CONFLICT, CLONING AND GENOME EVOLUTION IN THE CAPE HONEY BEE

Apis mellifera capensis

Part I: Maintenance of heterozygosity

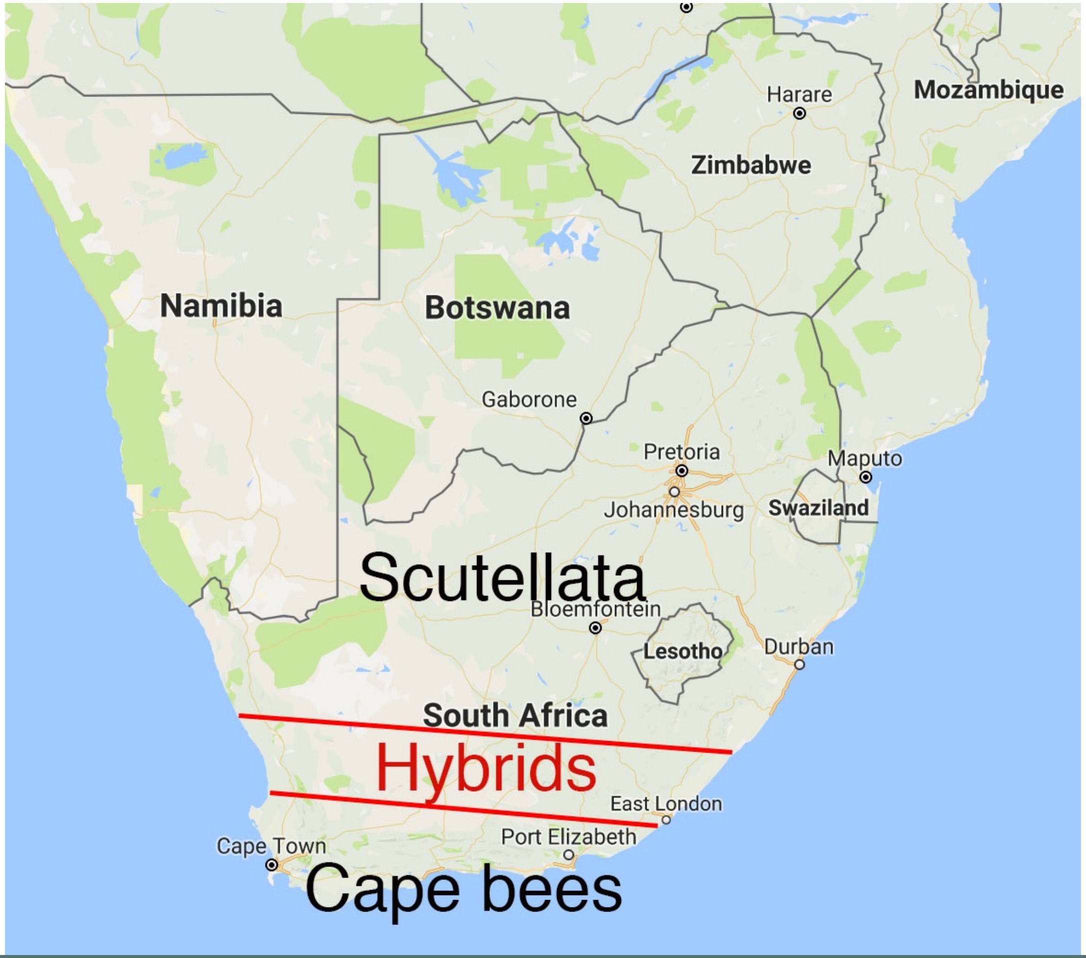
in a clonal system

Part II: Sexual conflict

in an asexual system

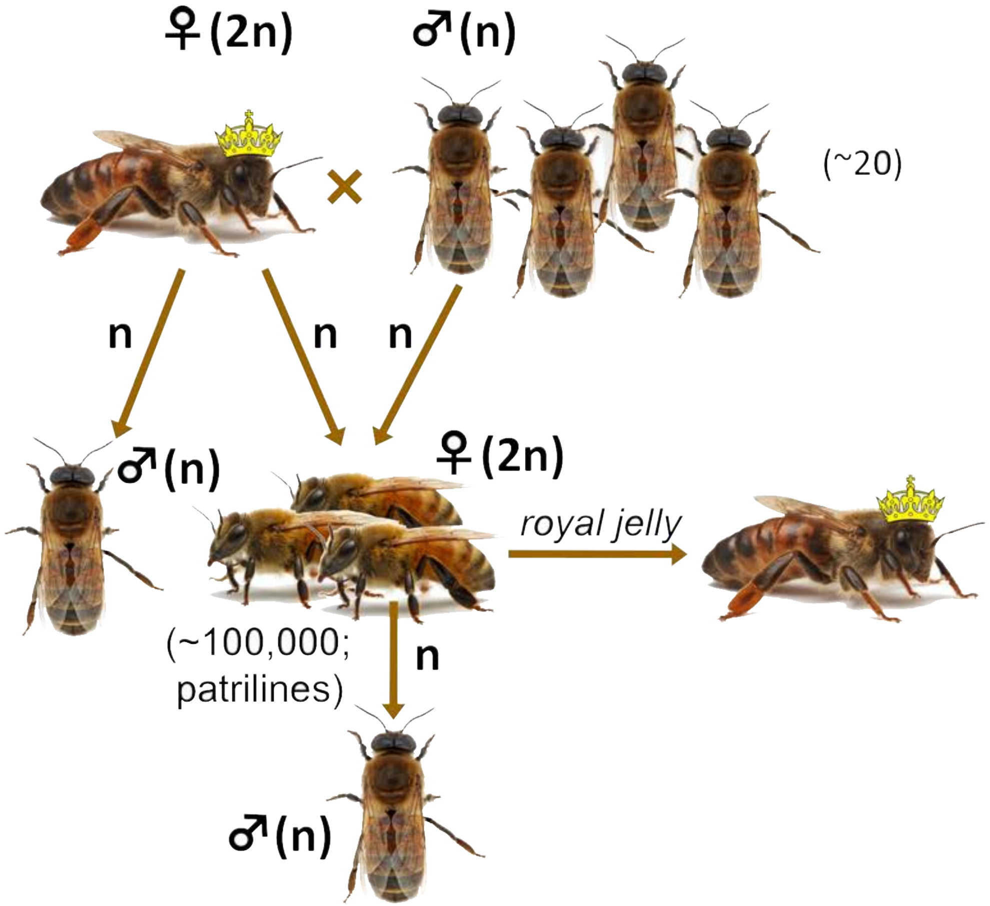
THE NEFARIOUS CAPE HONEY BEE CLONE – APIS MELLIFERA CAPENSIS

SOUTH AFRICAN HONEY BEES



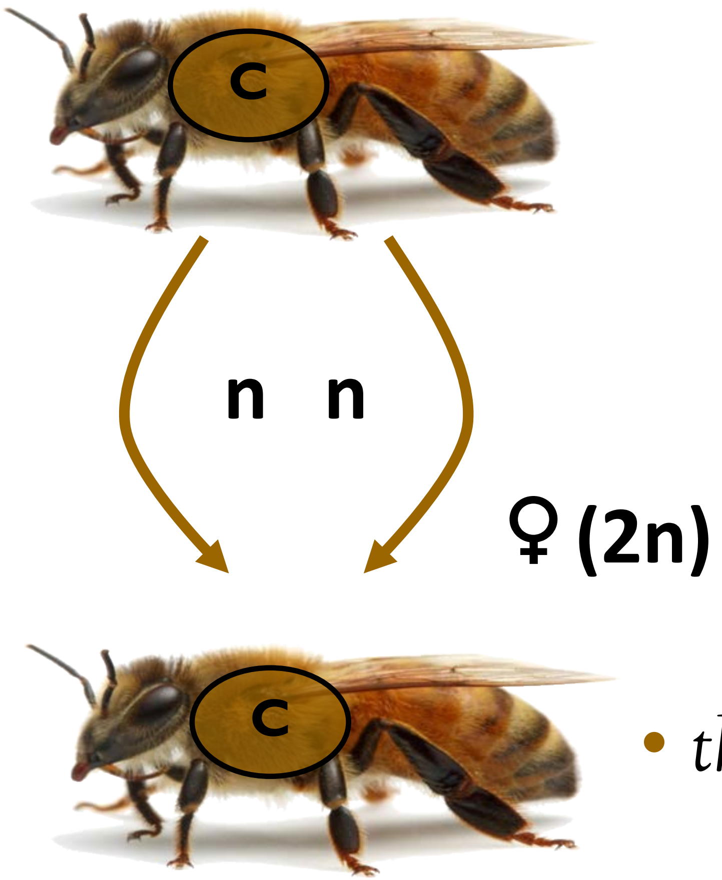
APIS MELLIFERA (MOST SUBSPECIES ARE LIKE THIS)

- *haplodiploid*
- *polyandrous*
- *arrhenotoky*



MEANWHILE, IN CAPE TOWN AND SURROUNDING AREAS…

A. m. capensis

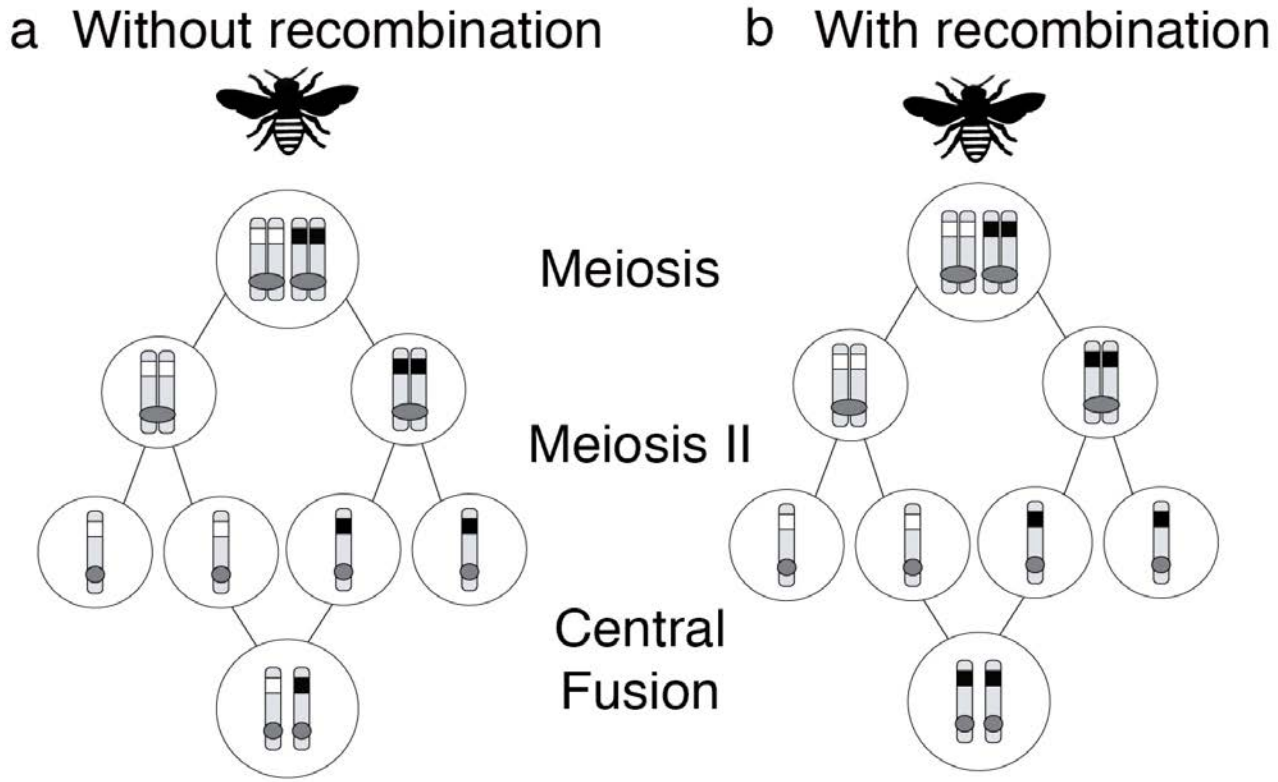


- *thelytoky*

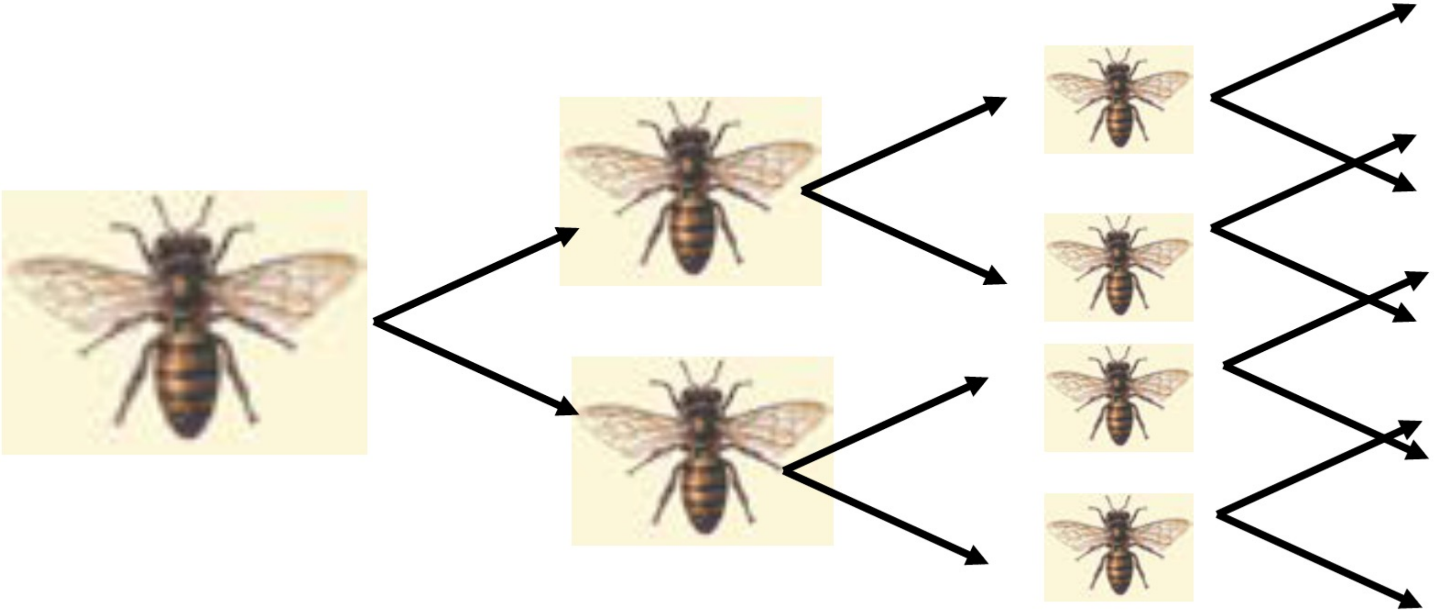
Thelytoky: two pronuclei of second division meiosis fuse to produce a clone of the mother

HOW ON EARTH DOES CAPENSIS DO THIS?

