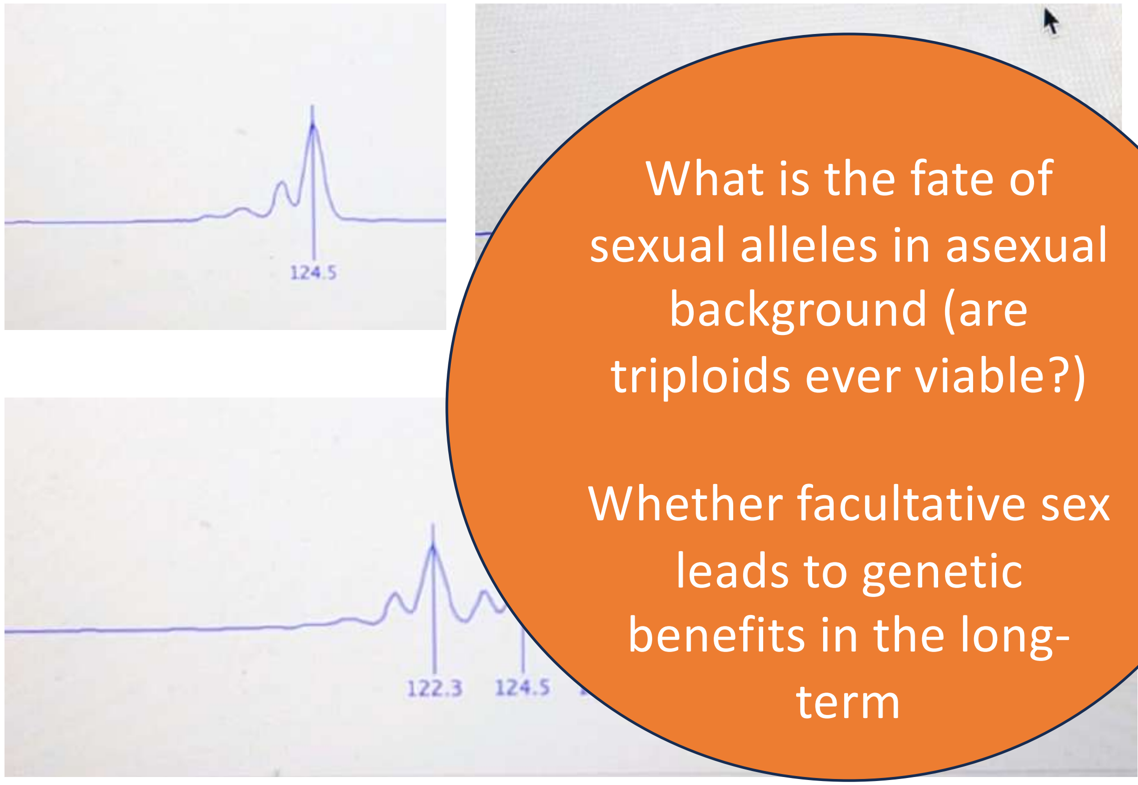
Facultative sex = the worst of both worlds

Facultative sex = the worst of both worlds

Results

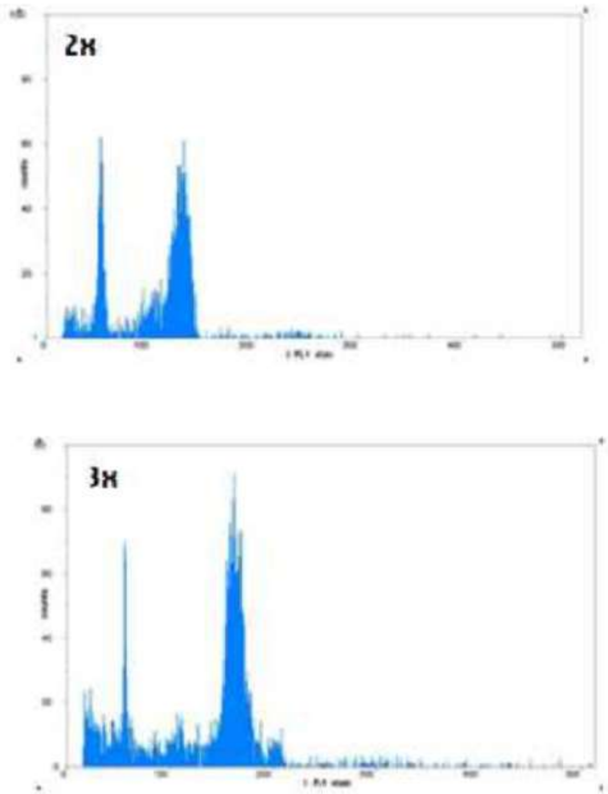
Gen 0

Gen 1



What is the fate of sexual alleles in asexual background (are triploids ever viable?)

Whether facultative sex leads to genetic benefits in the long-term



Can cryptic sex enhance the performance of an asexual aphid parasitoid?

- Short-term facultative sex is costly
- Long-term genetic benefits depend on offspring fertility – need more generations
- Facultative/cryptic sex as a tool for ‘genetic rescue’ of parthenogenetic commercially reared insects?


Arianna Chiti
Pauline Blaikie
Clare Bird
Taliesin Valencia
Laura Corral
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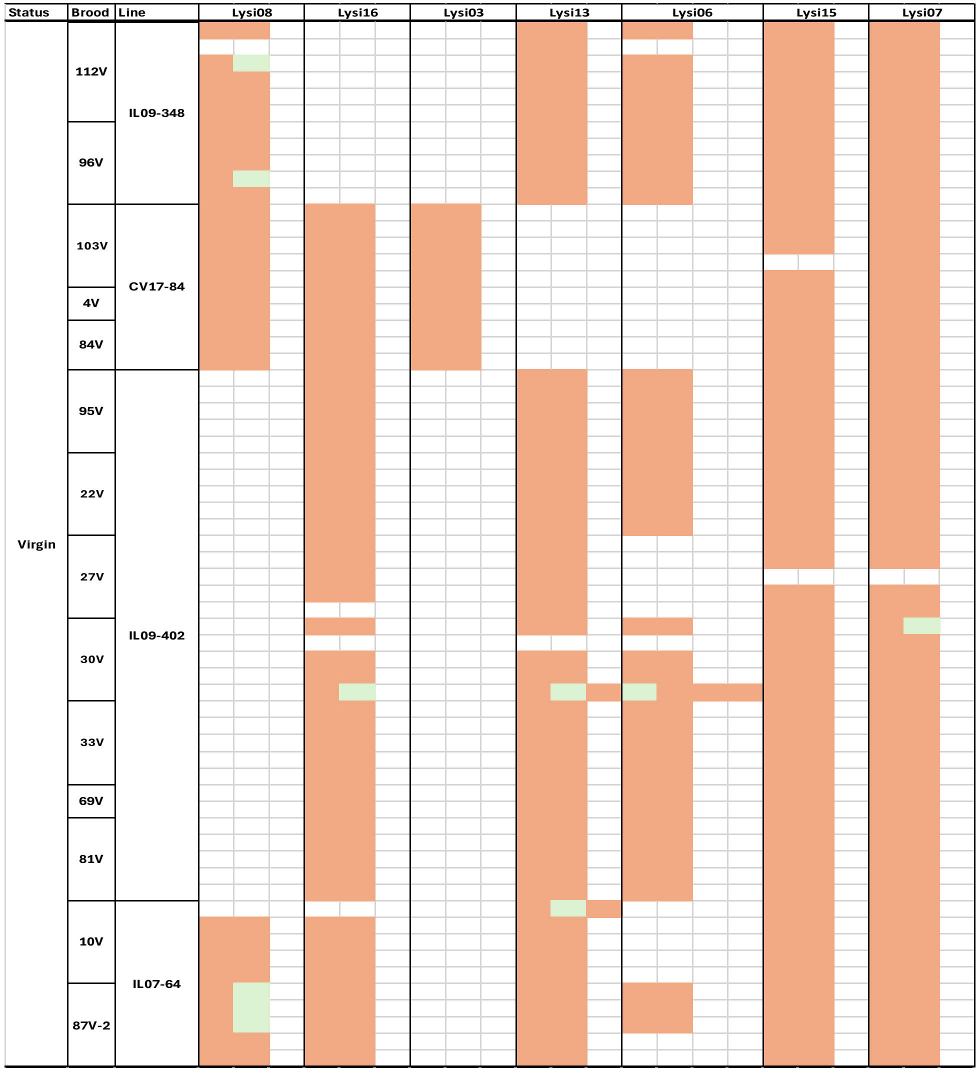
Thank you!
Bart Pannebakker
Kelley Leung
WAGENINGEN UNIVERSITY & RESEARCH
Christoph Vorburger
eawag aquatic research

Results

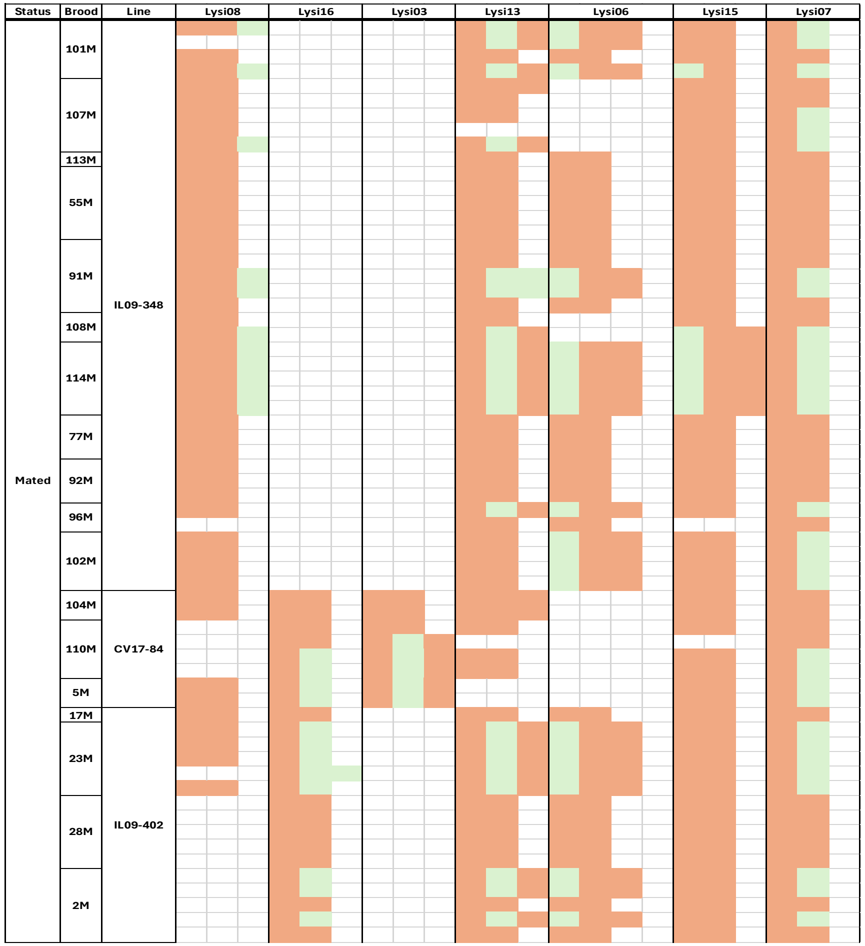


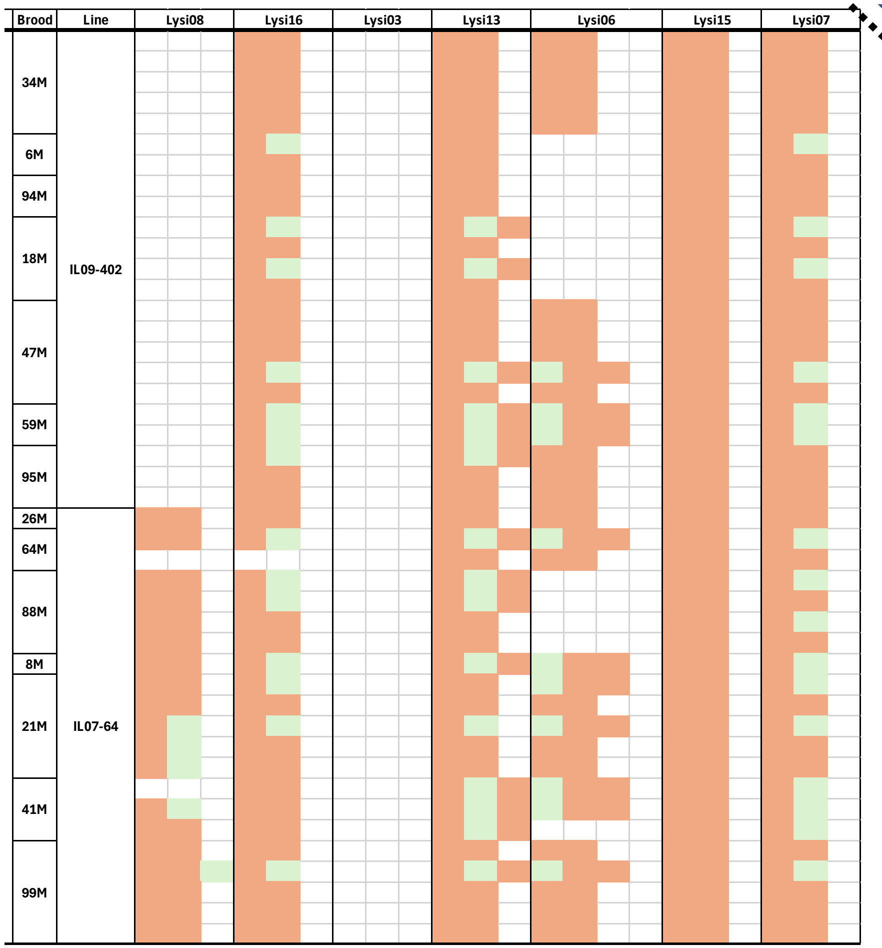
Allele from asexual mother

Allele from sexual population

63 females from 14 broods,
4 lines of unmated asexual mothers

10 alleles of potential sexual origin in 8 individuals
2 potential triploids





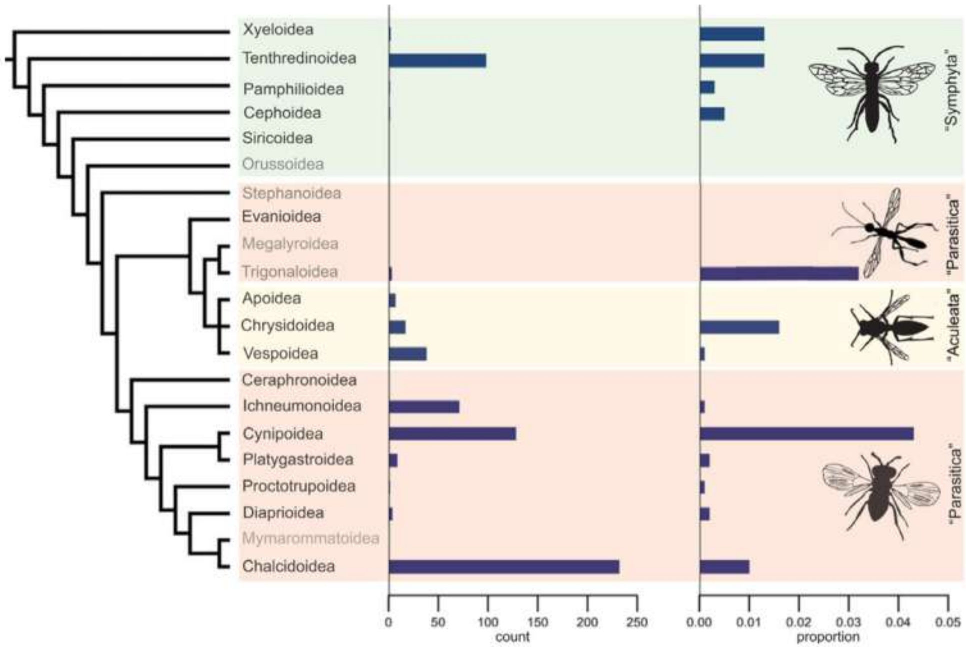
Results

Allele from sexual population

Allele from asexual mother

107 females from 32 broods,
4 lines of mated asexual mothers
121 alleles of potential sexual origin across 33 individuals

29 possible triploids, only 3 with no potential sexual alleles (only triploid at one locus)



High frequency of parthenogenesis in invertebrates

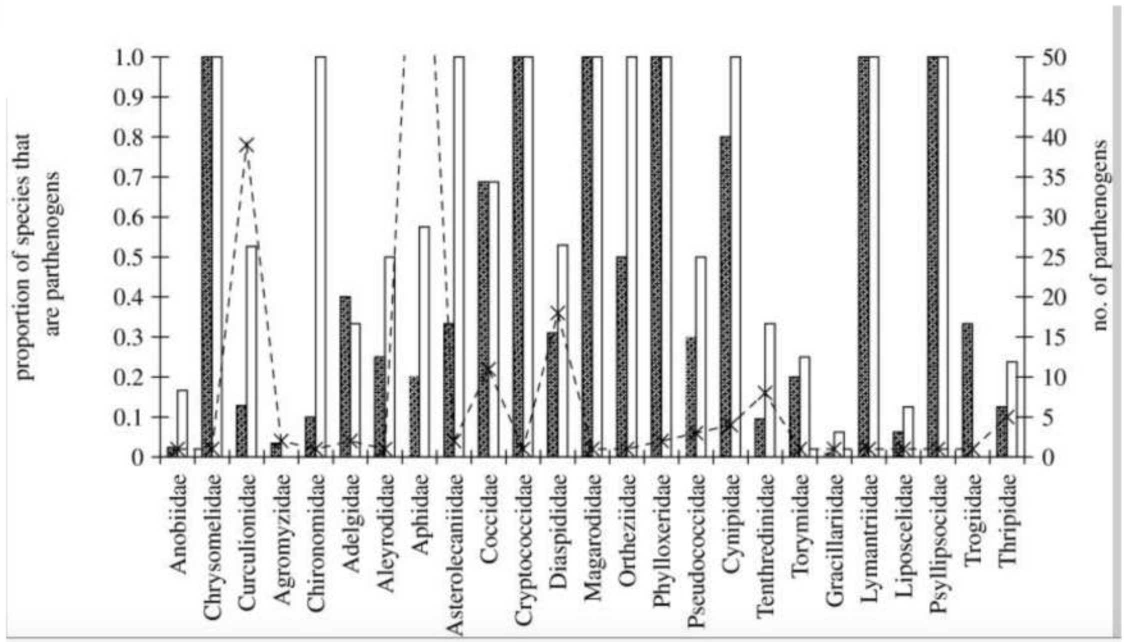
Variable across taxa, high in haplodiploids