Automixis central fusion



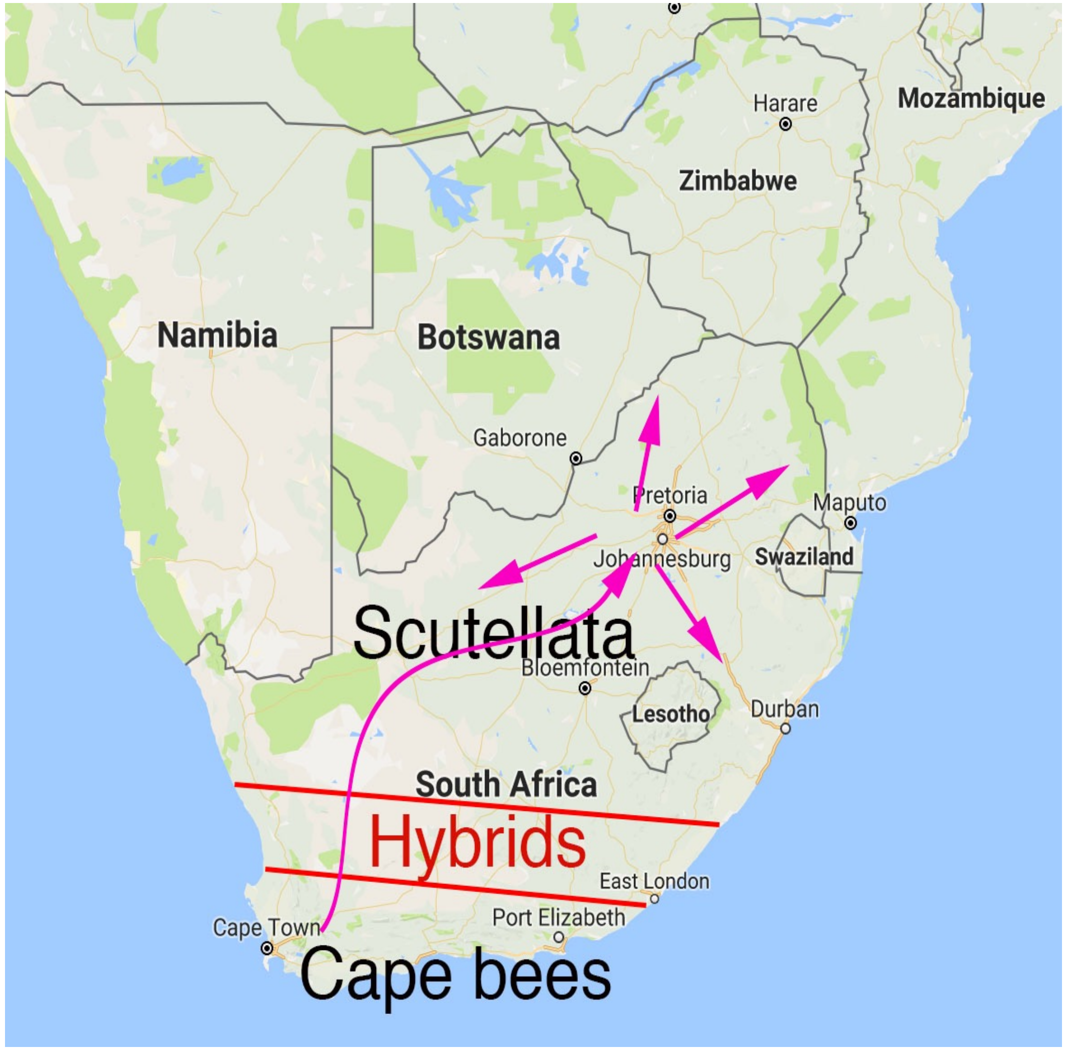
CONSEQUENCES OF THELYTOKY?



CONSEQUENCES OF THELYTOKY?

The emergence of Clonal lineages

WHERE DID THE CLONE COME FROM?

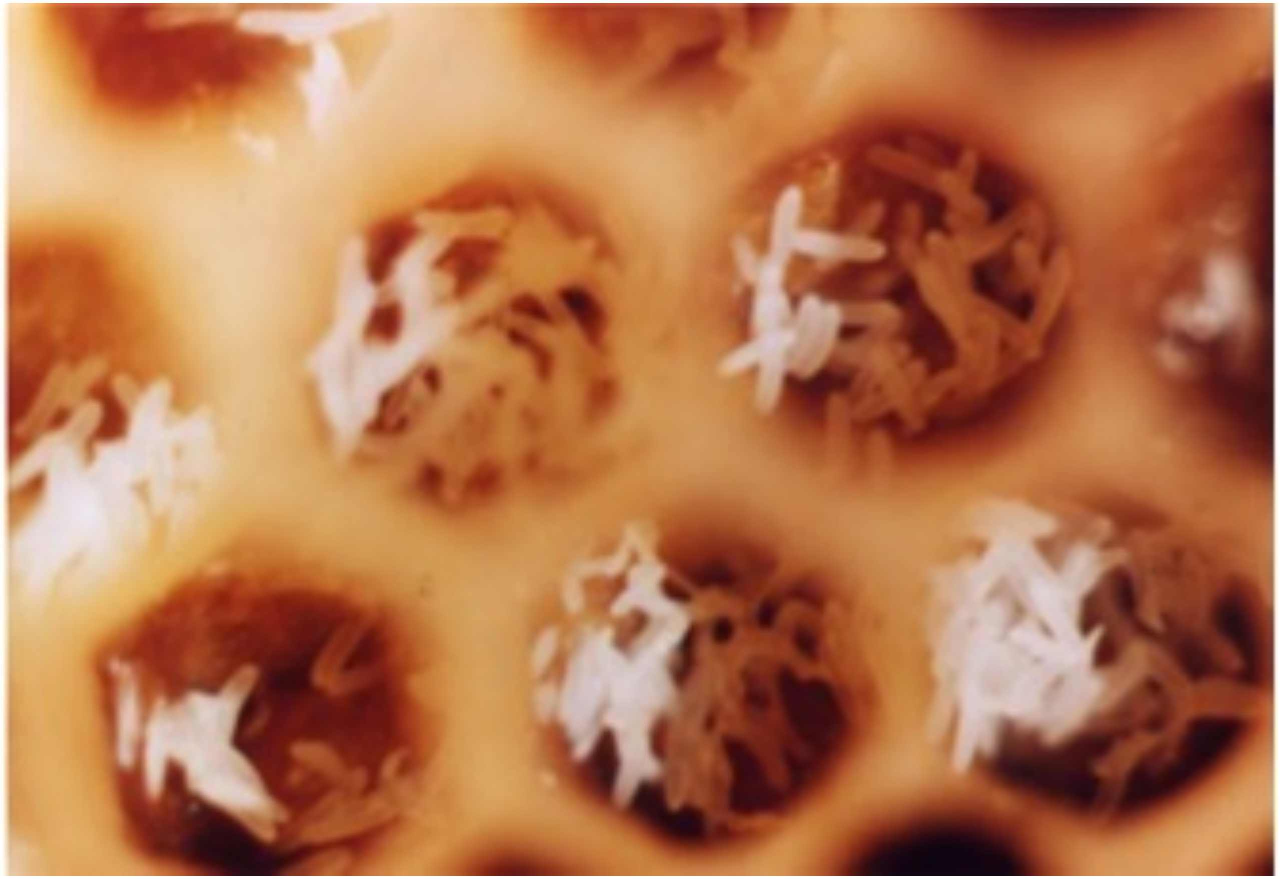


In 1990, 200 commercial Capensis colonies were introduced into the northern region of South Africa

Note: against the advice of many!

The current lineage consists of millions of workers that infest thousands of host colonies

all the descendants of a **single** worker!!!

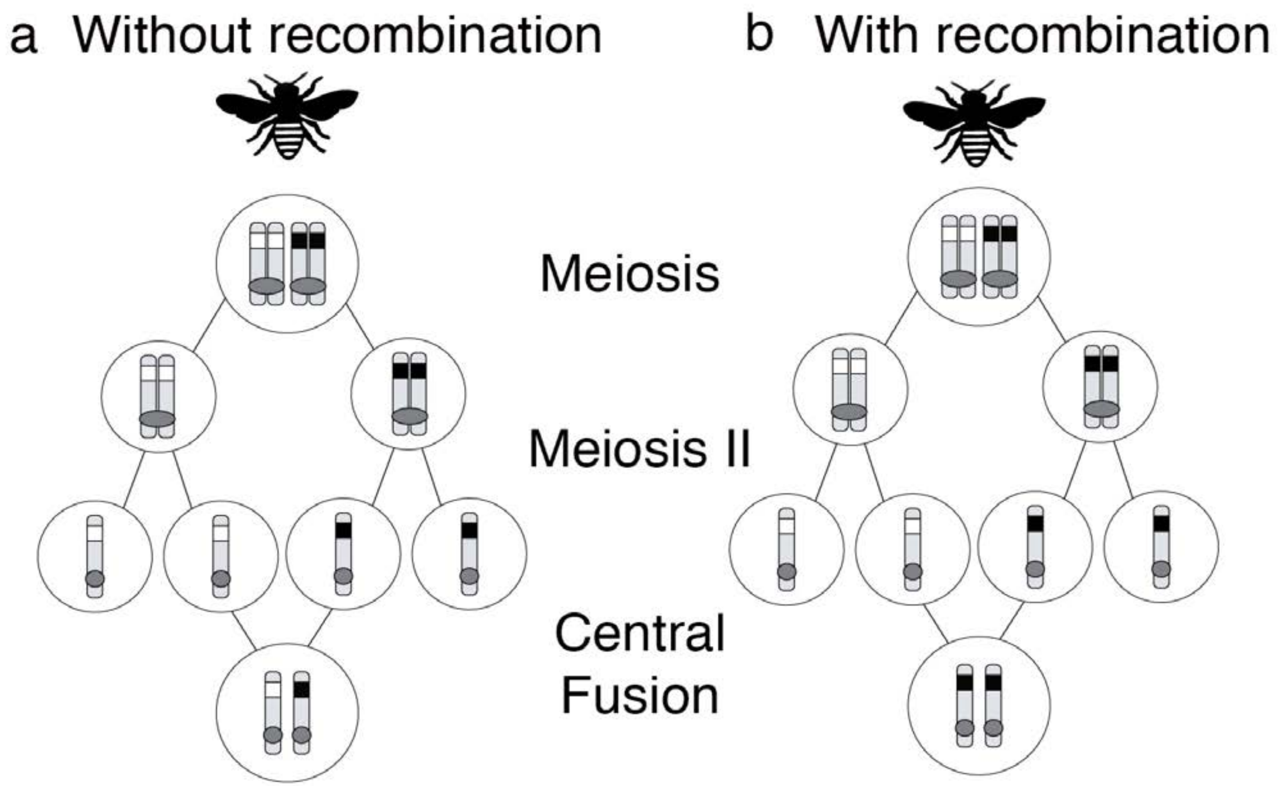


The invading clones and their offspring do zero colony work, all they do is lay eggs!

HOW THE CLONE CONTINUES TO FLOURISH IS BOTH INTRIGUING AND PUZZLING

REMEMBER IT AROSE IN 1990!

REMEMBER THIS SLIDE?

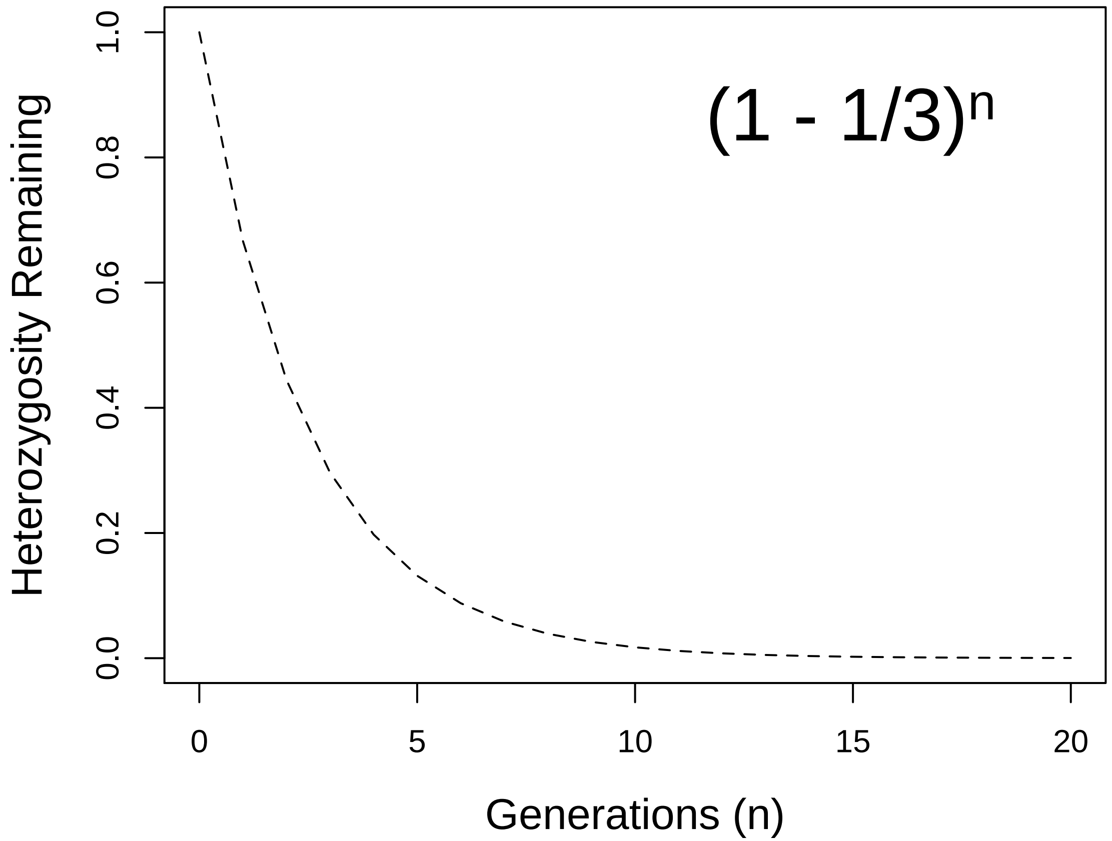


Honey bees have the highest rates of recombination that's ever been recorded!!