van der Kooi et al. 2017

45-48% of pest species sampled were parthenogenetic

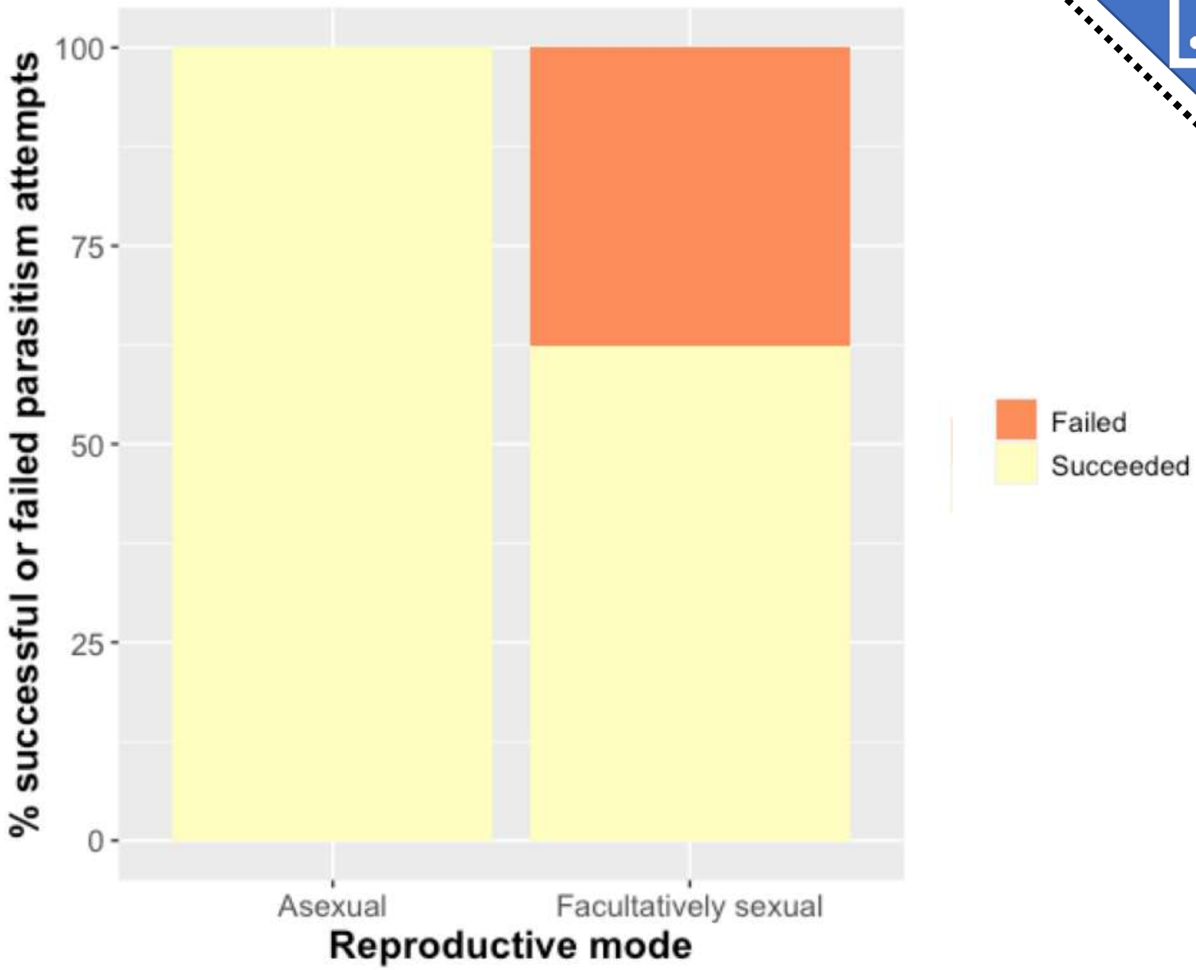
10-16% of non-pest species

Hoffman et al. 2008



Results

- After 4 generations of rearing as facultatively sexual still high rate of reproductive failure under facultative sex



$X^2 = 8.5484$, df = 1, p-value = 0.003

Triploidy is probably important, but it doesn't explain all the variation in reproductive failure

Genetic slippage - sets of genes work well together get reshuffled

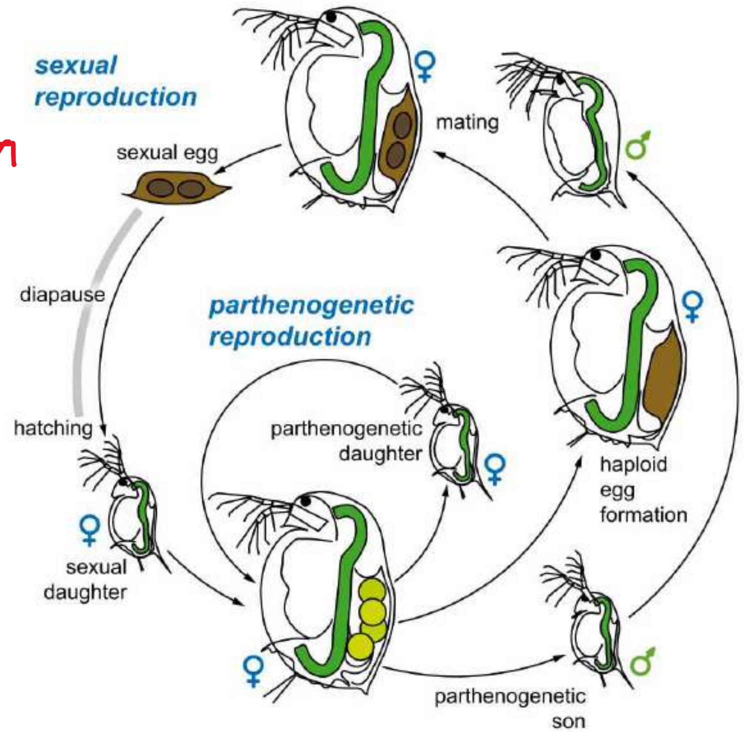
Facultative sex increases reproductive failure

Triploidy is probably important, but it doesn't explain all the variation in reproductive failure

Genetic slippage - sets of genes work well together get reshuffled

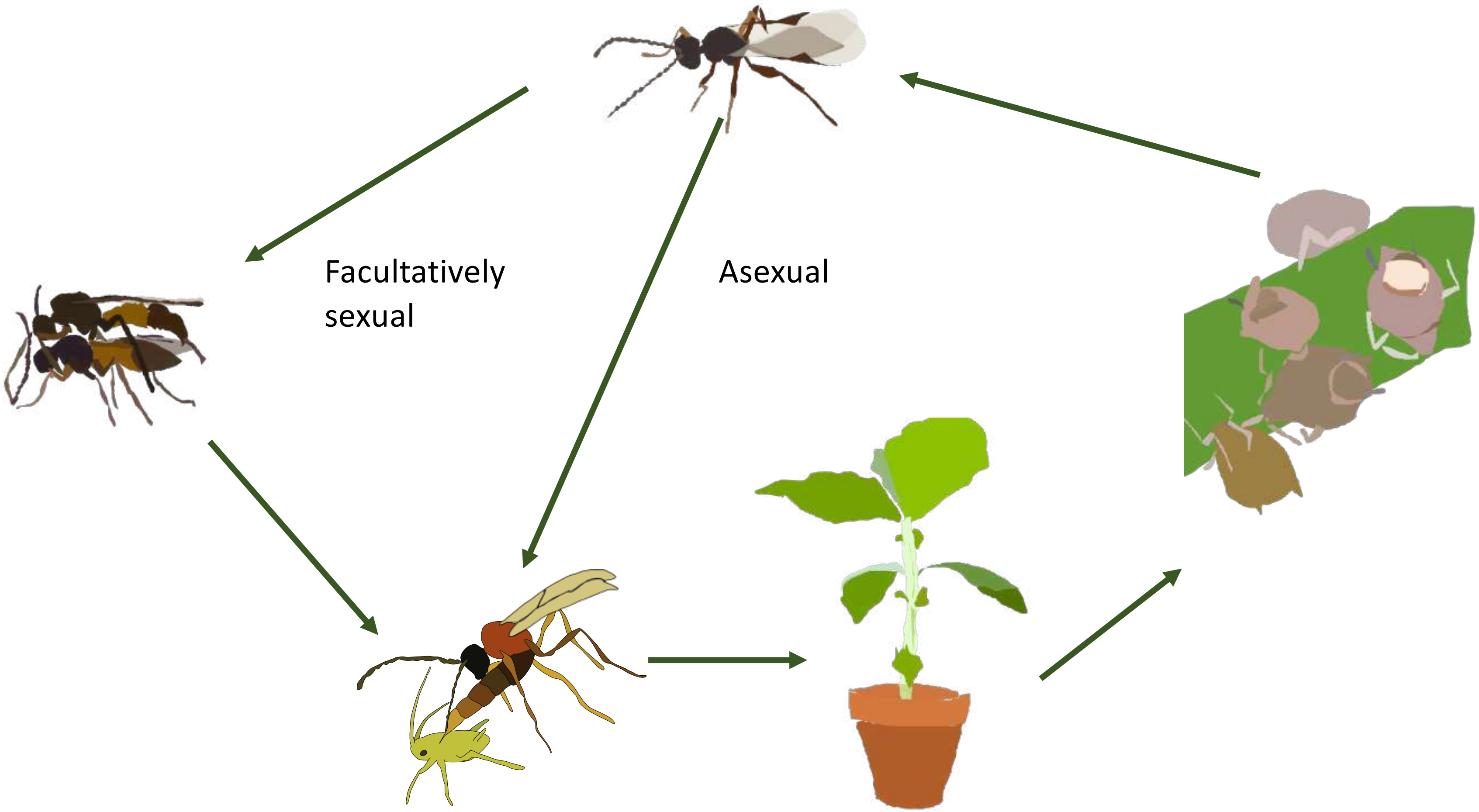
Cyclical parthenogenesis

Popn's w/ more frequent sex = reduced reproductive failure



Methods

Adding ~ 10% males to asexual cages every generation



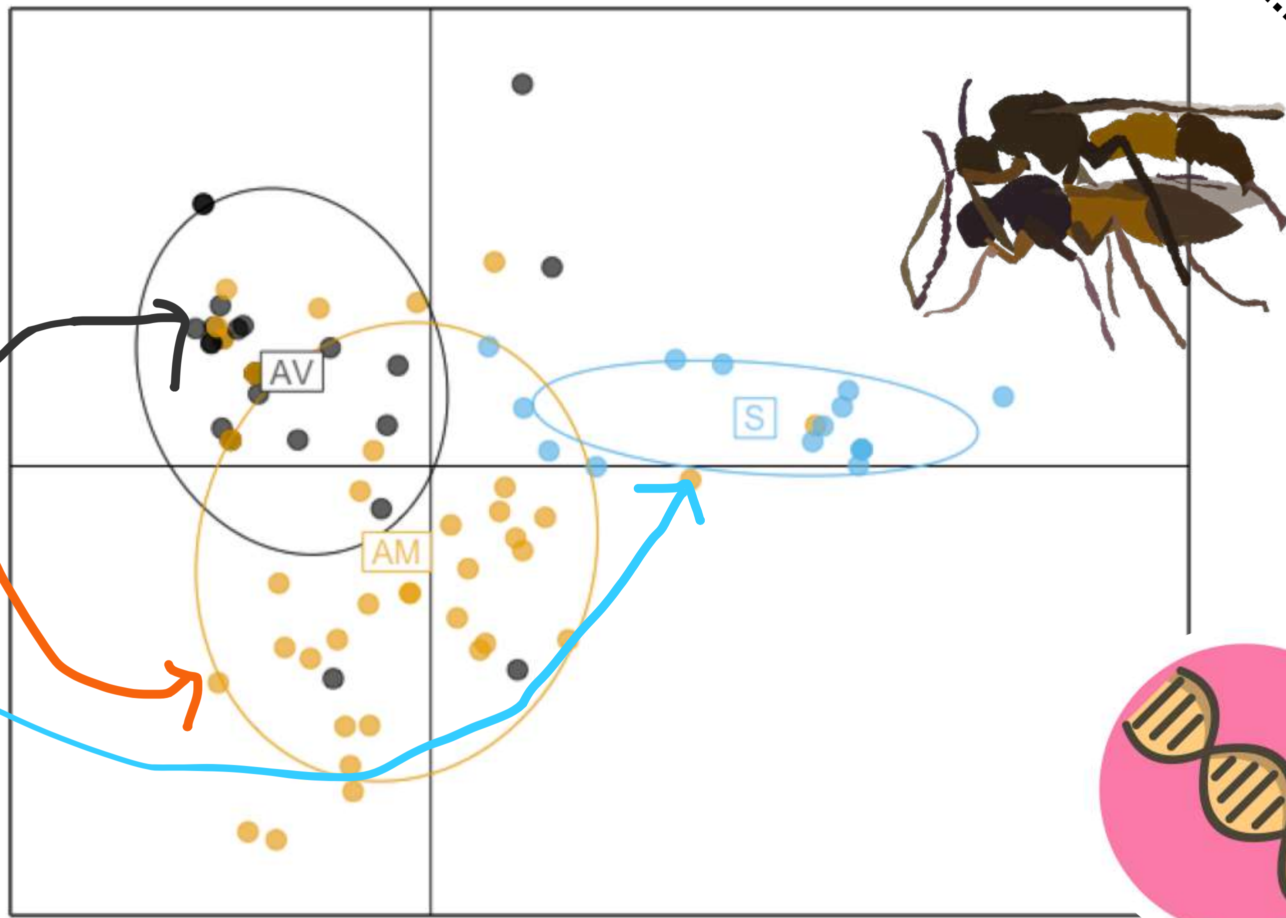
X 7 asexual lines

Gen 0

Gen 1

Results

Multilocus genotypes of broods from asexual mated females, virgin asexuals and sexual females

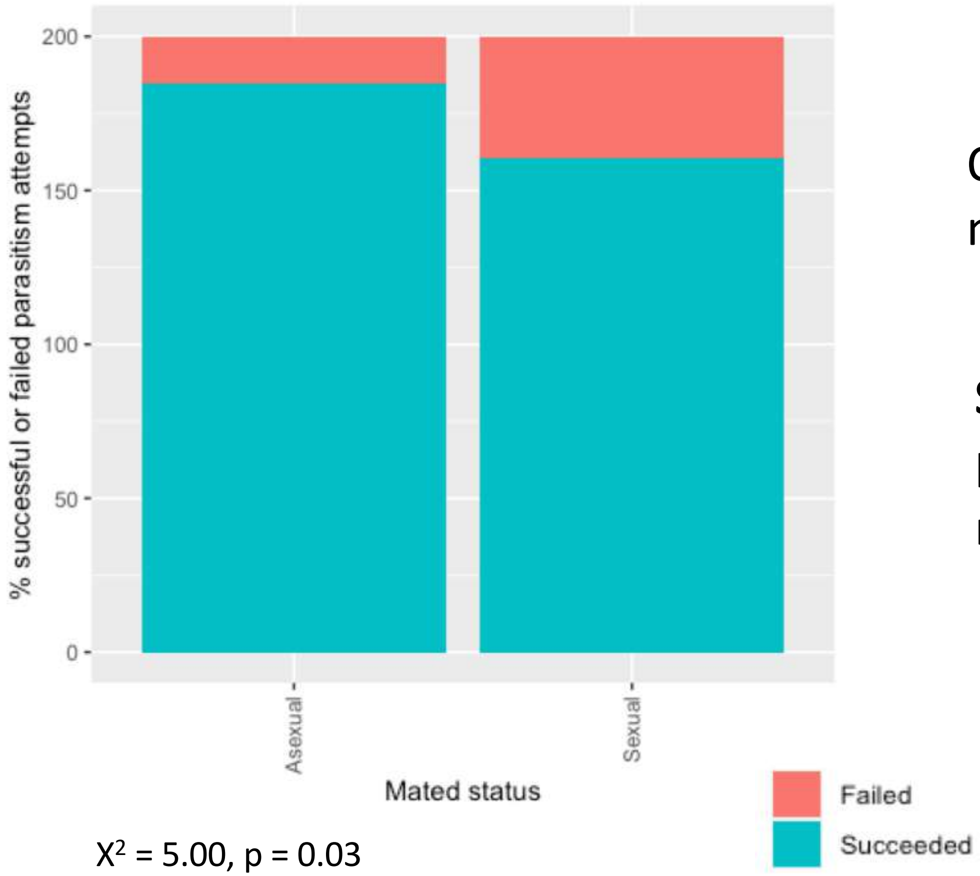


Results

Gen 0

Gen 1

Gen 2



$X^2 = 5.00$, $p = 0.03$

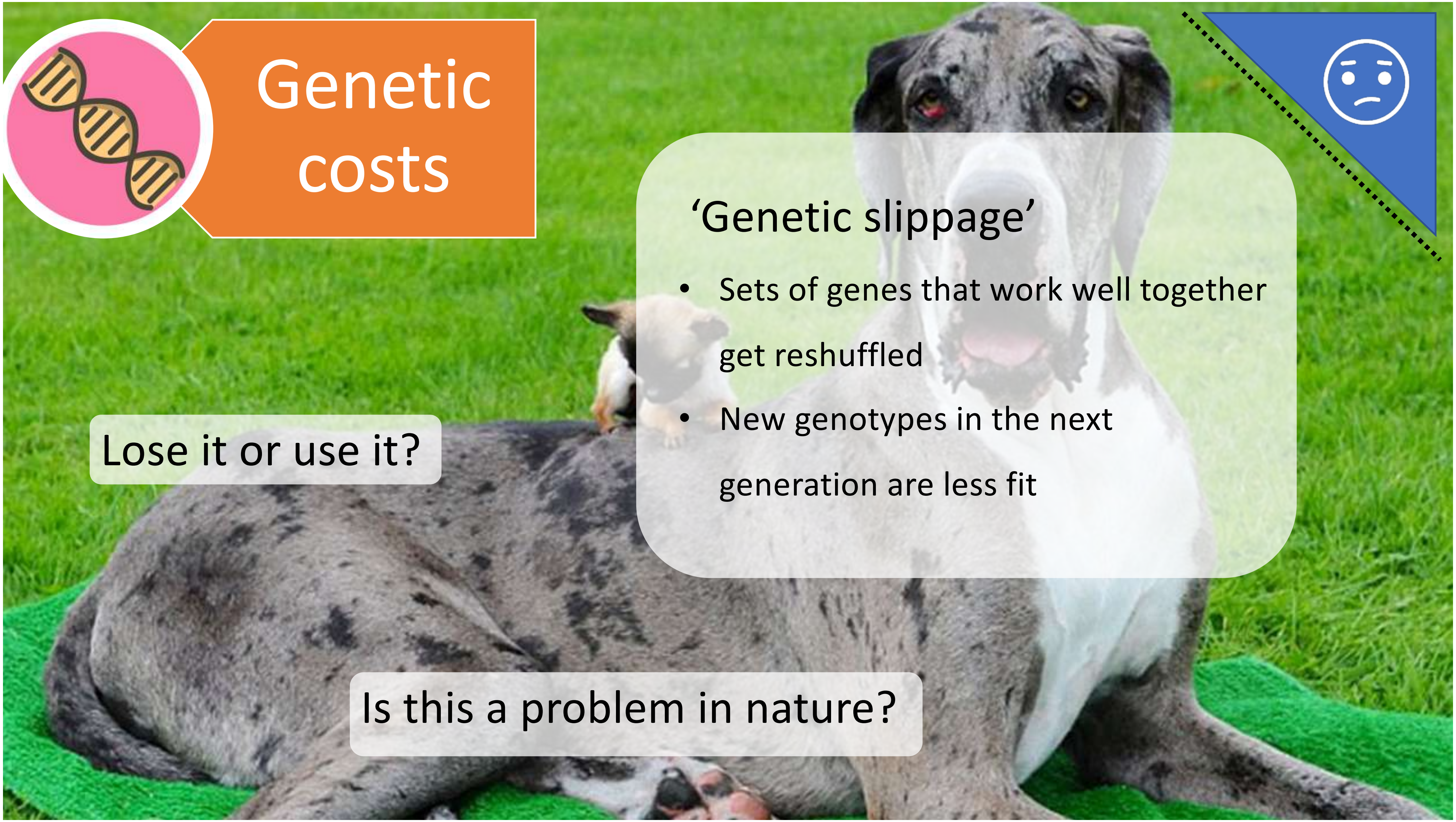
Only when females that failed to produce any mummies excluded, otherwise…

Sexual females more likely to fail to parasitise than asexuals regardless of their mated status

and

Costs of sex in *Lysiphlebus*

- Females produced sexually are more likely to fail
- This is the most extreme for sexually produced daughters of asexual females
- Why?
  - Genetic slippage – sets of genes work well together get reshuffled
- When sexual females do parasitise successfully they produce more offspring which gets rid of the cost of males
  - Sex purges deleterious recessives/fixes beneficial mutations
  - Not in the case of facultative sex?



Genetic costs

‘Genetic slippage’

- Sets of genes that work well together get reshuffled
- New genotypes in the next generation are less fit

Lose it or use it?

Is this a problem in nature?

Gen 1

- Sexual females more likely to fail to parasitise
  - A cost of sex, not a cost of mating
  - Just as bad for virgin sexual females
- When they do successfully parasitise, sexual females
  - Produce more mummies
  - Which more wasps emerge from
- This increased offspring production makes up for the 2-fold cost of males
  - Sexual females produce as many daughters as asexuals