HOW ON EARTH DOES CAPENSIS DO THIS?

Automixis central fusion

HETEROZYGOSITY SHOULD BE LOST EVERY GENERATION WHERE LOCI ARE FREE TO RECOMBINE



Even with one generation per year should still be completely homozygous!

Inbreeding is catastrophic for honey bees

Time

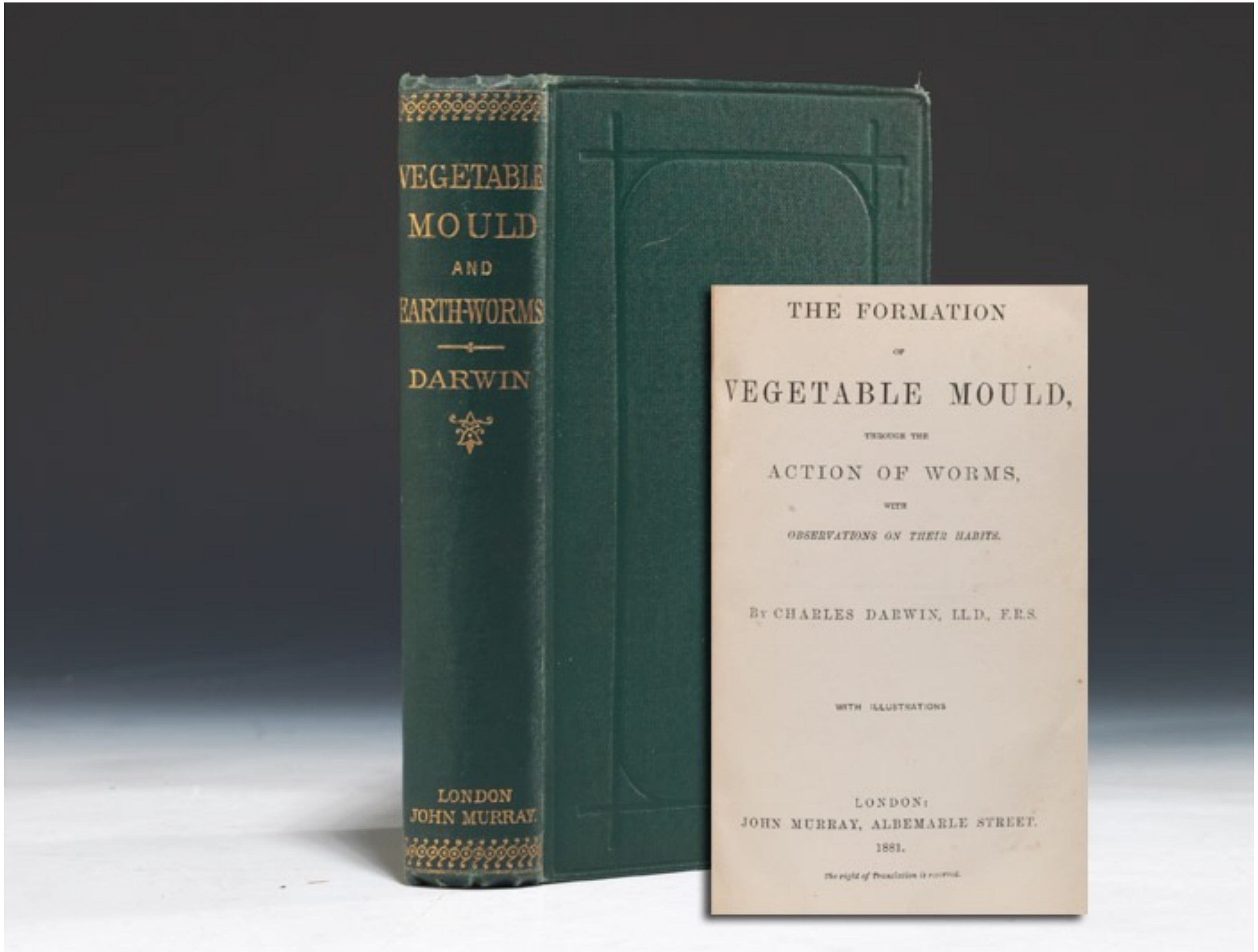
Expect fitness to decrease through time

Complementary *sex-determining* (CSD) locus

We know there must be heterozygosity in the Clone as she is female!

AB **Genotype** **AA**

Selection against homozygous individuals maintains heterozygosity at this locus



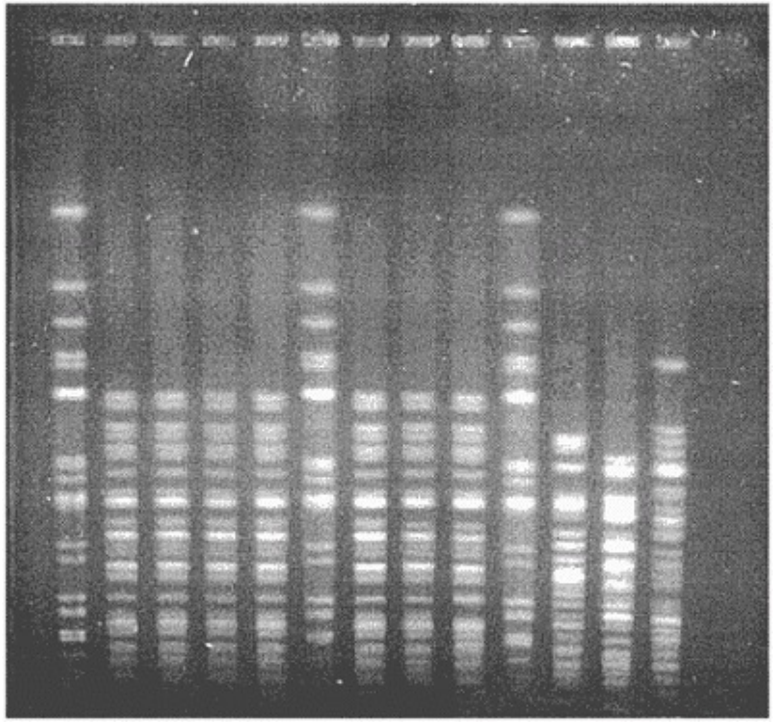
HETEROZYGOSITY, INBREEDING AND FITNESS

"It has been shown in the present volume that the offspring from the union of two distinct individuals, especially if their progenitors have been subjected to very different conditions, have an immense advantage in height, weight, constitutional vigour and fertility over the self-fertilised offspring from one of the same parents."

Heterozygosity and outcrossing

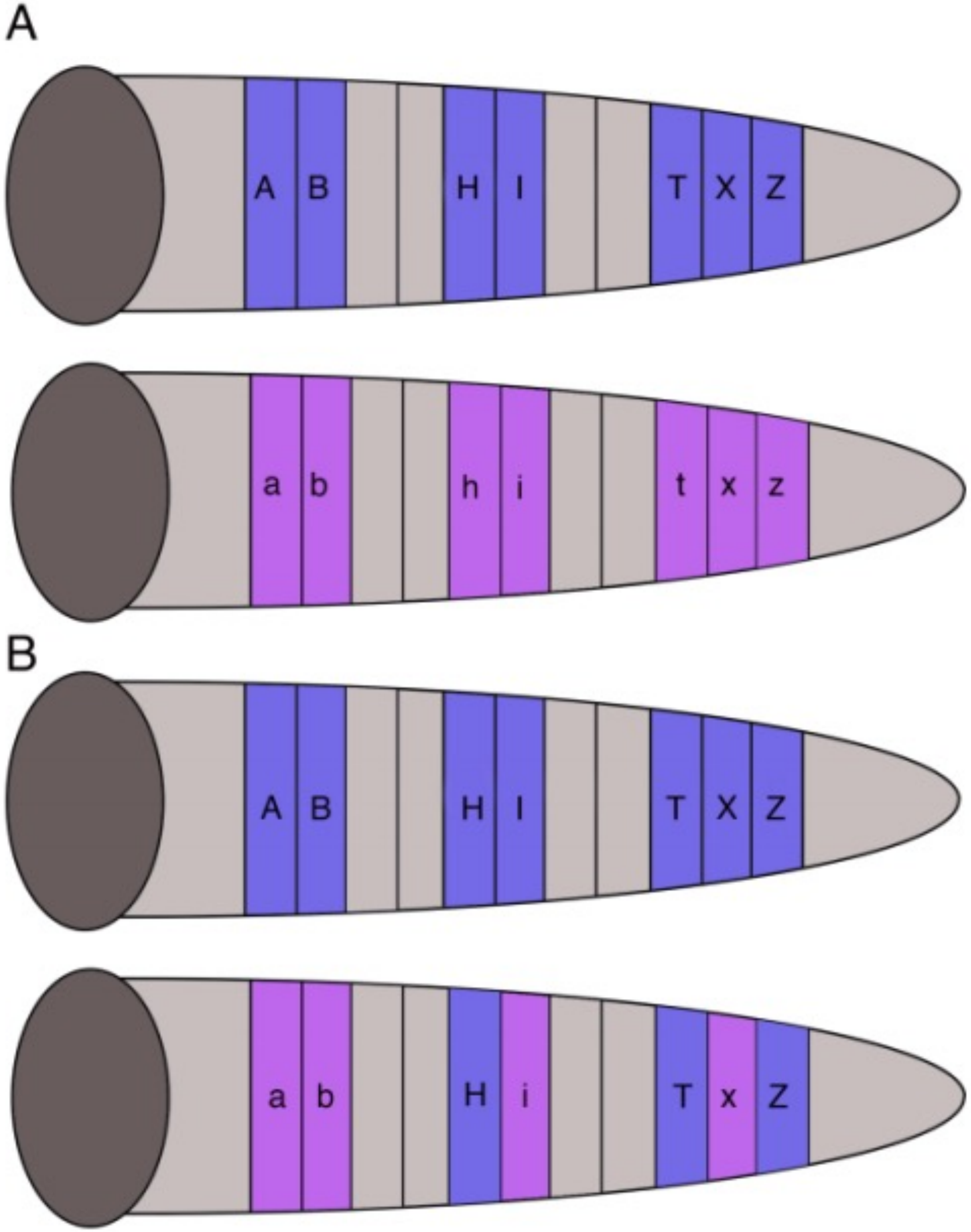
Homozygosity and inbreeding

HETEROZYGOSITY IS EVERYWHERE

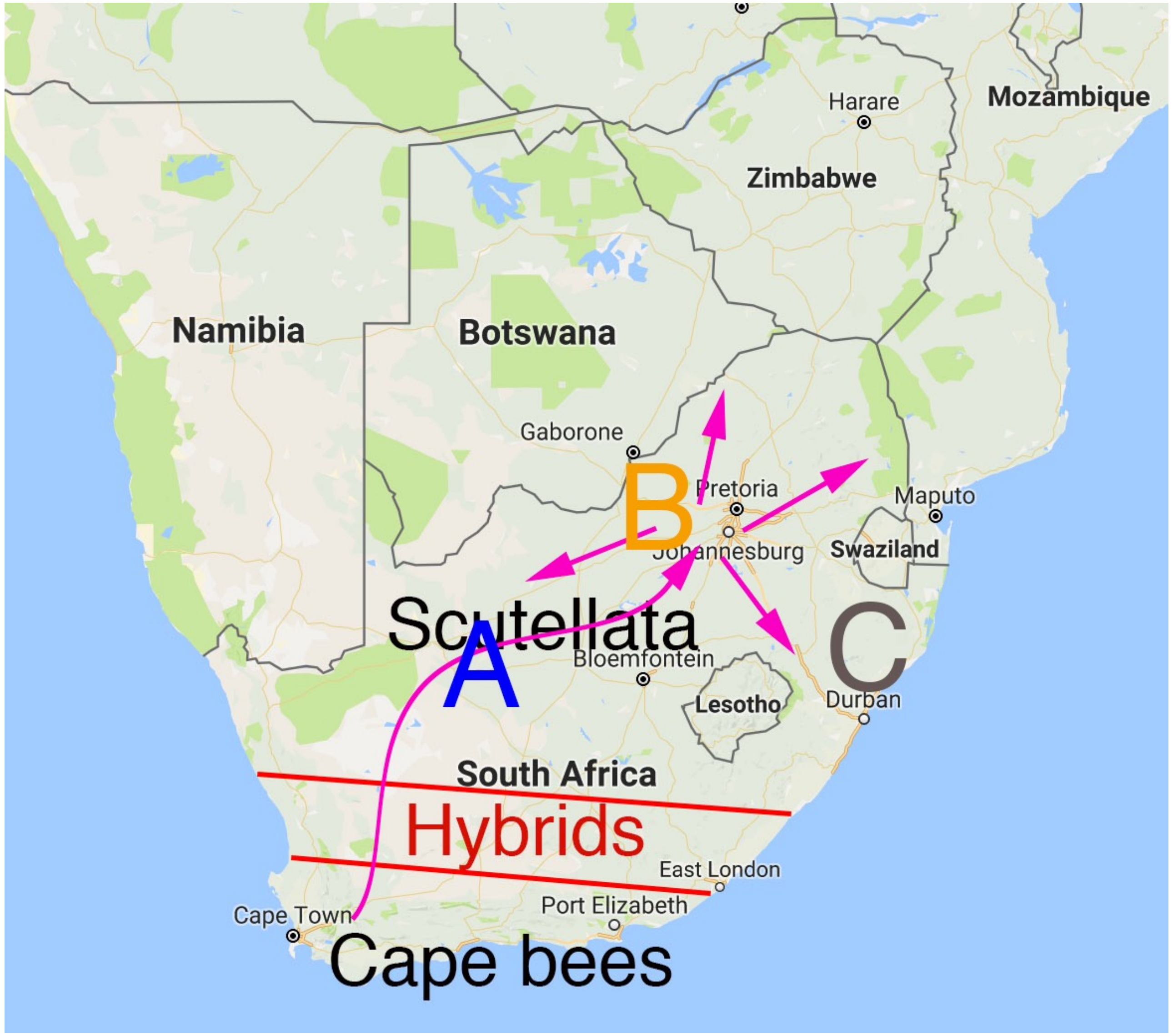


Lewontin and Hubby (1966)

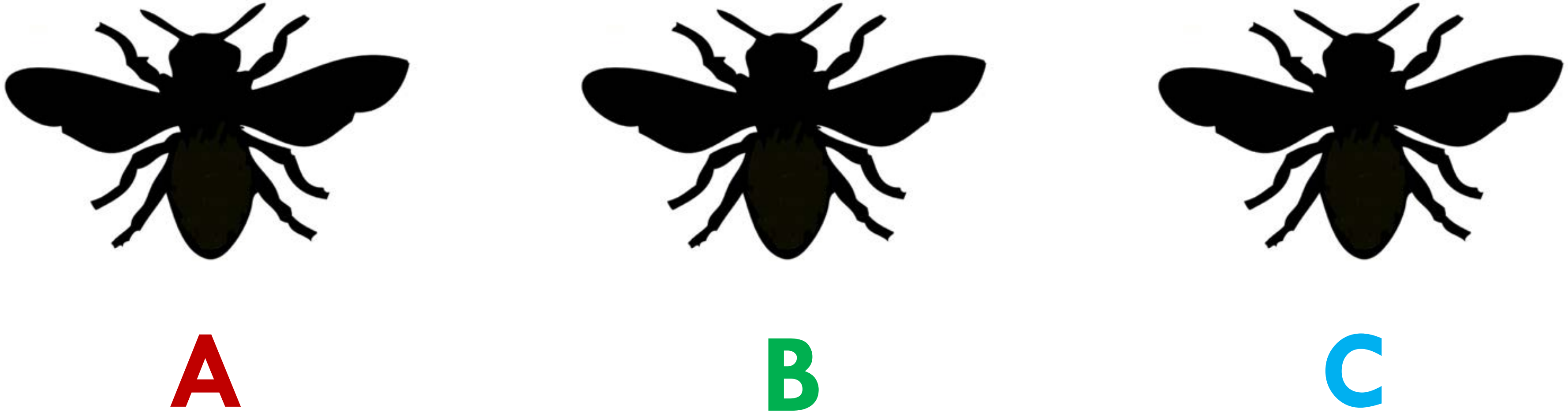
A LOT OR A FEW GENES NEED TO BE HETEROZYGOUS?

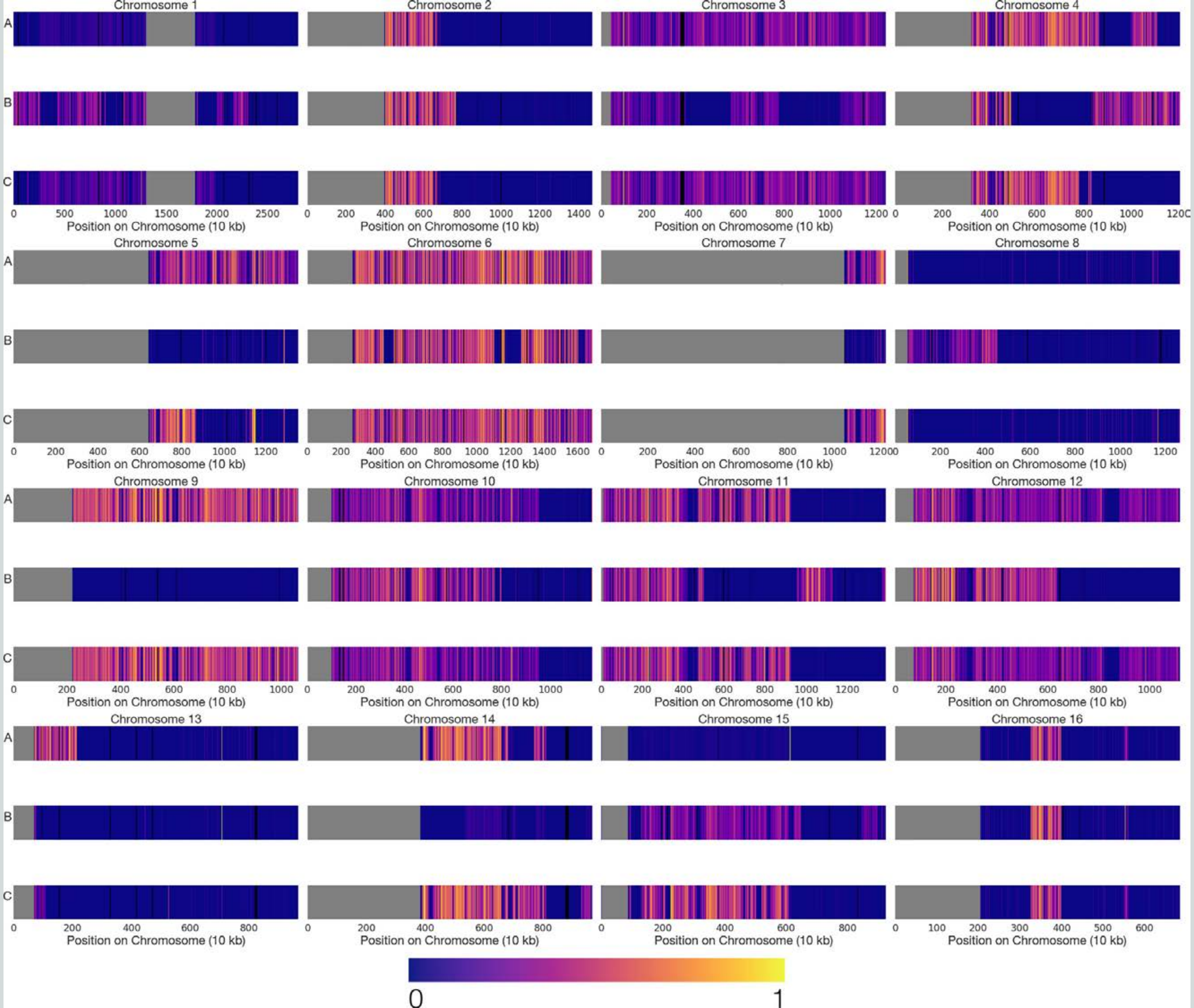


WHAT IS THE CLONE UP TO THESE DAYS?



Assessed genome-wide levels of heterozygosity in these three sublineages





Chromosome 1
Chromosome 2
Chromosome 3
Chromosome 4
Chromosome 5
Chromosome 6
Chromosome 7
Chromosome 8
Chromosome 9
Chromosome 10
Chromosome 11
Chromosome 12
Chromosome 13
Chromosome 14
Chromosome 15
Chromosome 16
A
B
C
Position on Chromosome (10 kb)
0
1

SUMMARY OF RESULTS

- Heterozygosity is maintained by heterozygote advantage at multiple loci on just about all chromosomes
- Vast heterogeneity among sublineages suggests that many of these over-dominant loci have only minimal fitness benefit
- Sub-lineage B is able to tolerate loss of heterozygosity at a number of these loci

INBREEDING EXPERIMENTS IN *DROSOPHILA* AND HETEROZYGOSITY

- *Drosophila* population inbred for 20 generations

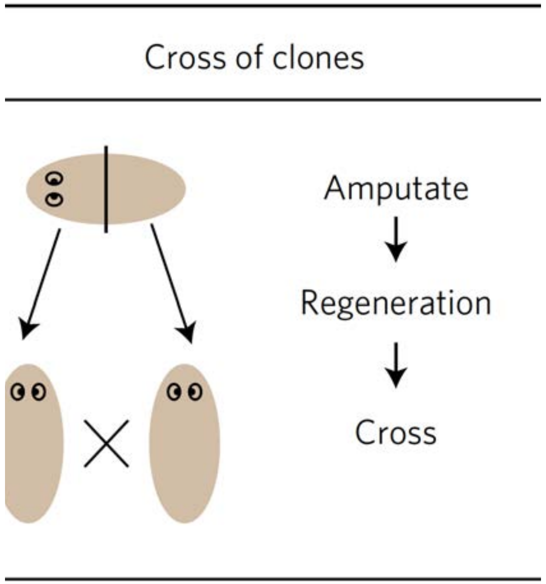
- After 20 generations, basically no heterozygosity left

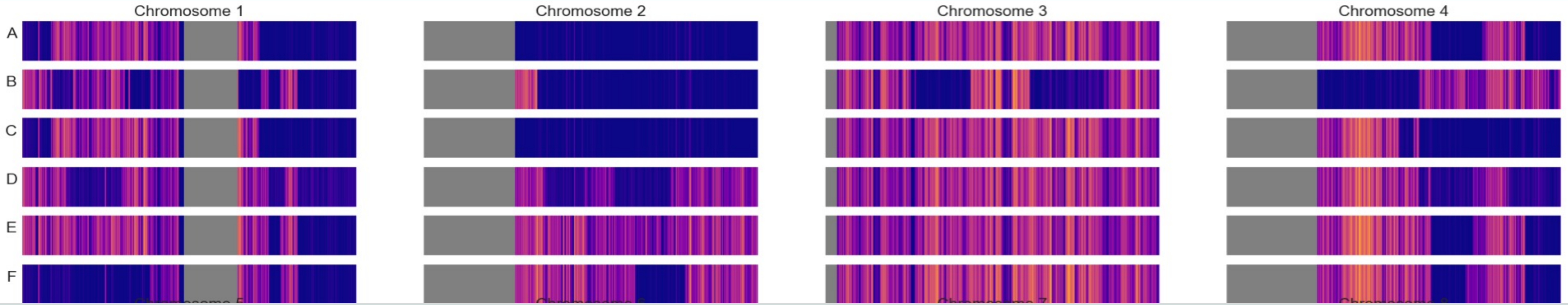
- Very different system to honey bees in some ways (population bottlenecks, low dispersal)

- Genetic architecture of *Drospohila* populations may reduce the importance of overdominant loci on genome evolution

INBREEDING EXPERIMENTS AND HETEROZYGOSITY IN PLANARIANS

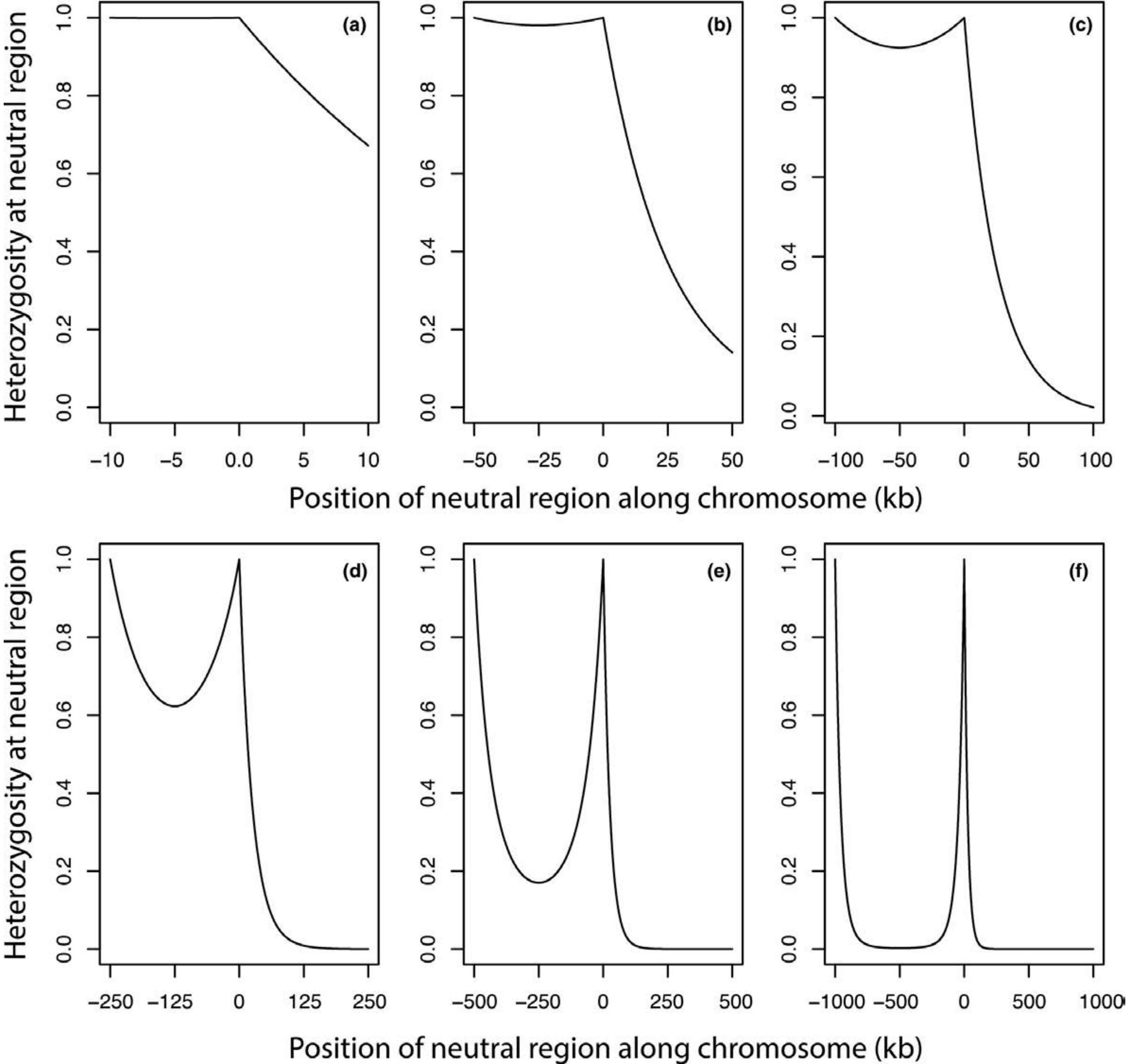
- Planarian population inbred for 10 generations
- Very little heterozygosity should remain
- 37.5% of genome remains heterozygous after 10 generations!!!
- Overdominant genes important for the survival and reproduction