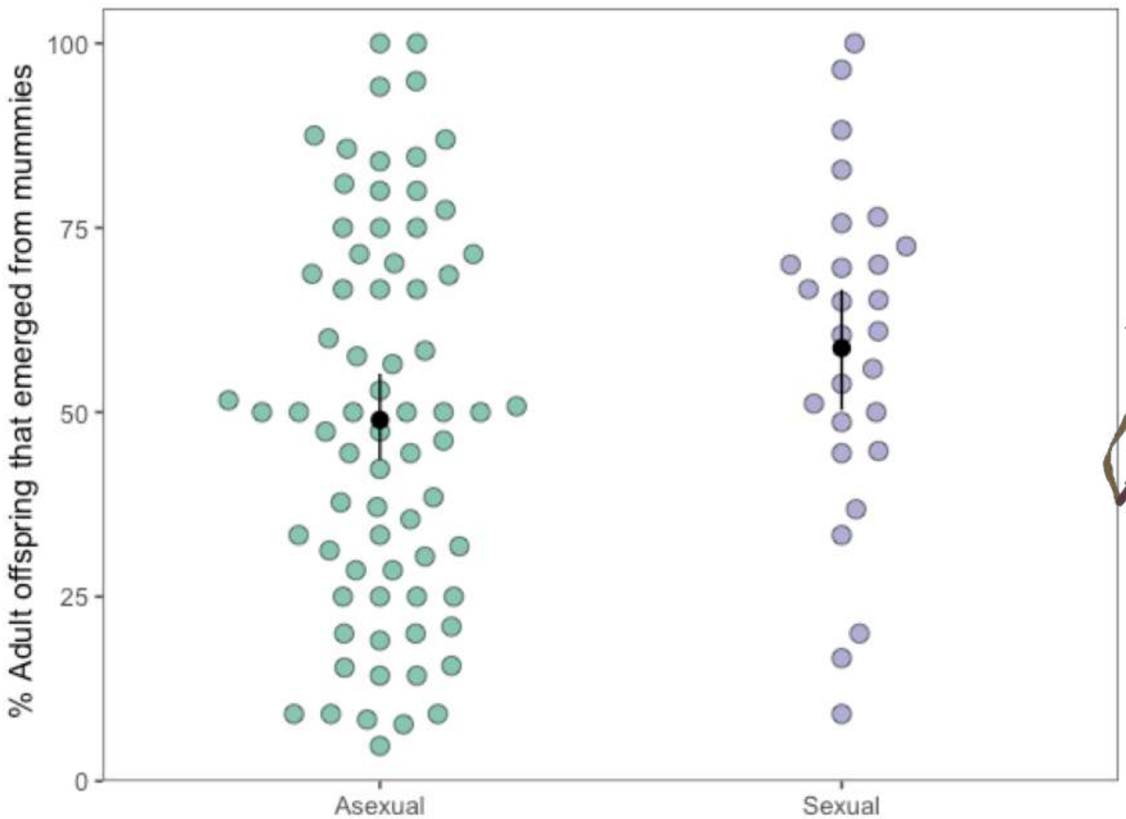
Gen 2

- Asexual females can still reproduce sexually
- Asexual females whose mothers mated much more likely to fail to parasitise than if their mothers remained virgin
  - Again, a cost of sex, not a cost of mating because it only showed up in the second generation
  - Cost more severe than in sexuals – points to genetic slippage/unmasking of deleterious recessives as the cause of the cost

Results

Gen 0 | Gen 1 | Gen 2

Probably because…



$X^2 = 5.03, p = 0.03$

Higher % emergence success from sexual mummies

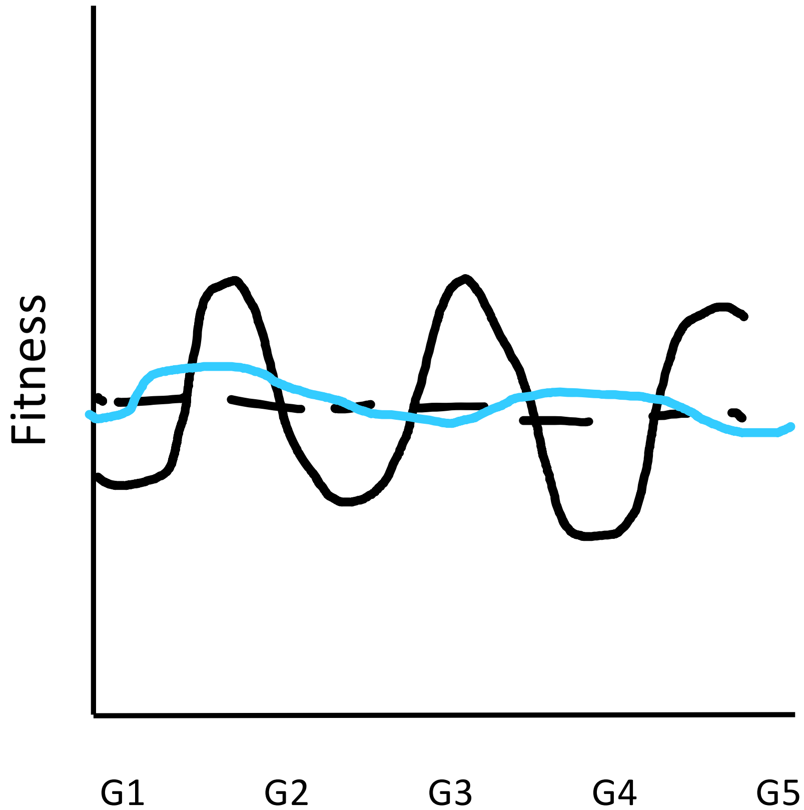
BUT

Wasp is the point of sex?

- If it happens often enough in the field it maintains genetic variation and heterozgosity
- Costs of genetic slippage may not be a problem in the field - if asexual females mate with (rare) closely related asexual males.
- Sex could be a bet-hedging strategy - persists at a low level despite the costs because it reduces variation in fitness over many generations

Sexual reproduction as bet-hedging

- Geometric mean fitness vs arithmetic mean fitness
- Geometric is measured as between generation fitness
- Across environments (and generations) bet-hedgers have higher fitness
- Bet-hedging (sex) favored in more variable environments



Wasp is the point of sex?

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- Sex could be a bet-hedging strategy - persists at a low level despite the costs because it reduces variation in fitness over many generations
- In *L. fabarum* if sex results in more diverse offspring – some of which do better in different environments, sex could be maintained by bet-hedging

Sexual reproduction as bet-hedging

- In *Lysiphlebus* if sex is a bet-hedging strategy could explain why sexuals are still around AND why asexuals haven't lost the ability to reproduce sexually

- Do asexual parasitoid wasps tend to inhabit more stable environments?
- Change in sexual vs asexual allele frequencies over the season?

Next steps

- Why are sexually produced females more likely to fail to parasitise?
  - Do they still sting hosts?
  - Do they still lay eggs?
  - When does failure occur and are they producing diapause eggs?
- Does the proportion of females that fail change if the environment changes?
  - Different host species/host adaptations?
    - *Hamiltonella?*
  - Host plant or temperature


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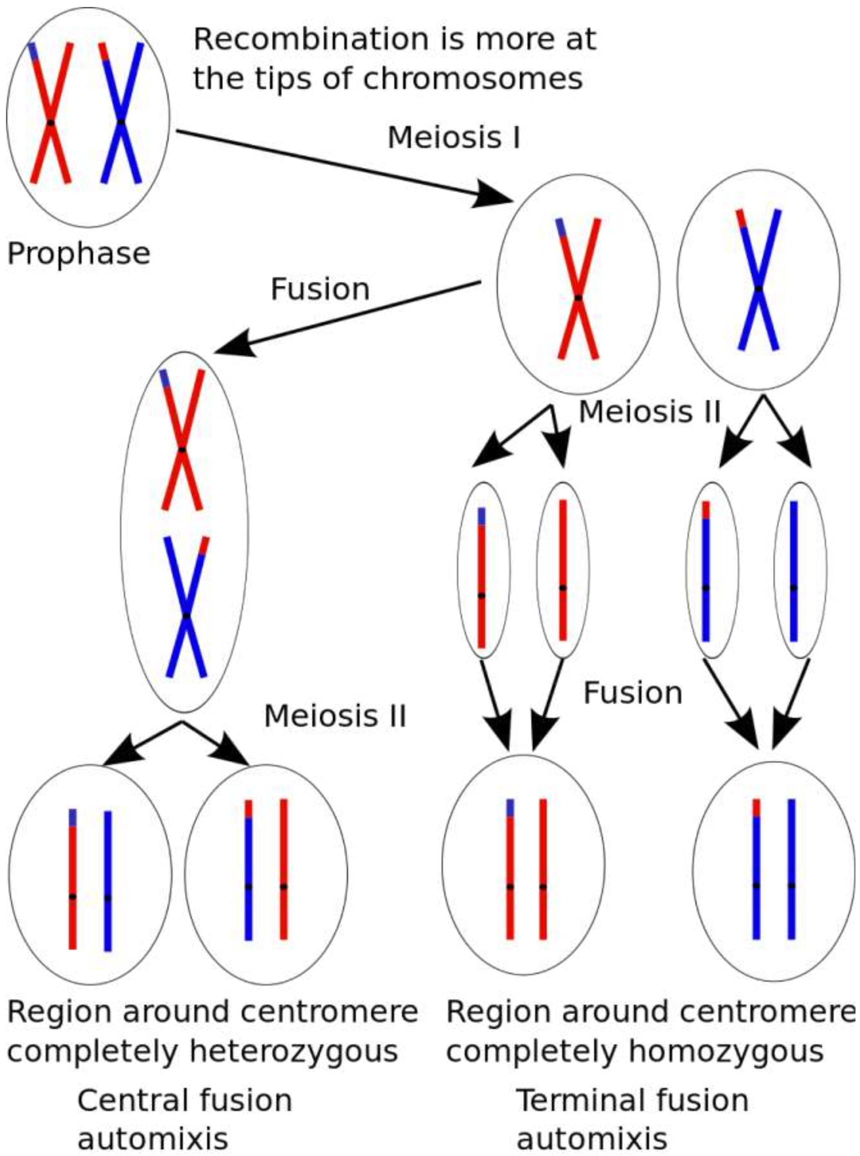