A, B, C = 2011

D, E, F = 2016



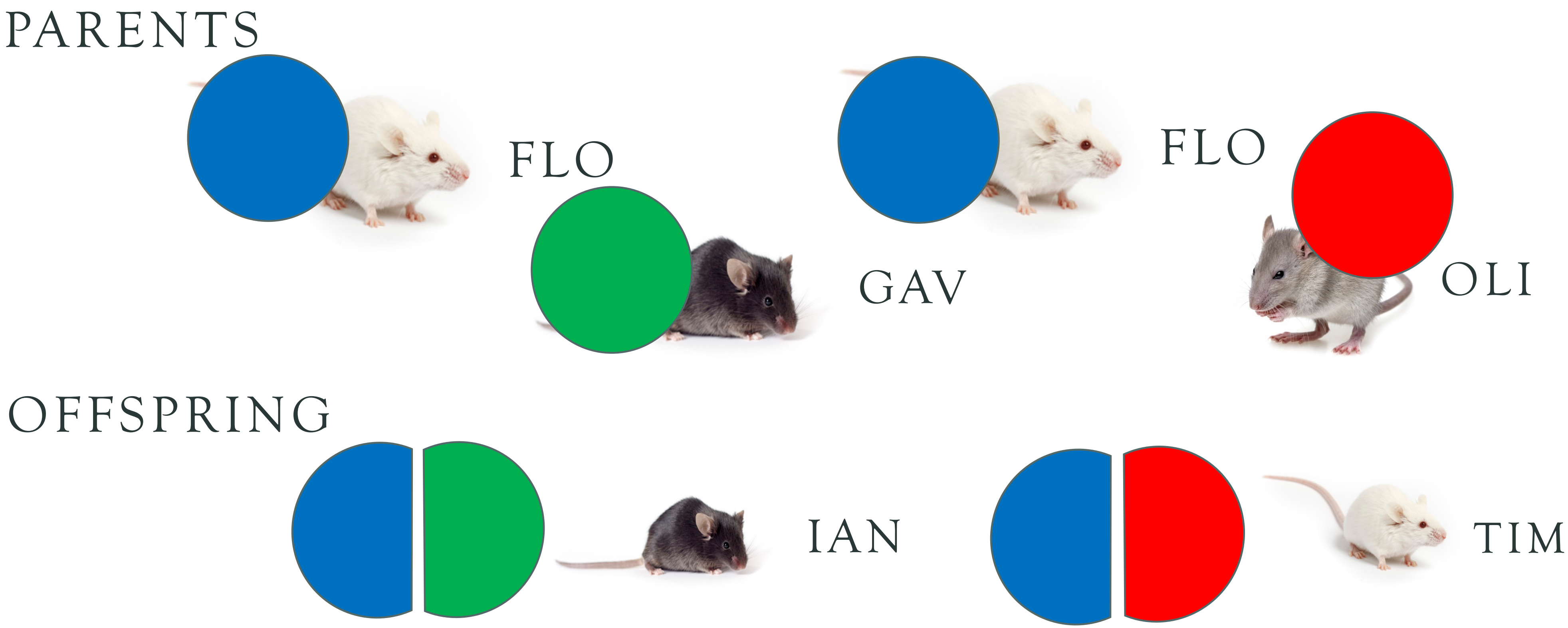
(a)
(b)
(c)
(d)
(e)
(f)
Heterozygosity at neutral region
Position of neutral region along chromosome (kb)

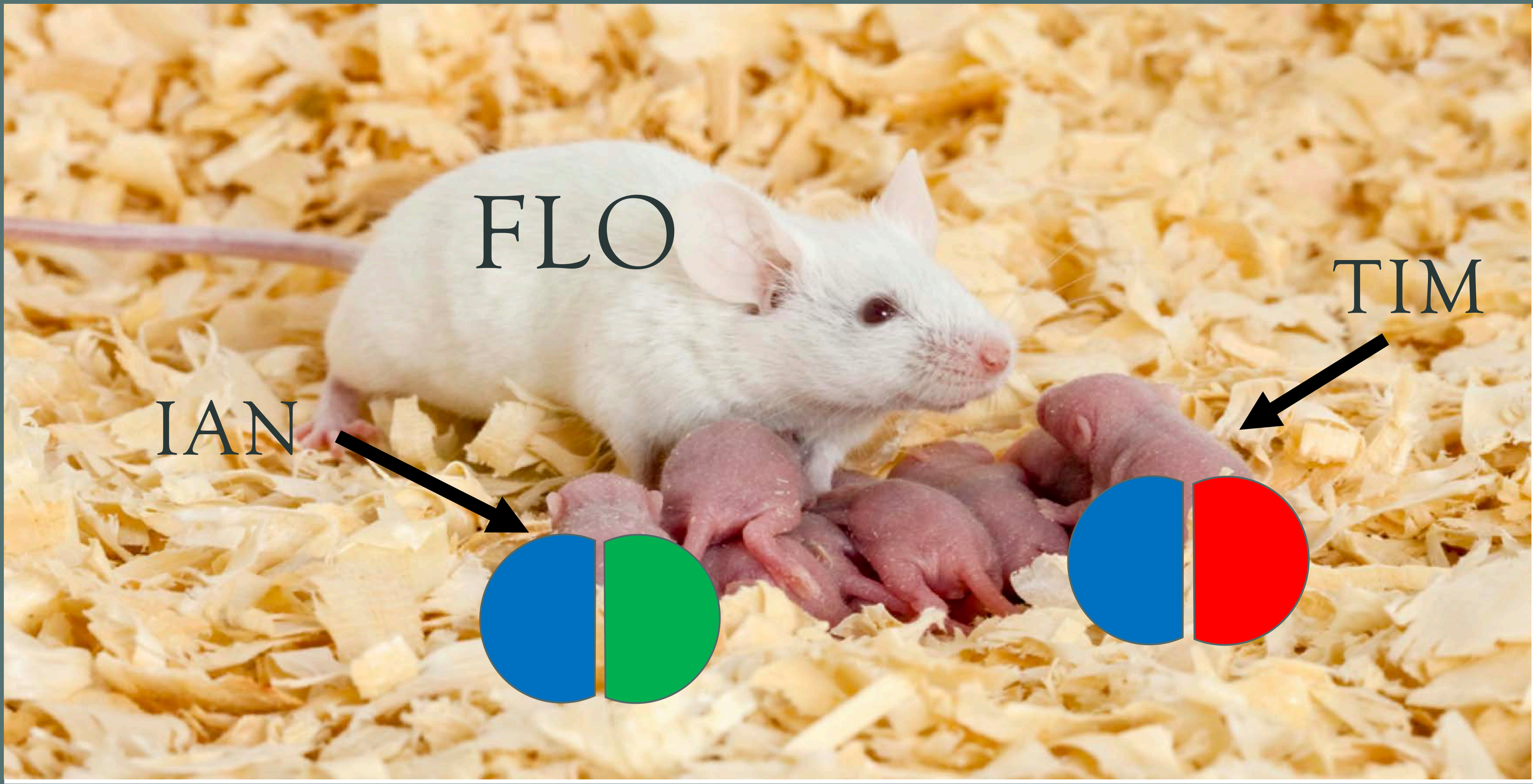
GENOMIC IMPRINTING IN HONEY BEES

POLYANDRY

FEMALES MATE WITH MULTIPLE MALES

POLYANDRY MEANS OFFSPRING HAVE A DIFFERENT FATHER




FLO
TIM
IAN

GAV WANTS HIS OFFSPRING (IAN) TO RECEIVE MORE RESOURCES THAN OLI'S (TIM)

GAV

OLI

FLO WANTS TO MAKE SURE HER OFFSPRING RECEIVE EQUAL RESOURCES

CONFLICTING PARENTAL ‘PLANS’ FOR OFFSPRING LEADS TO PARENT SPECIFIC GENE EXPRESSION

BOTH PARENTS GENES ARE NOT ALWAYS EQUALLY EXPRESSED IN OFFSPRING

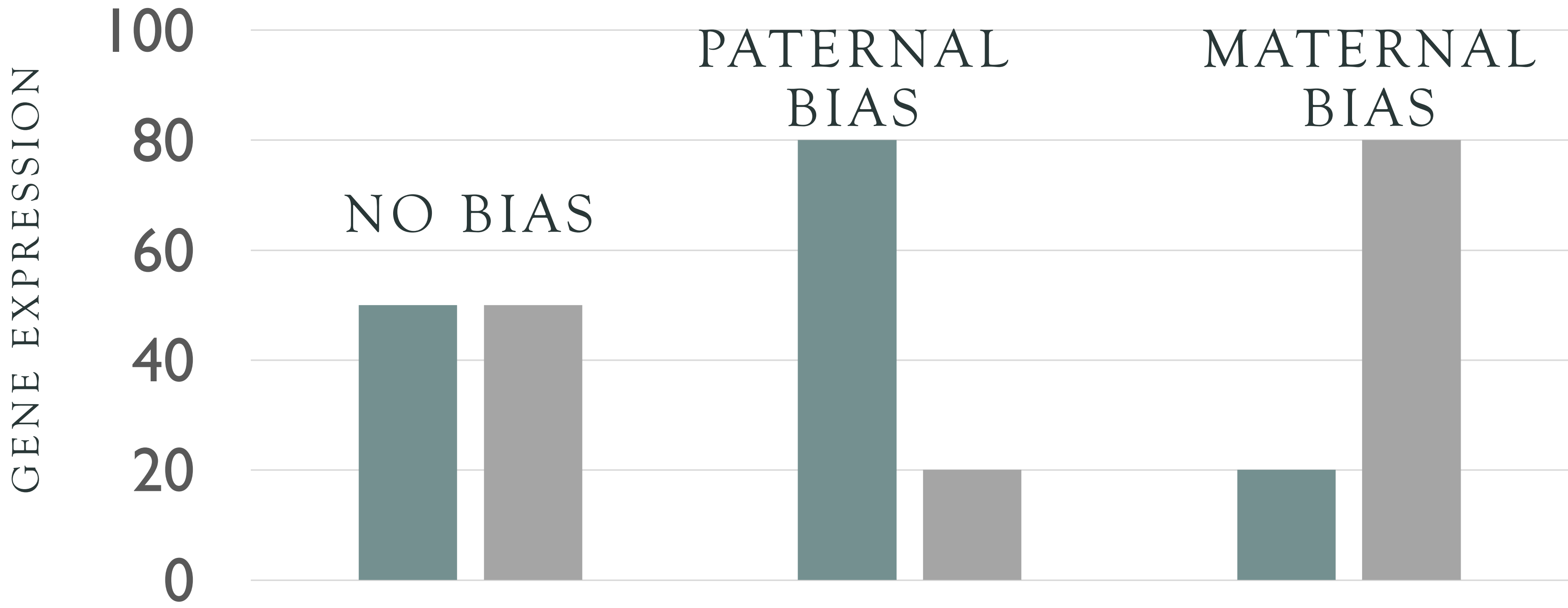
GENOME CAN BE DIVIDED INTO A PATERNAL AND MATERNAL CONTRIBUTION

PATERNAL

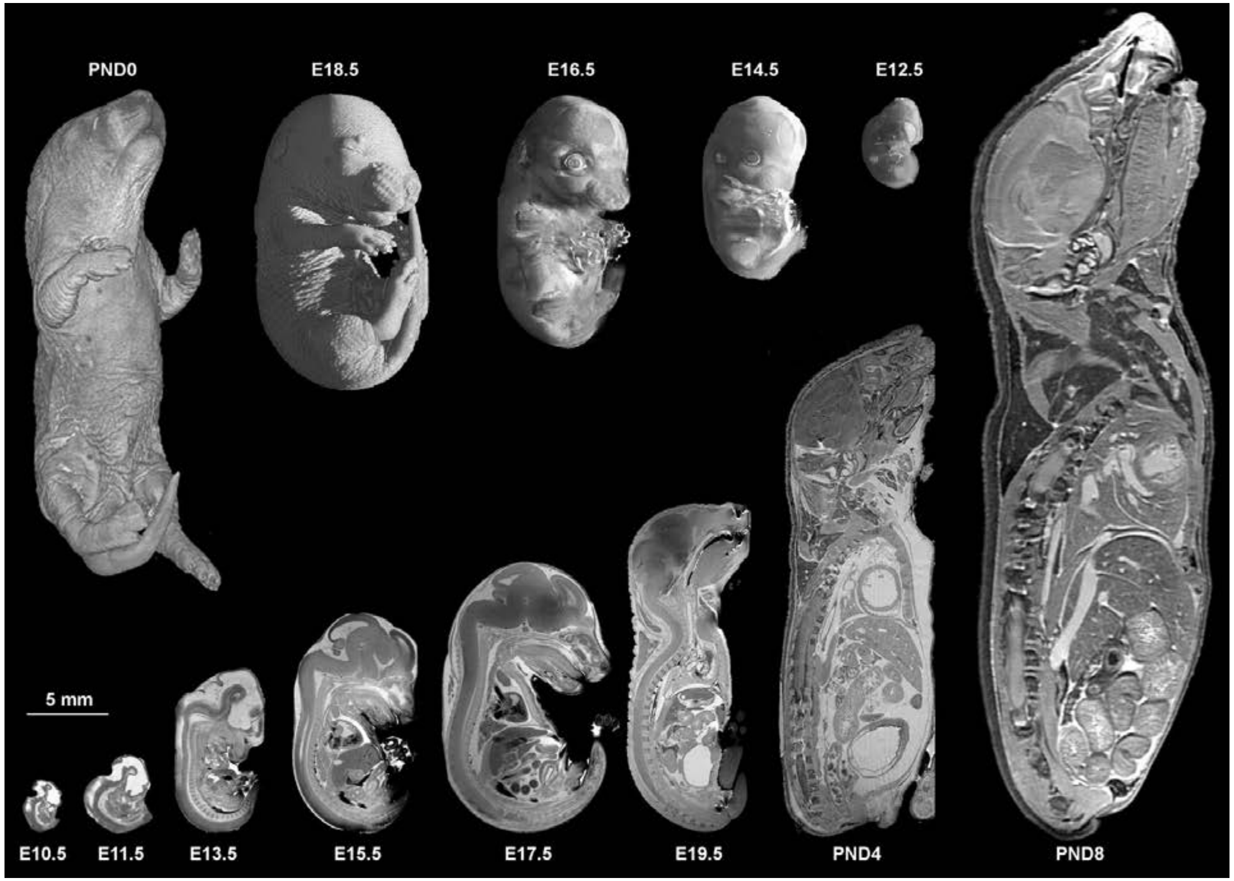
MATERNAL

BOTH PARENTS GENES ARE NOT ALWAYS EQUALLY EXPRESSED IN OFFSPRING

BOTH PARENTS GENES ARE NOT ALWAYS EQUALLY EXPRESSED



WHAT ARE MUM AND DAD'S GENES DOING WHEN MUM PROVISIONS HER OFFSPRING?



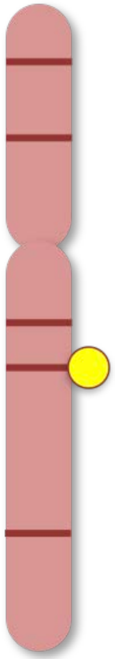
PREDICTION: PATERNAL BIAS IN EXPRESSION OF GENES THAT ARE ASSOCIATED WITH RESOURCE ACQUISITION

FLO WANTS TO MAKE SURE HER OFFSPRING RECEIVE EQUAL RESOURCES

CONFLICTING PARENTAL 'PLANS' FOR OFFSPRING LEADS TO PARENT SPECIFIC GENE EXPRESSION

RED = CHROMOSOME FROM FLO

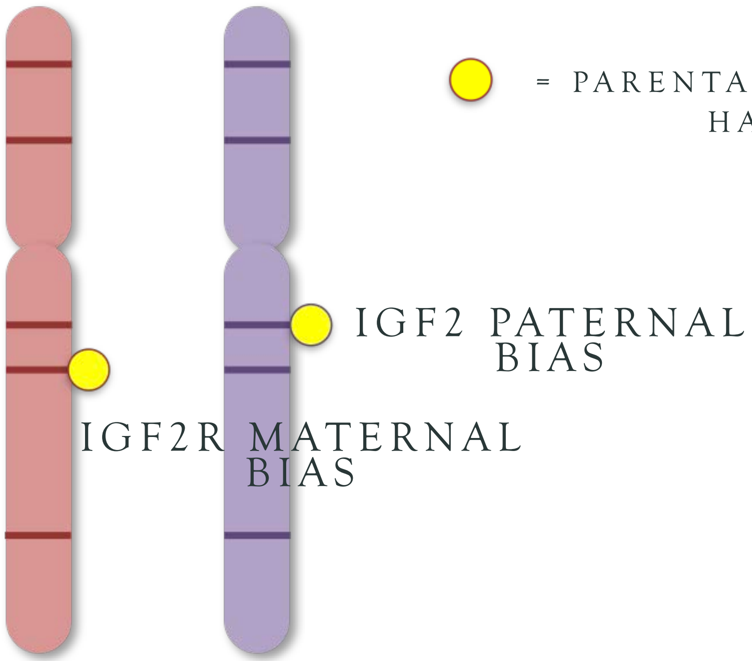
FLO



PURPLE = CHROMOSOME FROM GAV

GAV

CONFLICTING PARENTAL ‘PLANS’ FOR OFFSPRING LEADS TO PARENT SPECIFIC GENE EXPRESSION



= PARENTAL BIAS IN GENE EXPRESSION HAS BEEN IDENTIFIED

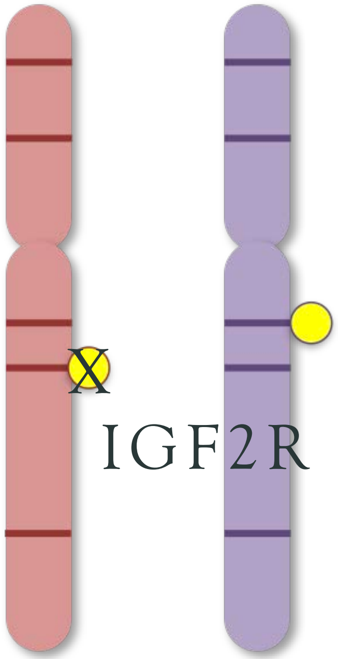
WHAT ARE THESE TWO GENES?

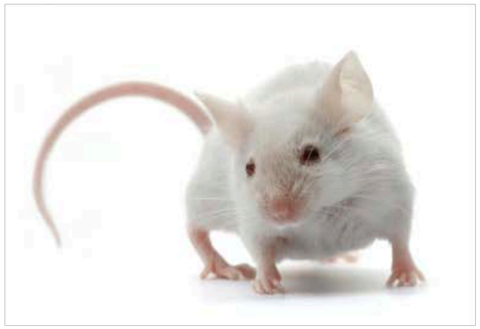
INSULIN LIKE GROWTH FACTOR (IGF2)

WHAT ON EARTH DOES IT DO?

HOW DO WE KNOW WHAT THEY DO?

LET'S DELETE IGF2R AND SEE WHAT HAPPENS TO AN INDIVIDUAL'S WEIGHT



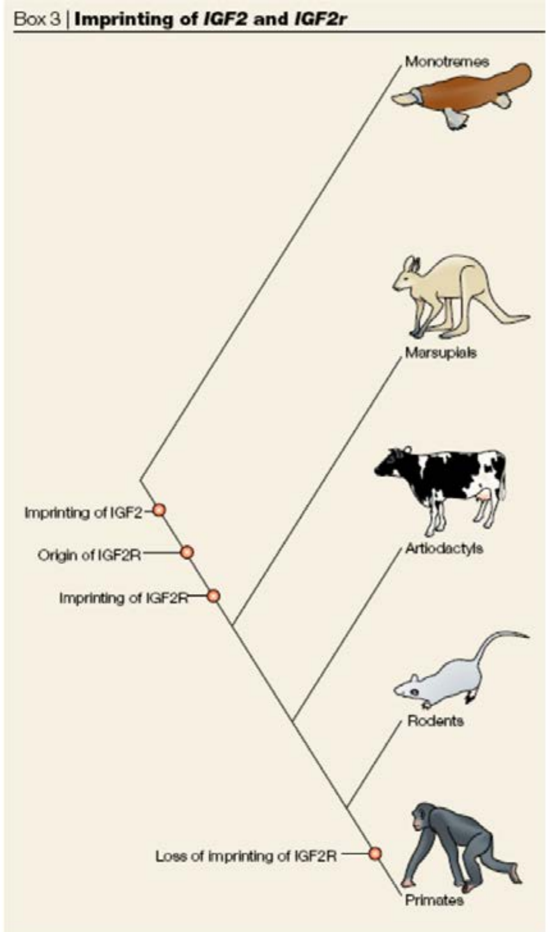


Normal weight (IGF2 and IGF2r)

125-130% of normal weight (Deletion of IGF2r)

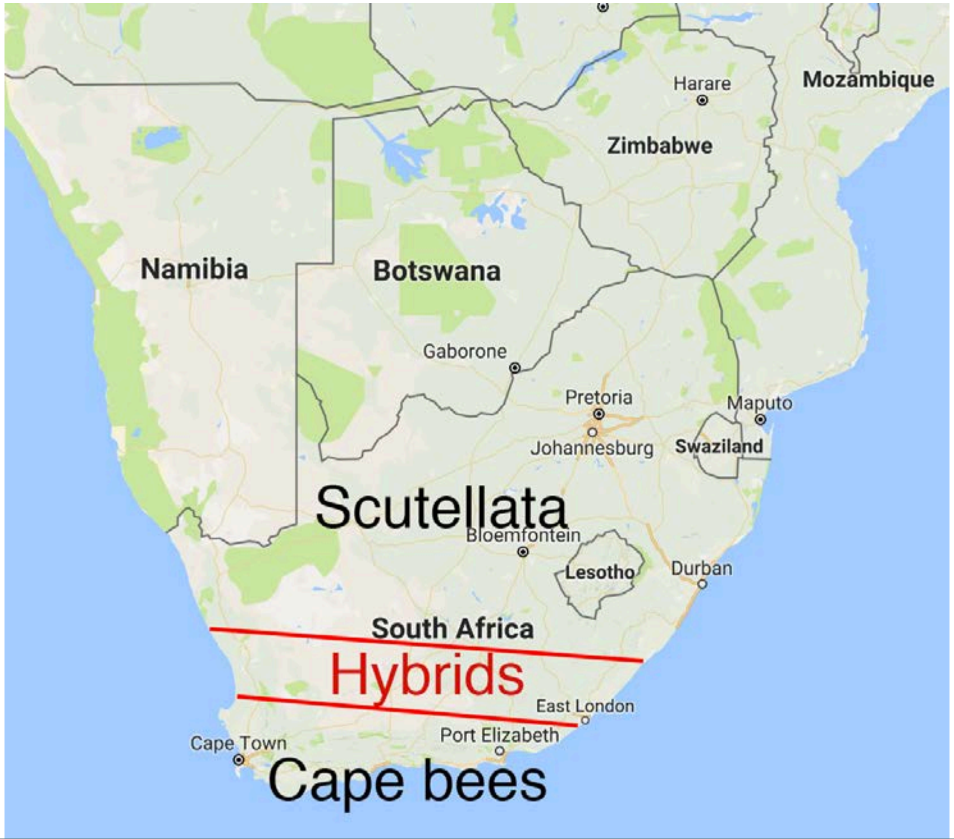
THESE PARENT SPECIFIC GENE EXPRESSION PATTERNS ARE DEEPLY CONSERVED

BUT WHAT ABOUT OTHER ORGANISMS?