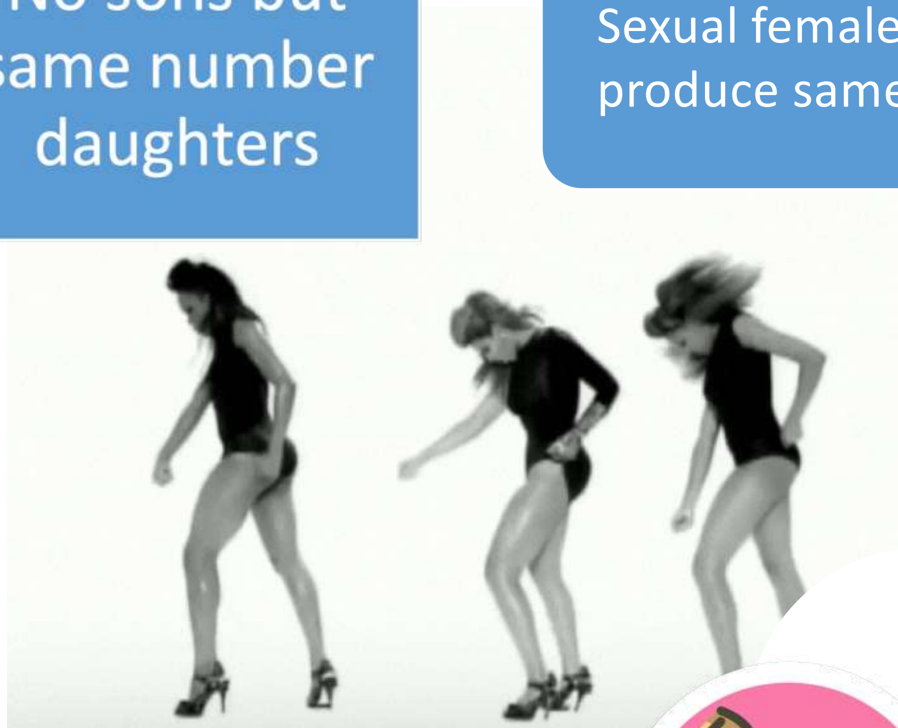
Central fusion automixis

Mostly maintains heterozygosity

Recombination can lead to reduced heterozygosity at the tips

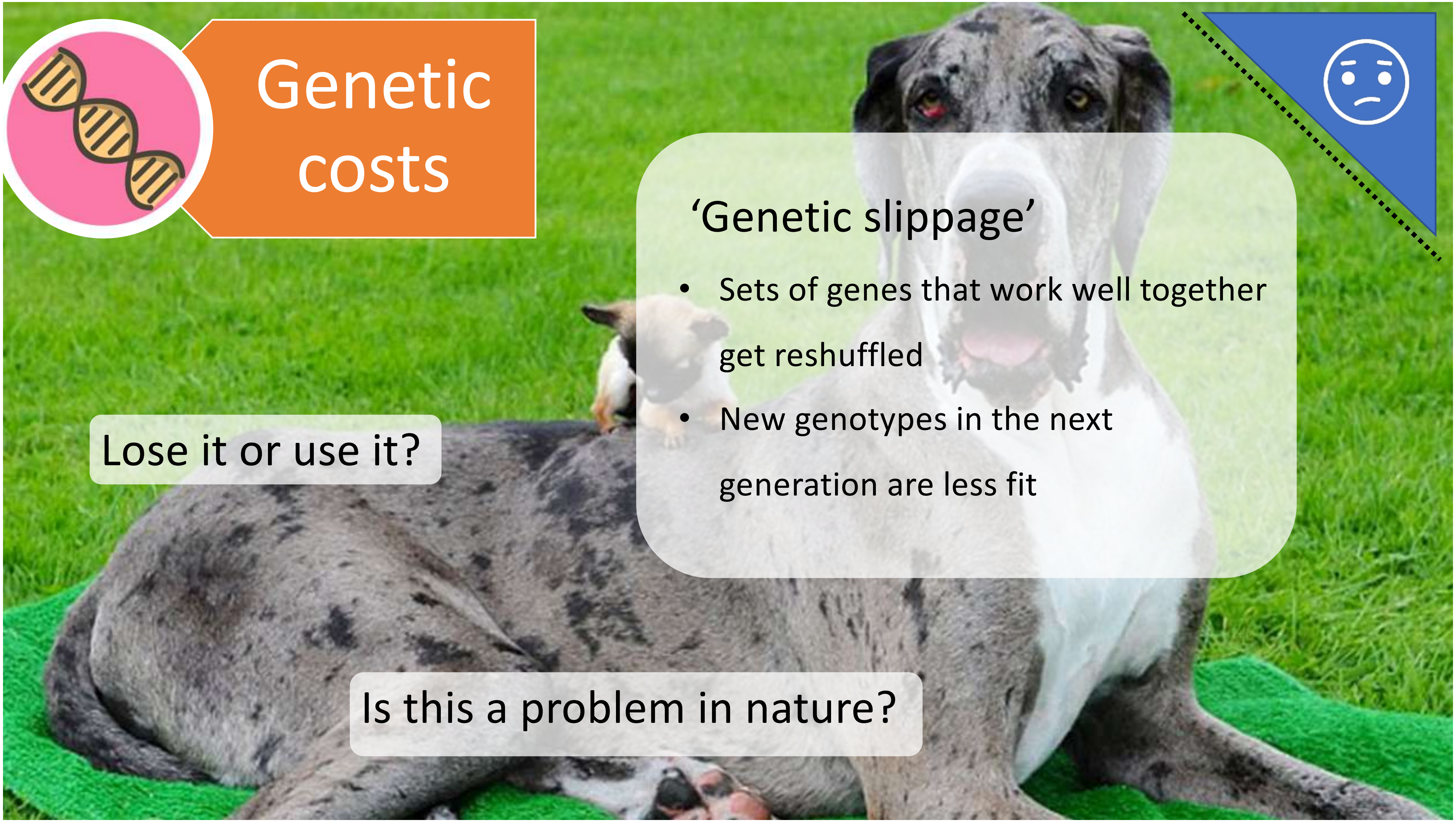
No sons but same number daughters

Sexual females more fecund so they produce same number daughters

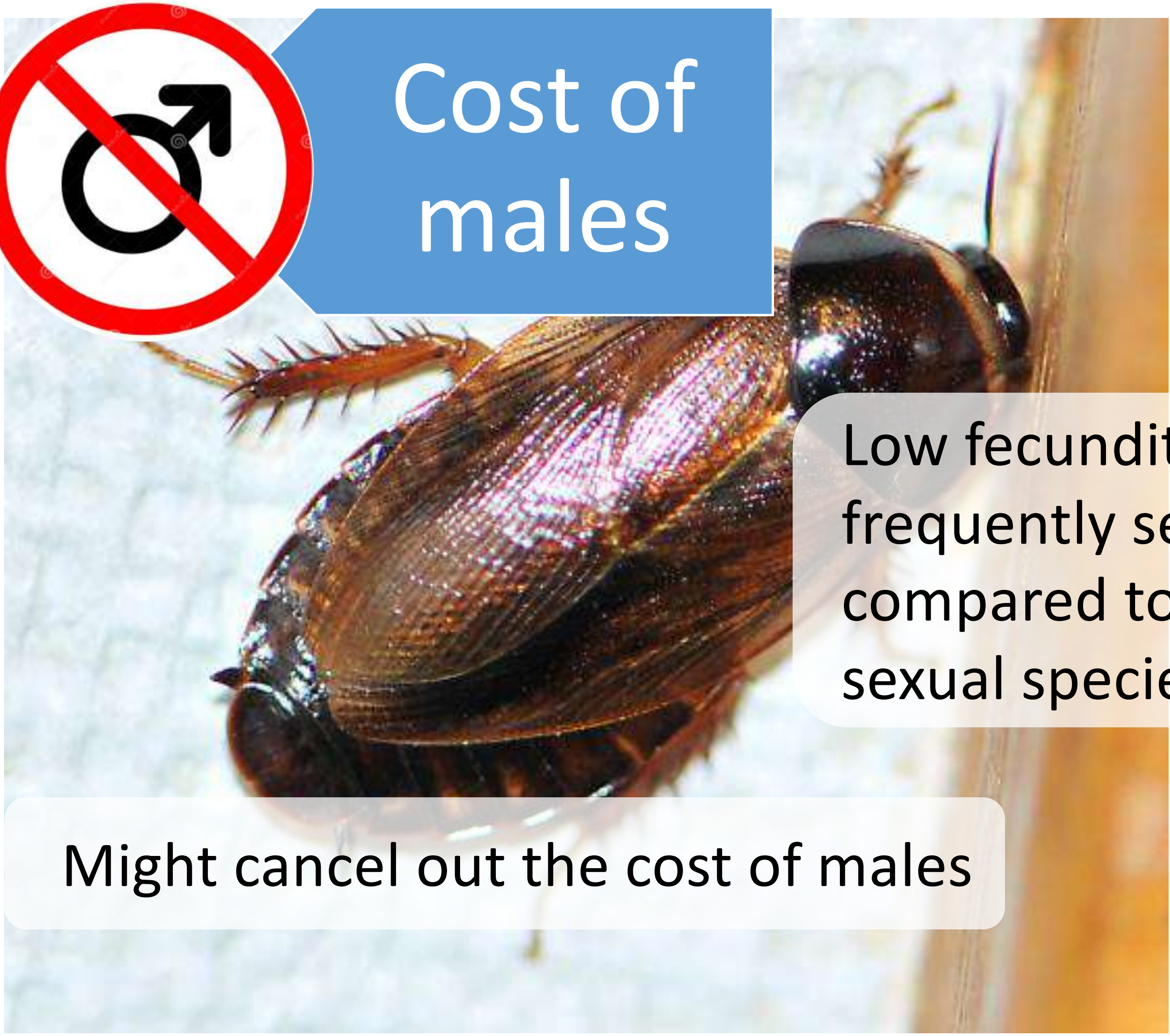


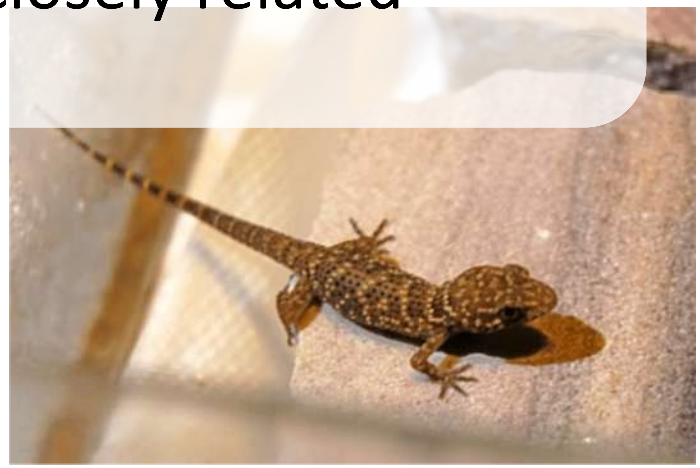
Mating increases reproductive failure

Genetic costs


Genetic costs
'Genetic slippage'
• Sets of genes that work well together get reshuffled
• New genotypes in the next generation are less fit
Lose it or use it?
Is this a problem in nature?

Cost of males





Low fecundity and high mortality frequently seen in asexual compared to closely related sexual species

Might cancel out the cost of males

Why have sex if you don't need to?

Asexual female *Lysiphlebus* accept matings from males produced by sexual females

Benefits only accrue when environment changes

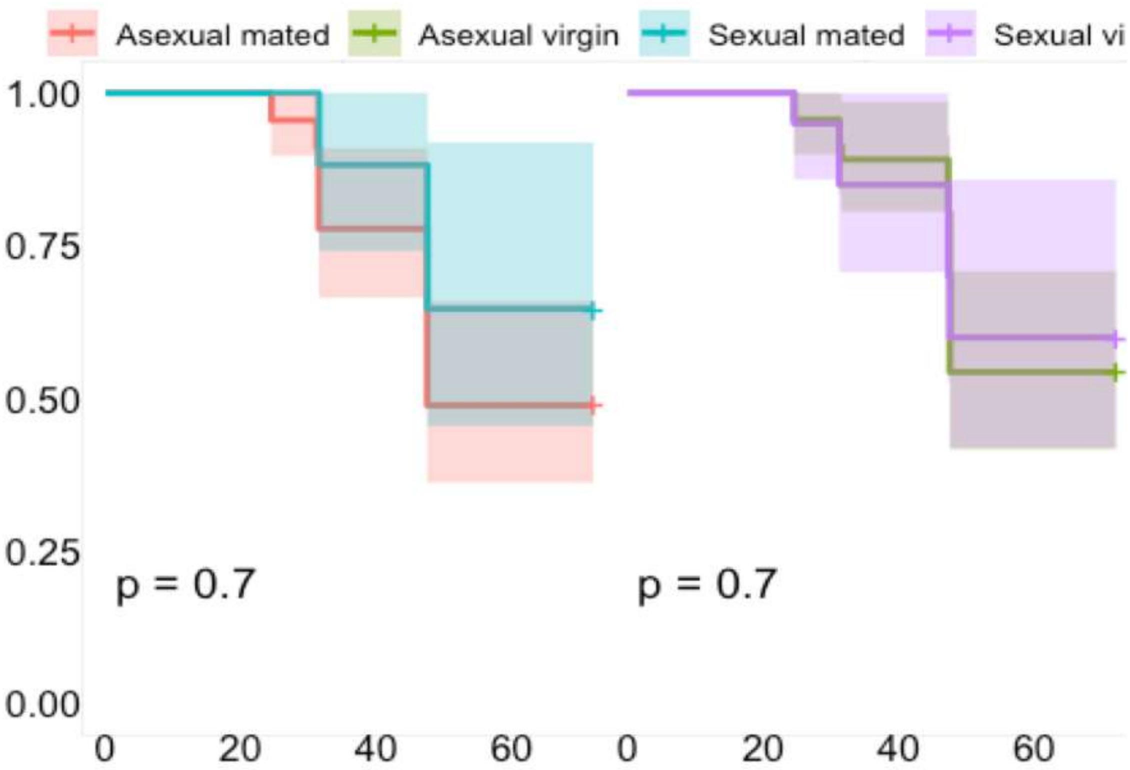
Insufficient costs/time to erode sexual traits

Results

Gen 0

Gen 1

Gen 2



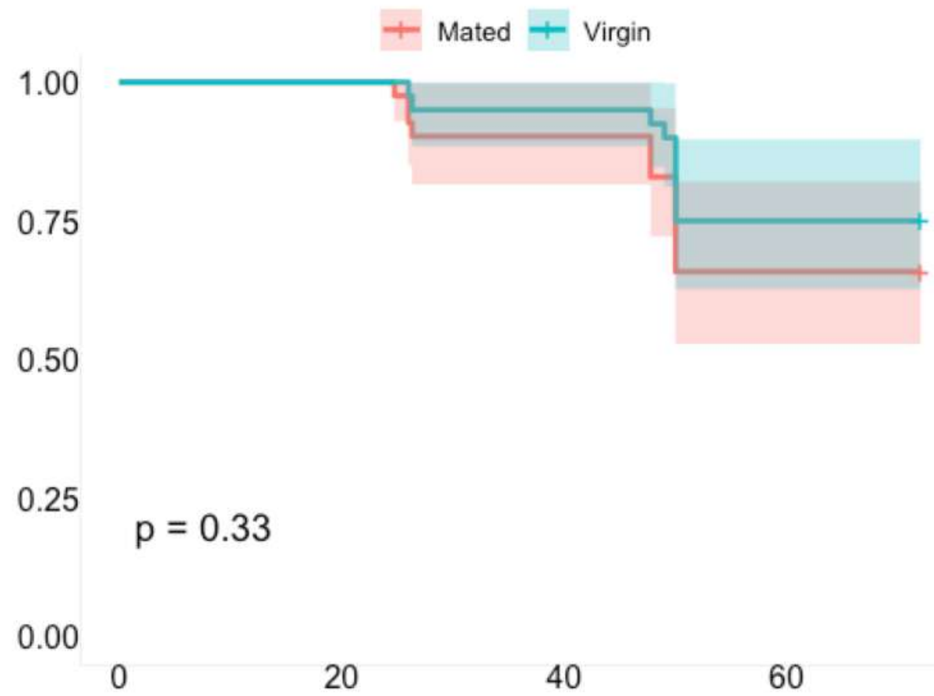
Survival

Gen 0

Gen 1

Gen 2

Results



Results

Gen 0 | Gen 1 | Gen 2

Line	Remained virgin	Attempted matings	Successful matings	proportion attempts successful
348	10	14	8	0.57
402	10	20	10	0.50
554	5	5	5	1.00
64	11	25	10	0.40
658	3	5	5	1.00
66	5	5	5	1.00
84	4	6	5	0.83
Sexual	18	23	22	0.96

Mating rates

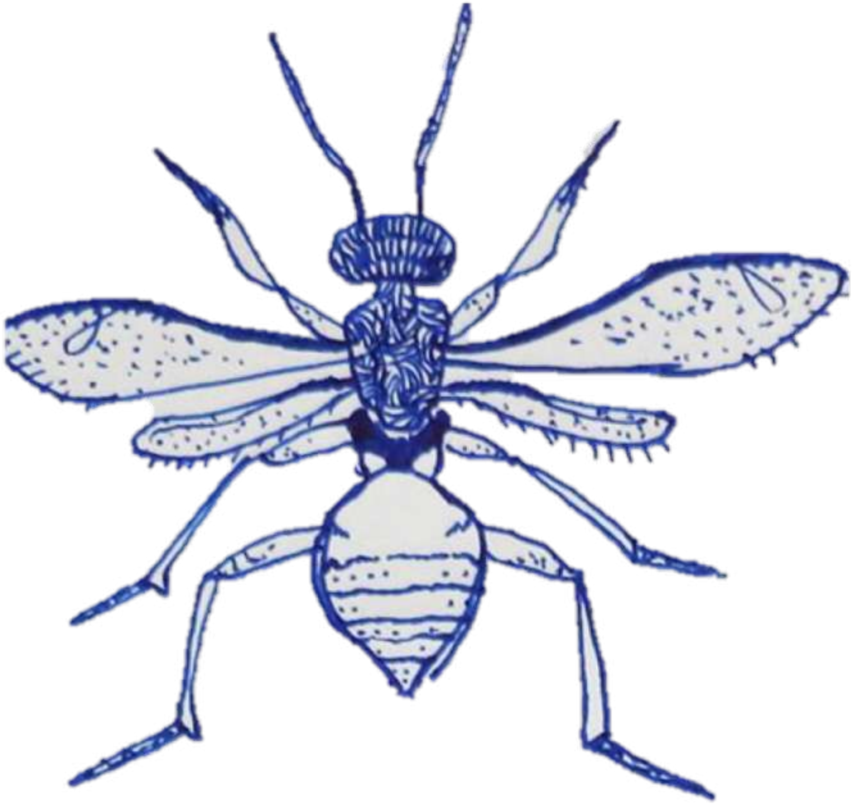
N = 128

What	When	Who
• Higher fitness	G2	Daughters of asexual mated females
• More daughters	G1 & G2	Asexual females