18.19. The phylogenetic sequence of evolution of genomic imprints

SOUTH AFRICAN HONEY BEES



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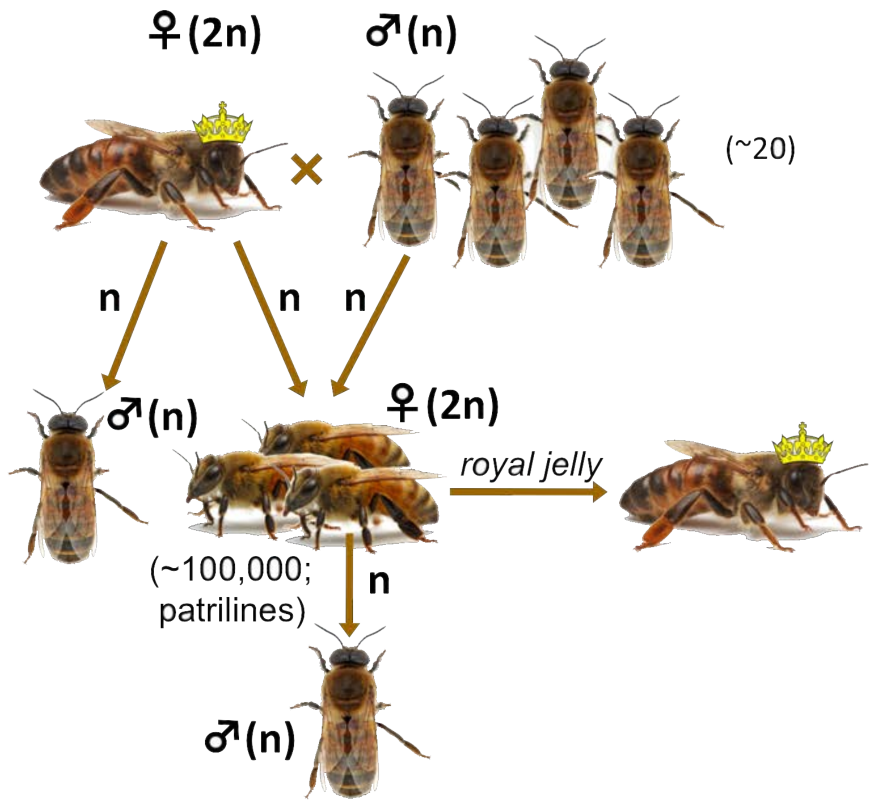
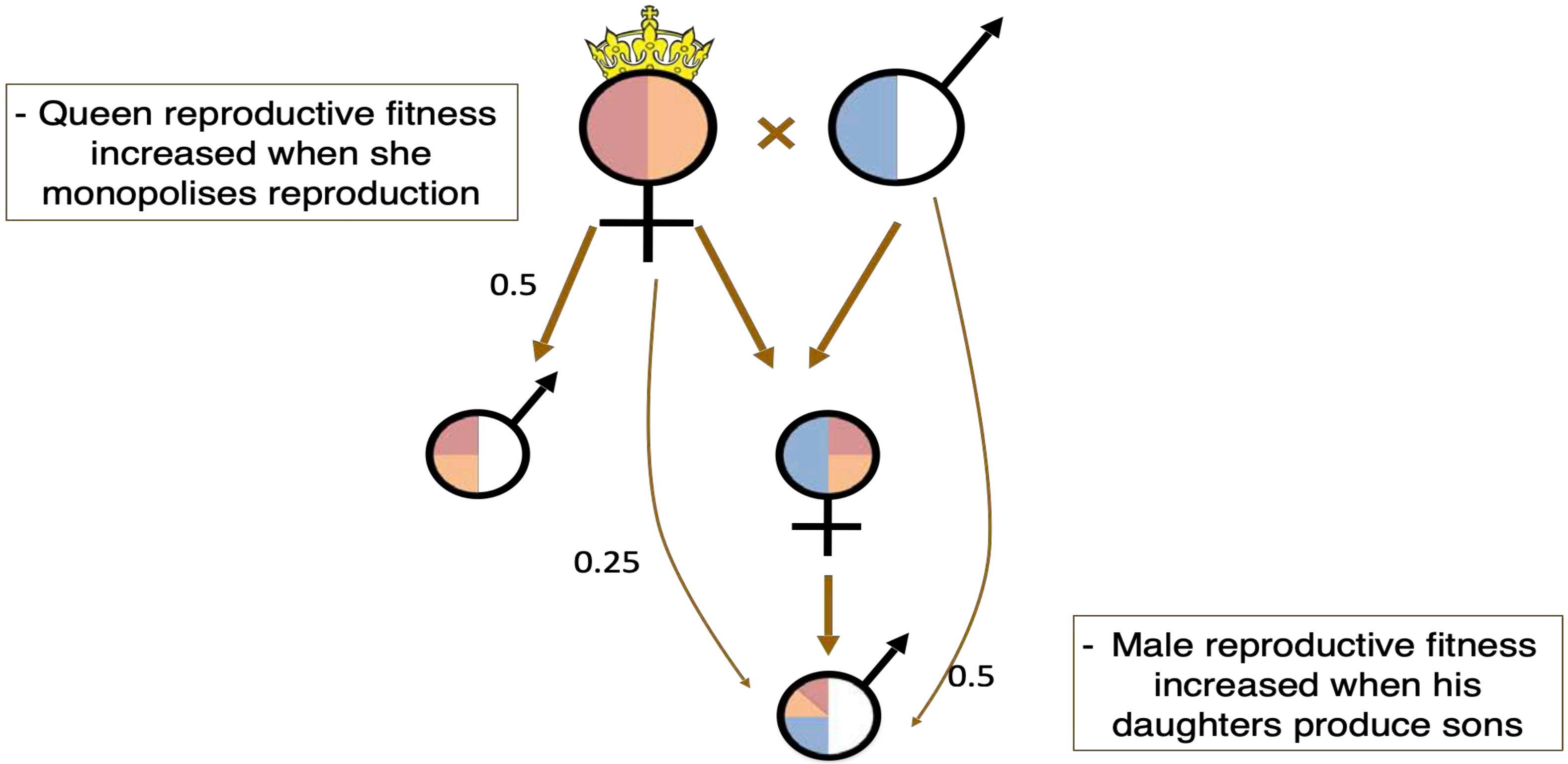


Reproductive conflict in honey bees



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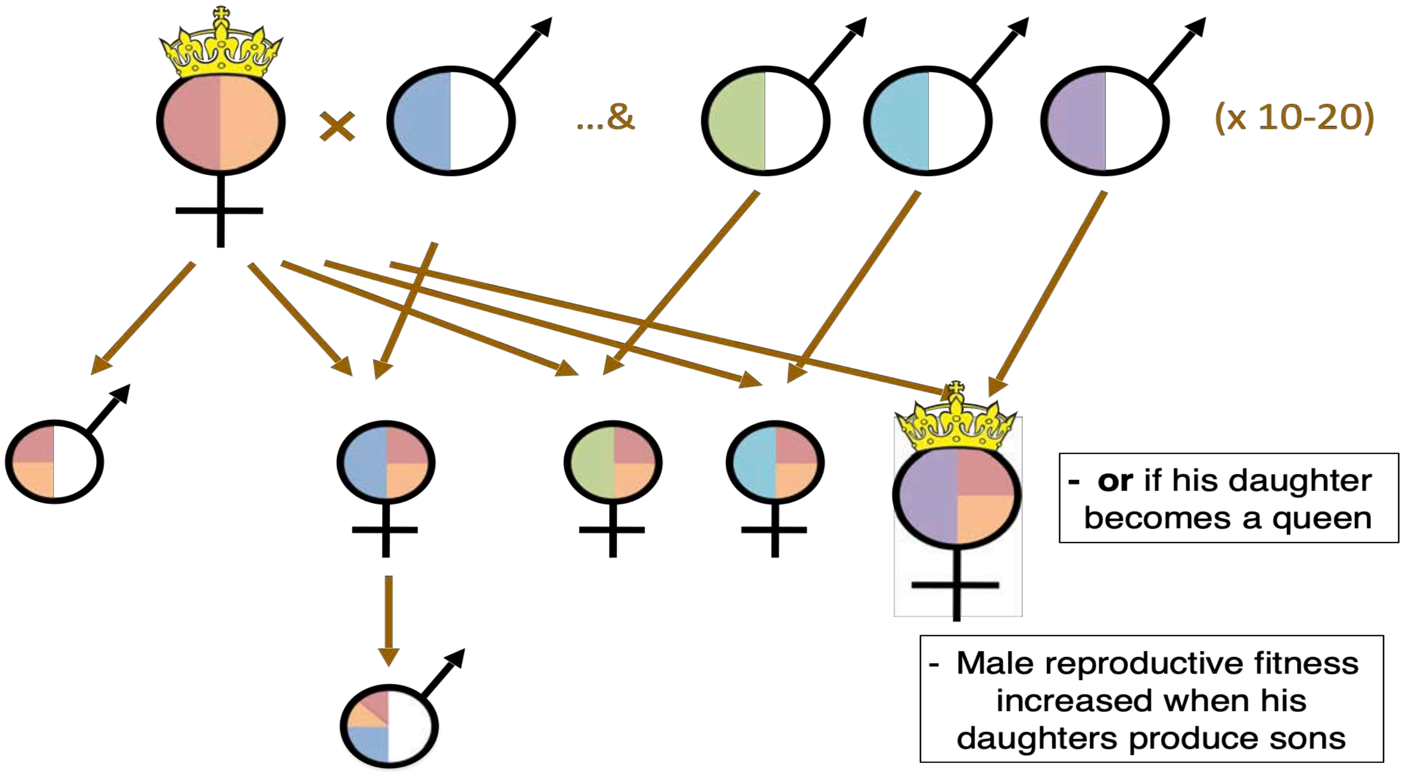
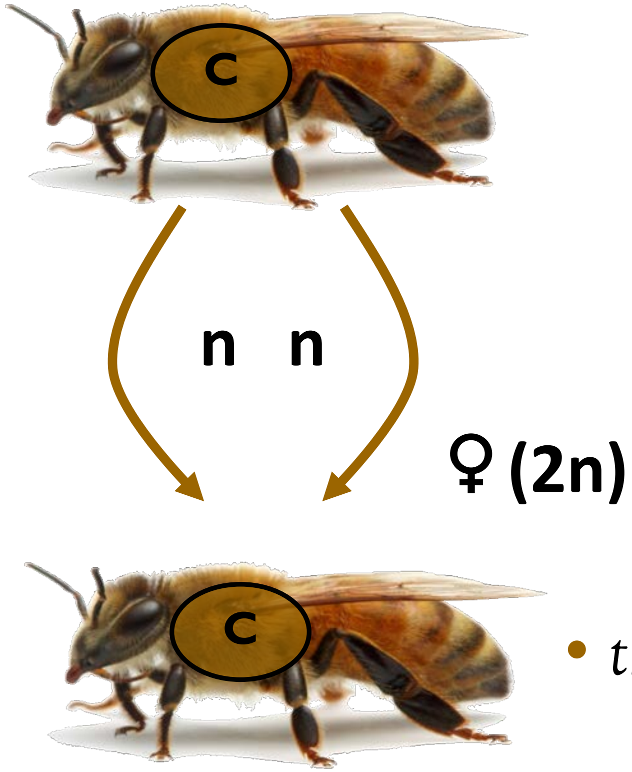


MEANWHILE, IN CAPE TOWN AND SURROUNDING AREAS…

A. m. capensis



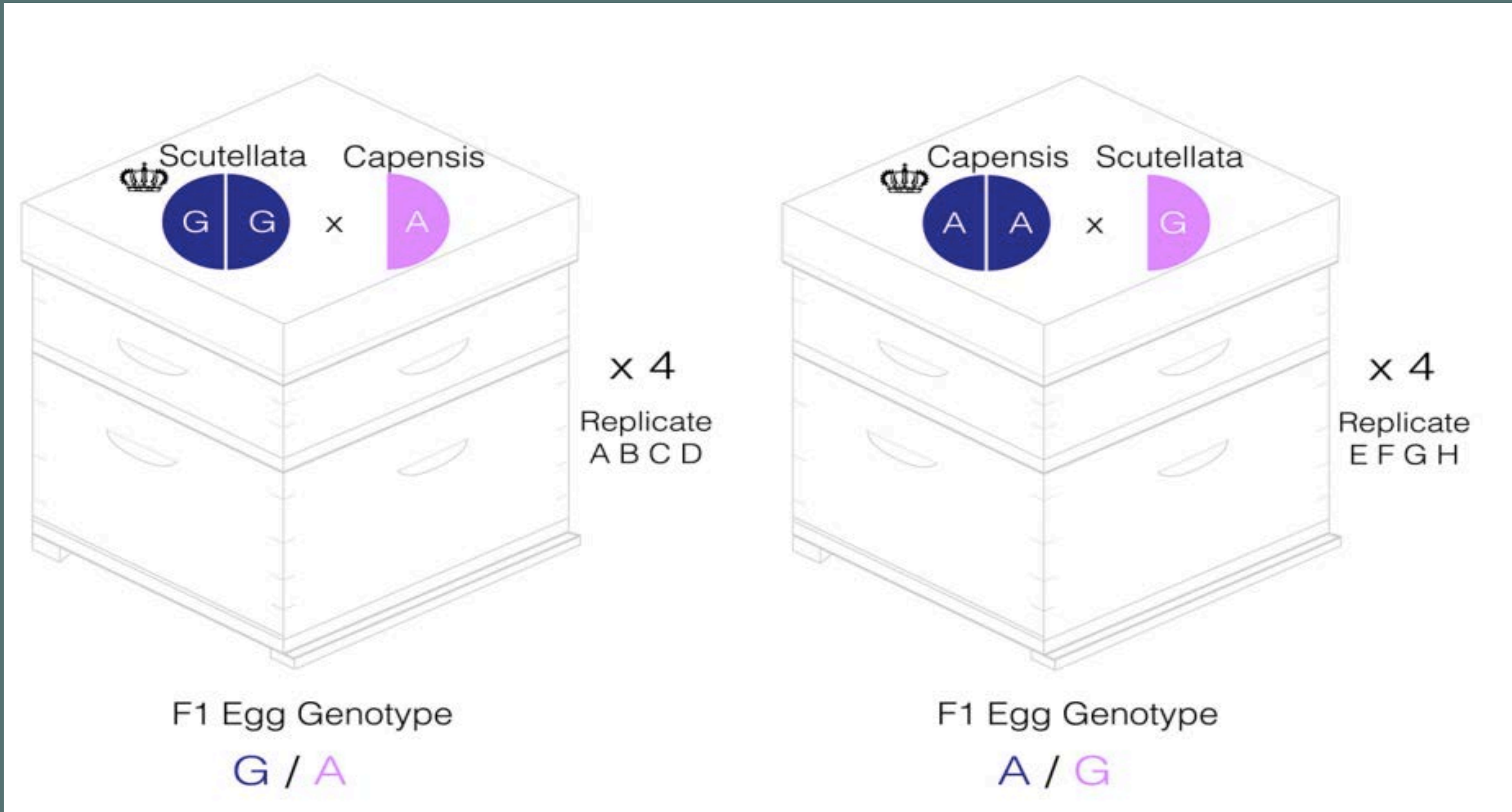
- *thelytoky*

Thelytoky: two pronuclei of second division meiosis fuse to produce a clone of the mother

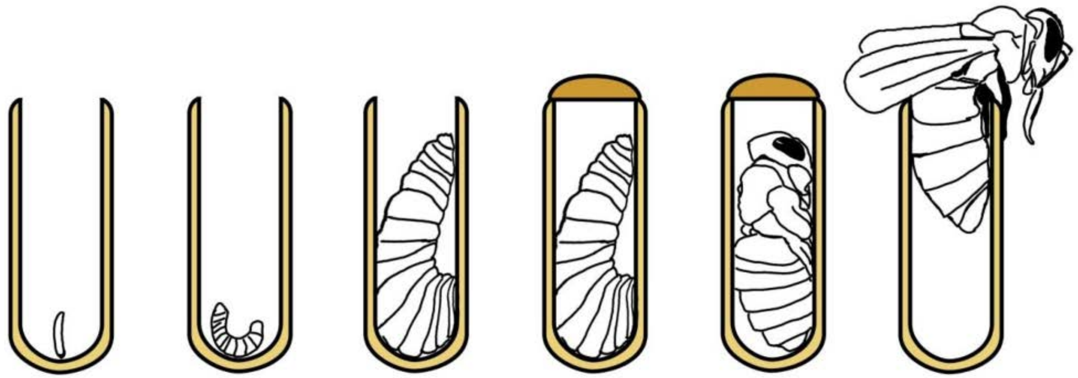
CONSEQUENCES OF THELYTOKY?