Predictions

Genetic benefits

No males



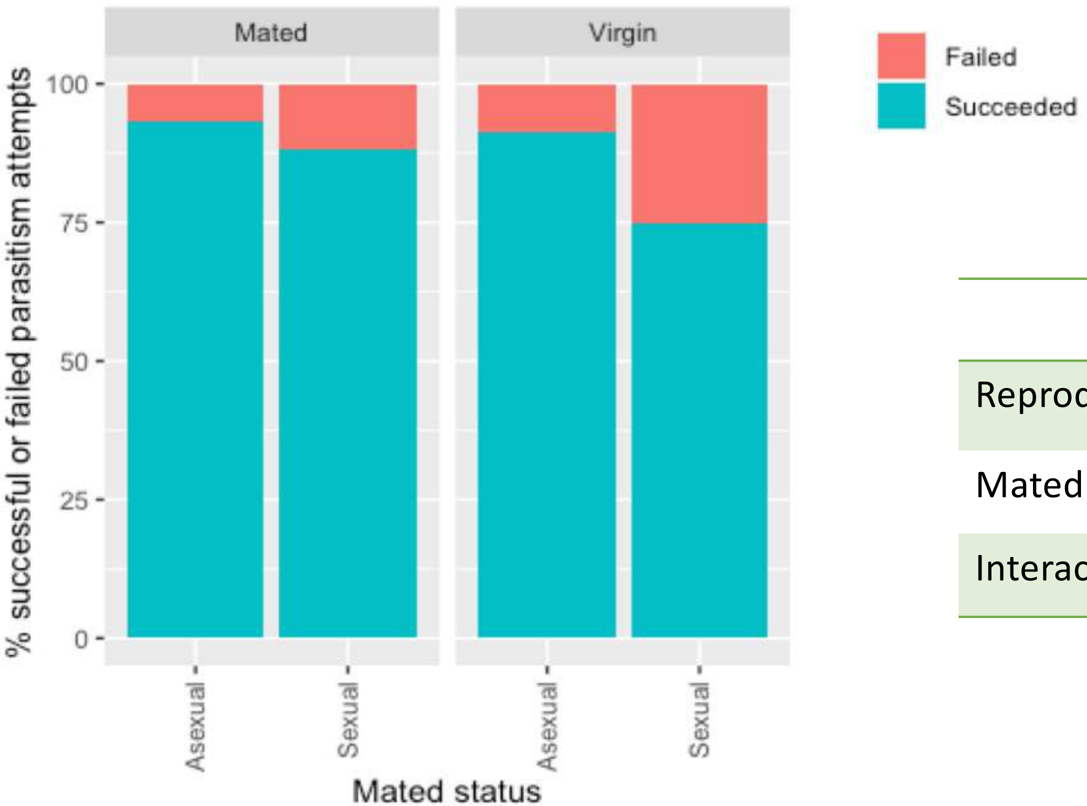
Parasitoid wasps

Diverse reproductive modes and mating systems

Results

Gen 0 | Gen 1 | Gen 2

Sexual females more likely to fail to parasitise than asexuals



	X^2	p
Reproductive mode	4.02	0.045
Mated status	1.35	0.245
Interaction	0.3	0.586

Results

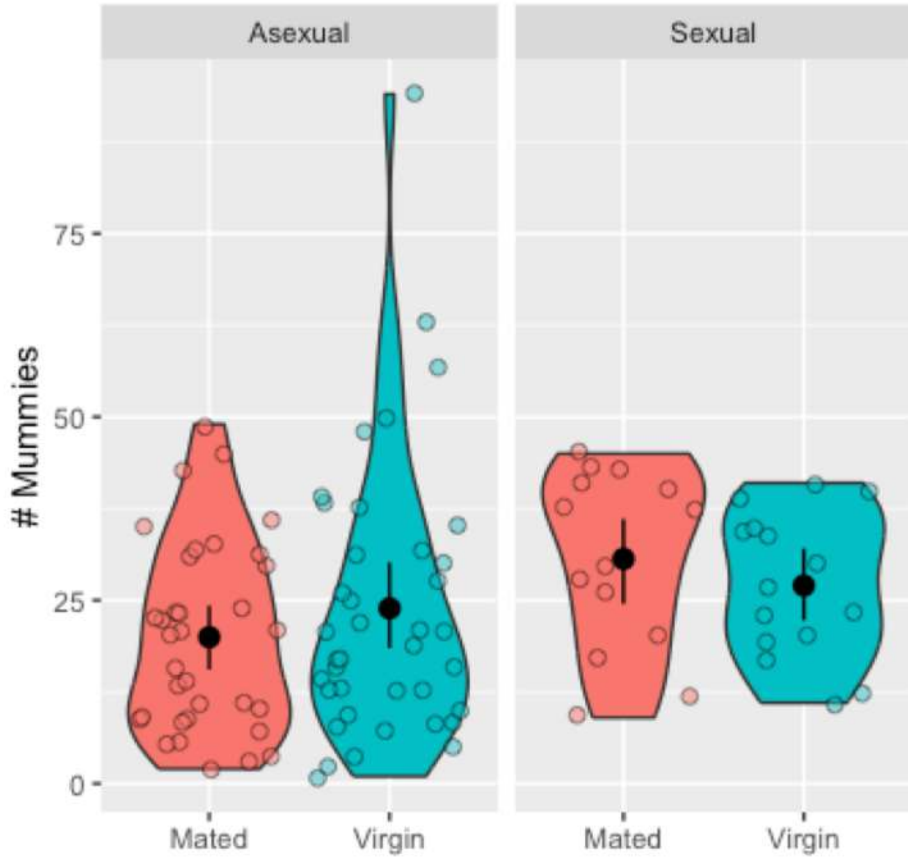
Gen 0

Gen 1

Gen 2

	X^2	p
Reproductive mode	5.29	0.021
Mated status	0.33	0.564
Interaction	0.24	0.627

Of the females that were successful (N = 102), sexuals produced more mummies

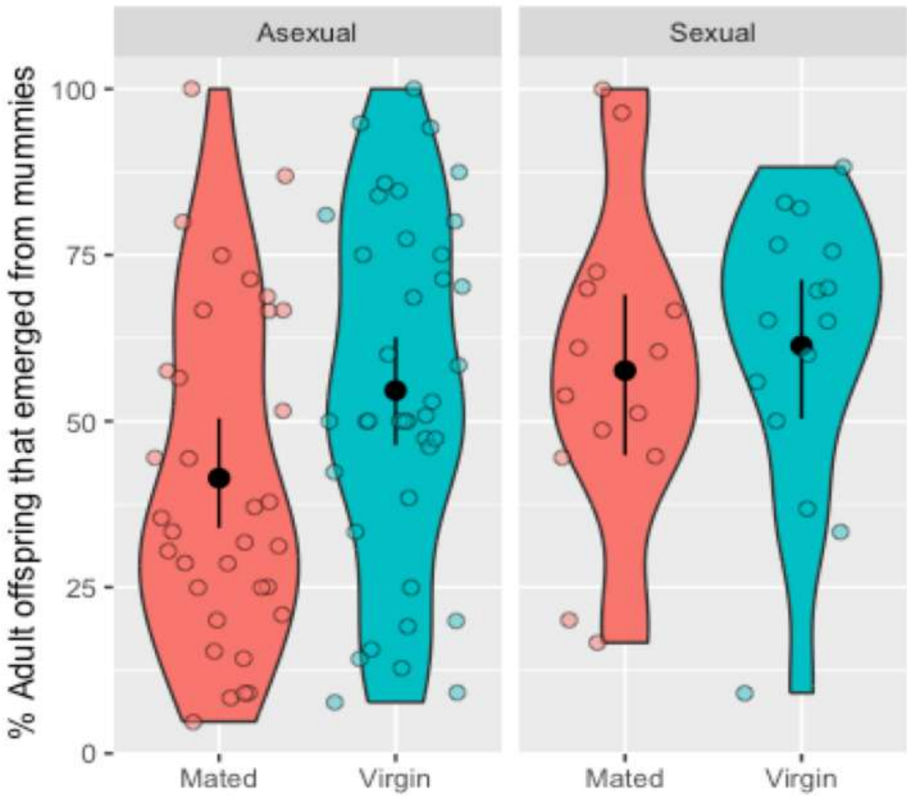


Gen 0

Gen 1

Gen 2

Results



	X^2	p
Reproductive mode	5.16	0.023
Mated status	4.25	0.039
Interaction	0.58	0.445

Higher proportions of adult wasps emerged from mummies produced by sexual females and by virgin females (sexual and asexual)

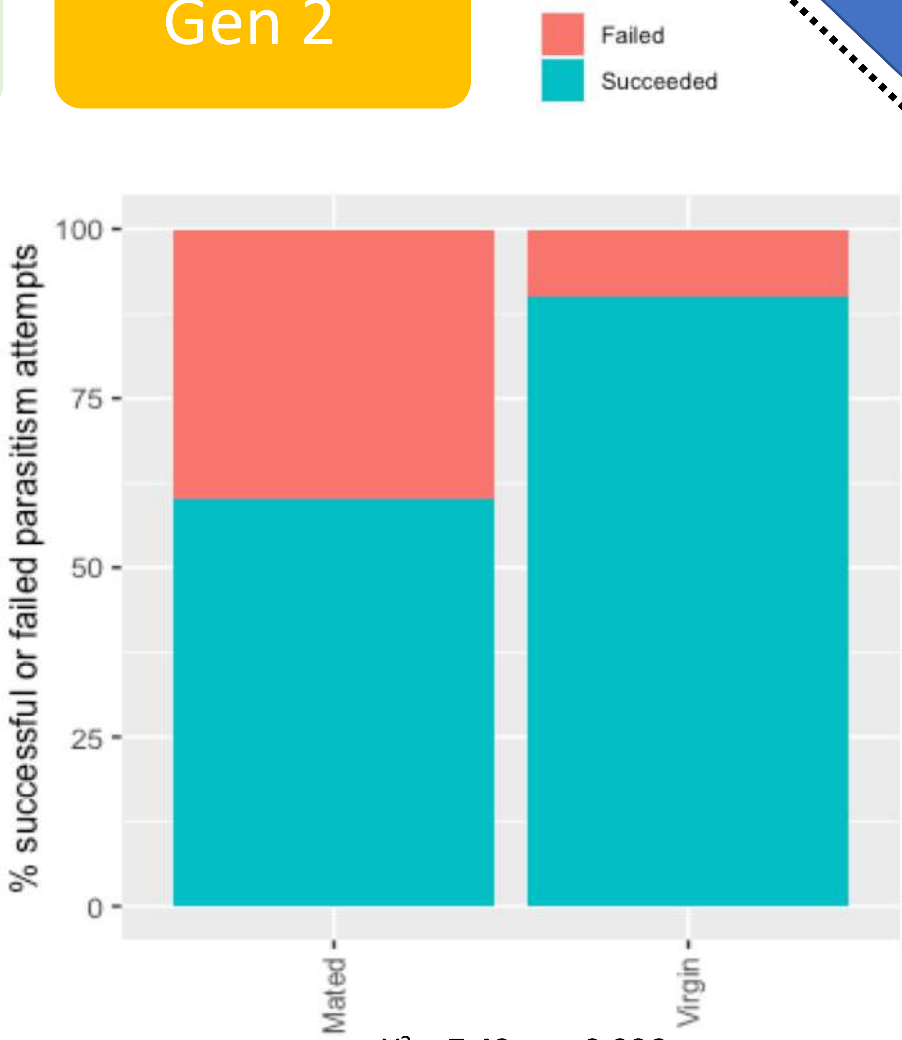
Gen 0

Gen 1

Gen 2

Results

Daughters of mated asexual females more likely to fail



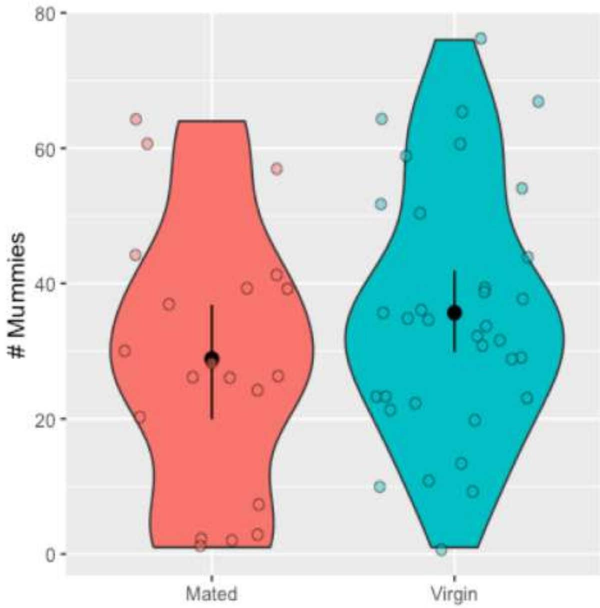
$X^2 = 7.43$, $p = 0.006$

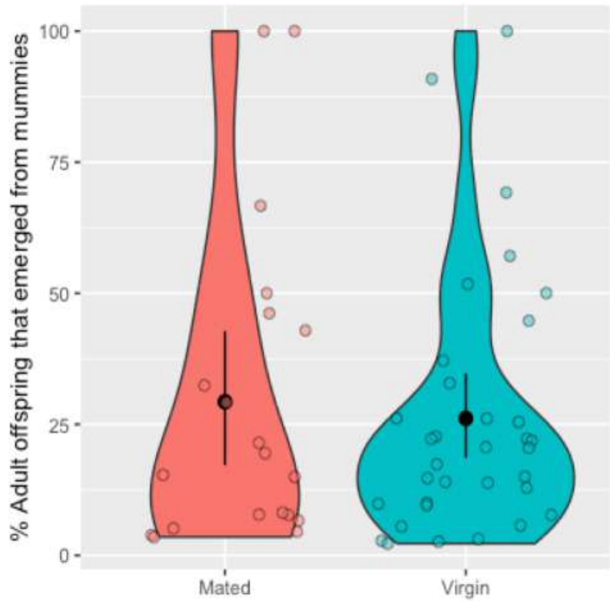
Gen 0

Gen 1

Gen 2

Results





For females that did successfully parasitise (N = 54) there was no effect of mothers mated status on mummy production or the proportion of mummies that successfully emerged

		X^2	p
Mummy production	Mothers mated status	2.41	0.12
Proportion emerged		0.20	0.64