GENOMIC IMPRINTING RESEARCH IN THE BEE LAB AT UNIVERSITY OF SYDNEY

- We performed reciprocal crosses between *Apis mellifera capensis* and *Apis mellifera scutellata*
- 4 colonies in each direction
- 8 colonies in total
- Sequenced parents from each colony and the transcriptome of F1 eggs

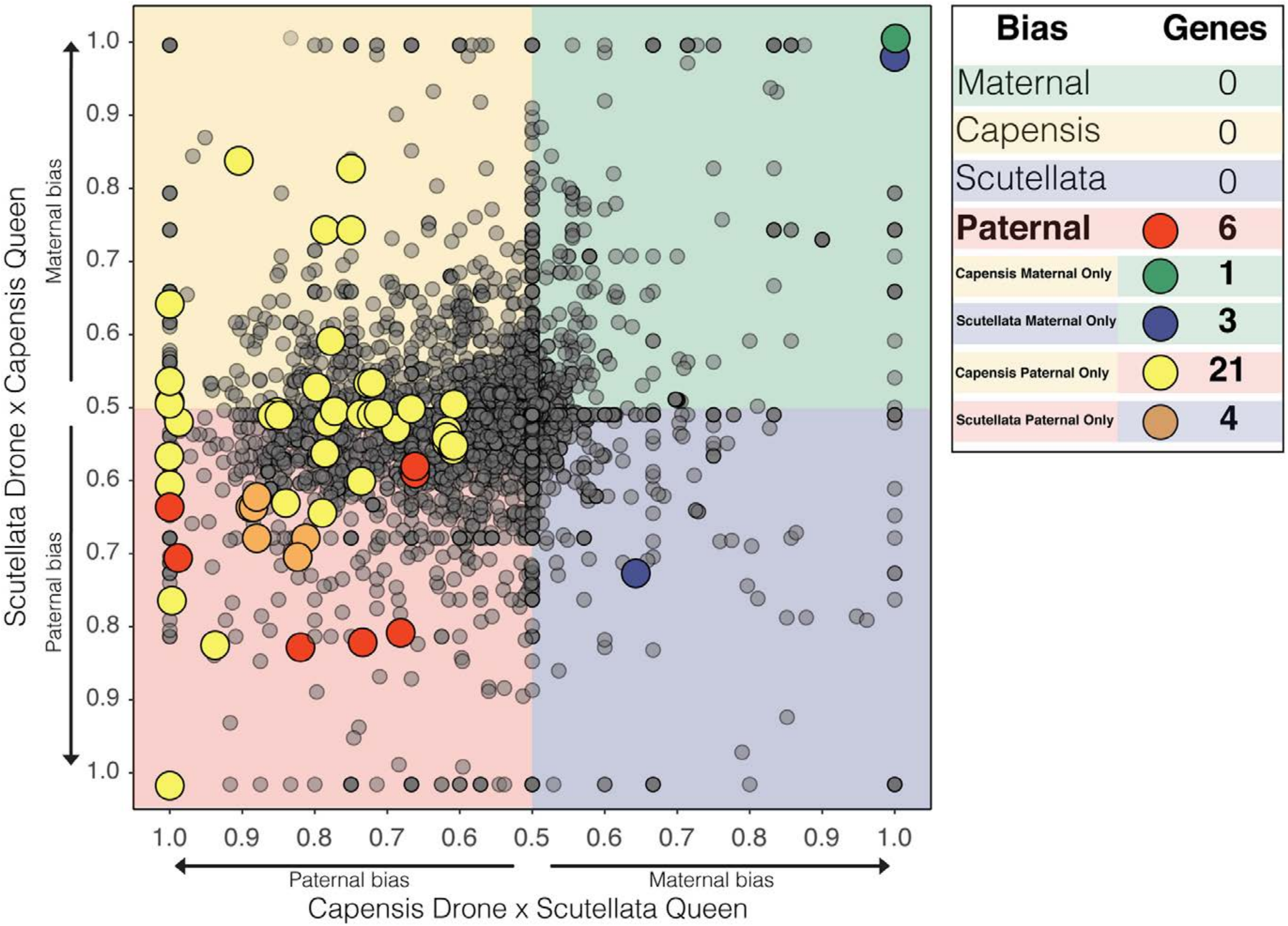

Scutellata
Capensis
G
G
×
A
× 4
Replicate
A B C D
F1 Egg Genotype
G / A
Capensis
Scutellata
A
A
×
G
× 4
Replicate
E F G H
F1 Egg Genotype
A / G

LET'S LOOK AT WHAT MUM AND DAD'S GENES ARE DOING DURING DEVELOPMENT IN BEES



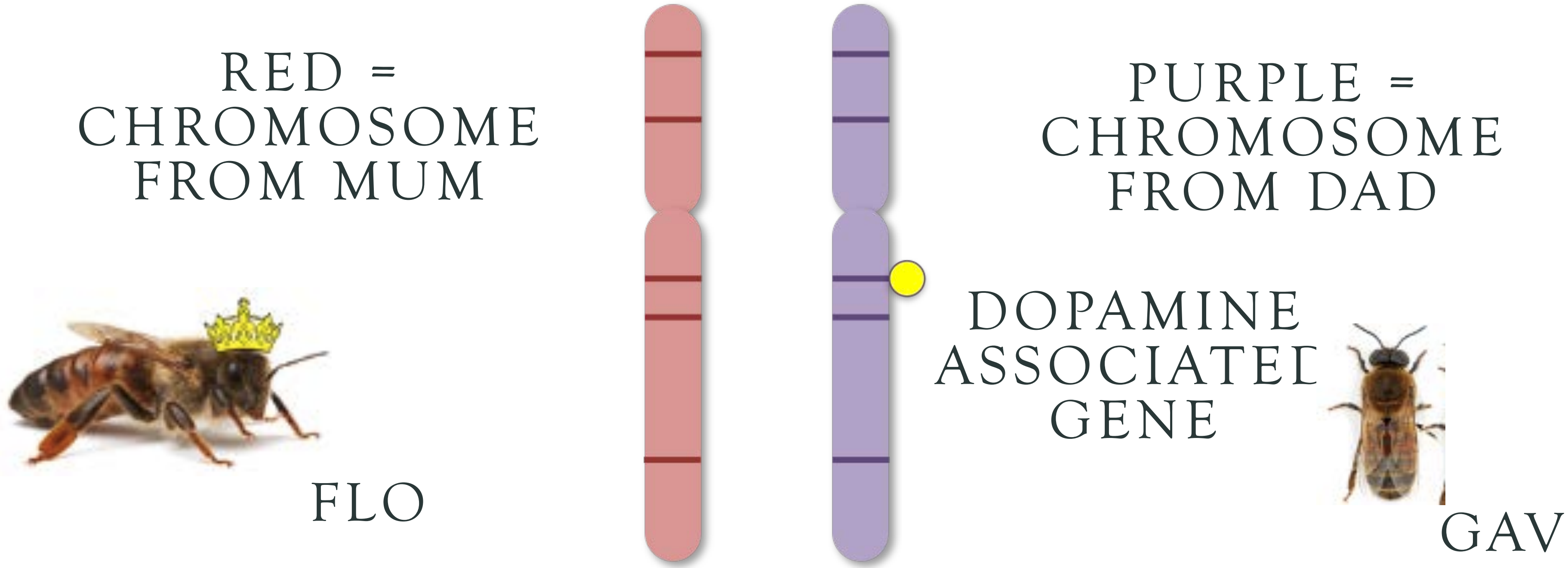
	Egg	Larva	Pupa	Total
Worker	3 days	5.5 days	11-12 days	21 days


IBM

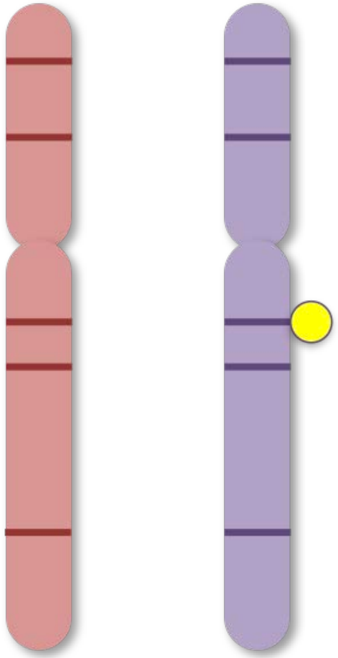


Bias
Genes
Maternal 0
Capensis 0
Scutellata 0
Paternal 6
Capensis Maternal Only 1
Scutellata Maternal Only 3
Capensis Paternal Only 21
Scutellata Paternal Only 4
Scutellata Drone x Capensis Queen
Maternal bias
Paternal bias
1.0
0.9
0.8
0.7
0.6
0.5
0.6
0.7
0.8
0.9
1.0
1.0 0.9 0.8 0.7 0.6 0.5 0.6 0.7 0.8 0.9 1.0
Paternal bias
Maternal bias
Capensis Drone x Scutellata Queen

CONFLICTING PARENTAL 'PLANS' FOR OFFSPRING LEADS TO PARENT SPECIFIC GENE EXPRESSION IN BEES TOO



CONFLICTING PARENTAL 'PLANS' FOR OFFSPRING LEADS TO PARENT SPECIFIC GENE EXPRESSION IN BEES TOO



WHAT IS THIS GENE?

DOPAMINE GENE

WHAT ON EARTH DOES IT DO?

INCREASES PROBABILITY OF WORKER REPRODUCTION

WHAT IS THE MECHANISM????????

- Assessed DNA methylation state at these genes from previous studies (Remnant et al. 2016; Yagound et al. 2020)
- No overlap with DNA methylation and genes with parent-of-origin effects that we found
- Assessed histone modifications at these genes from a previous study (Wojciechowski et al. 2018)
- No overlap with histone modifications and genes with parent-of-origin effects that we found

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ORIGINAL ARTICLE

MOLECULAR ECOLOGY WILEY

Paternally-biased gene expression follows kin-selected predictions in female honey bee embryos

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ARC • LNR

Excellence in Research and Development

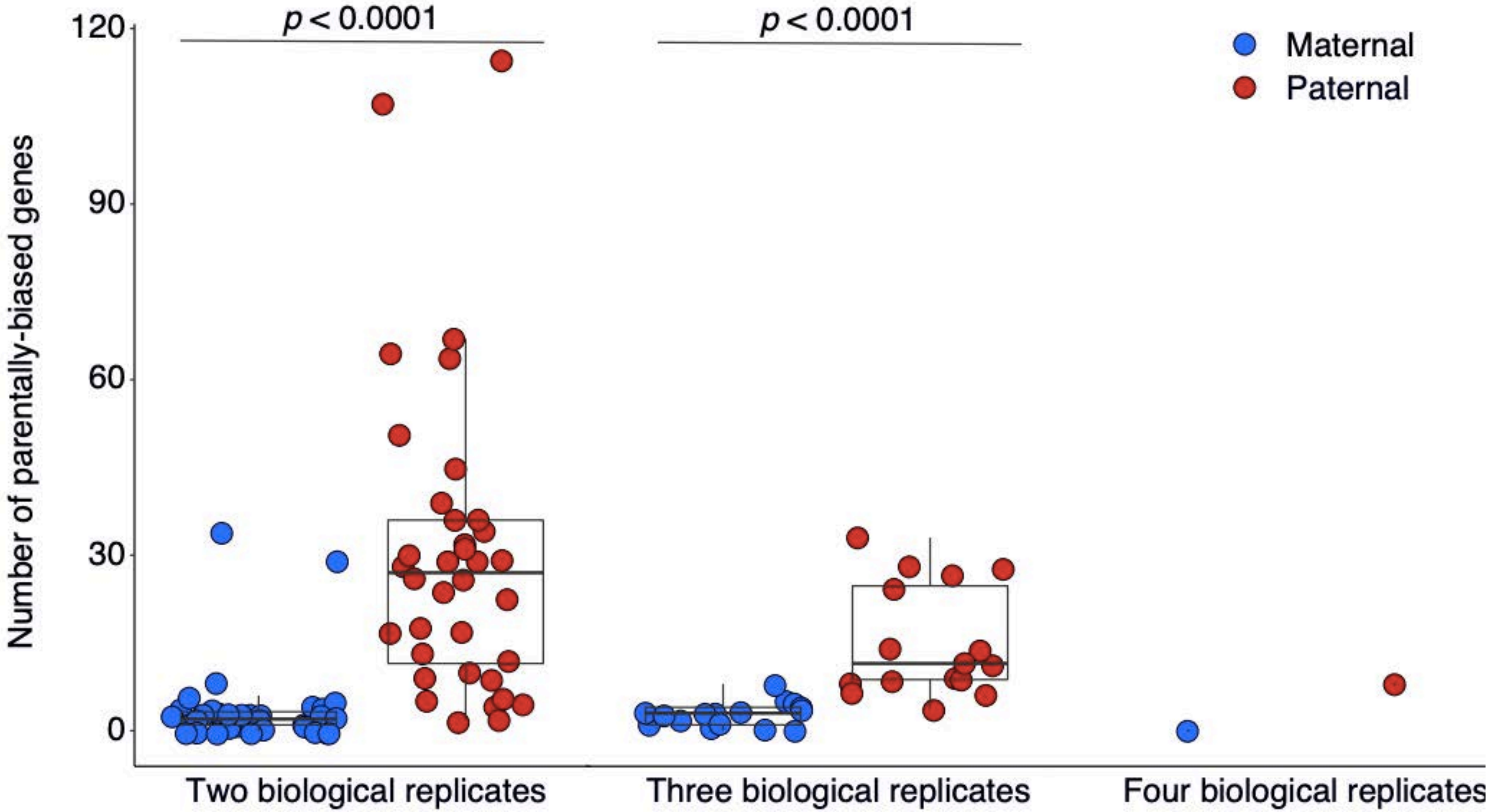
WOSSLER

BEHAVIOURAL ECOLOGY GROUP

THE UNIVERSITY OF SYDNEY

Amro Zayed's Laboratory

Department of Biology, York University



p < 0.0001
p < 0.0001
Maternal
Paternal
Number of parentally-biased genes
120
90
60
30
0
Two biological replicates
Three biological replicates
Four biological replicates