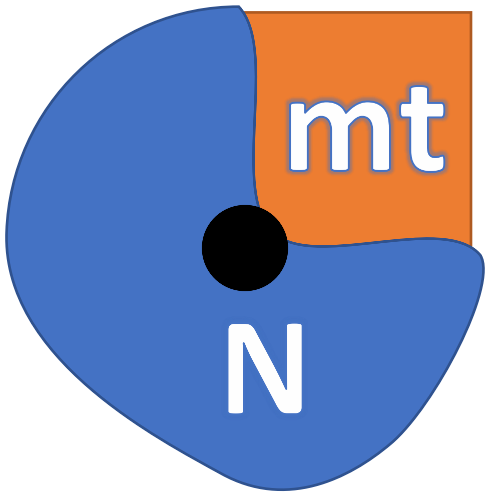
Coevolution, co-transmission, and conflict

Co- Co- Co-

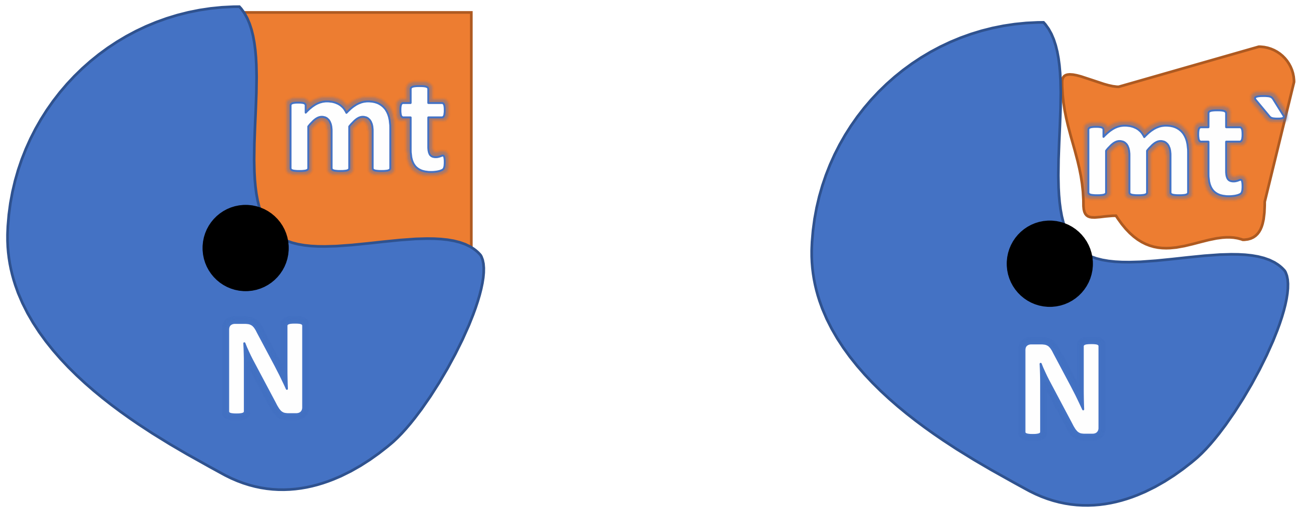
evolutionary time



Co-function
requires
Co-adaptation

Co- Co- Co-

evolutionary time

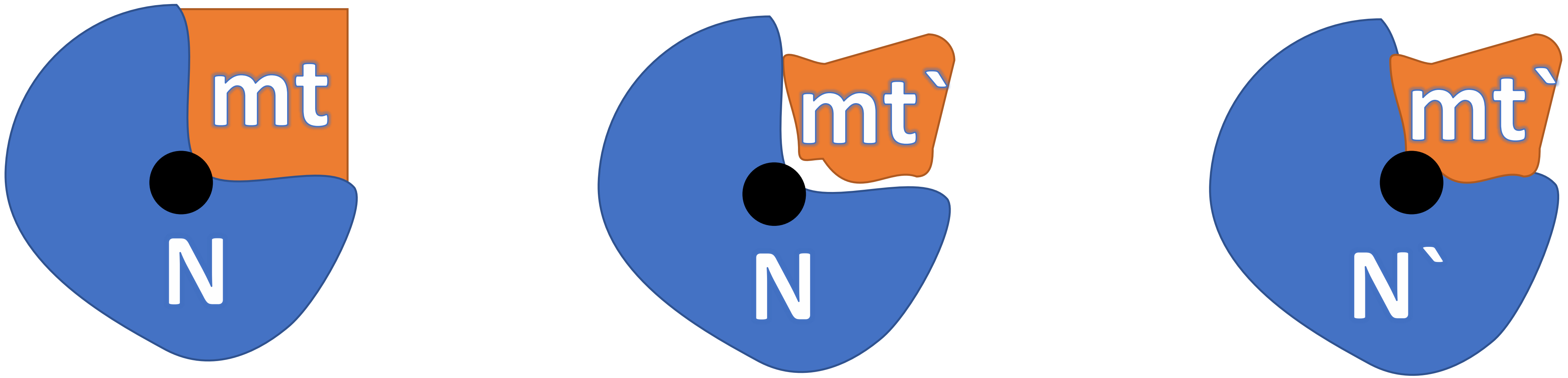


Separate genomes evolve at different rates

Co- Co- Co-

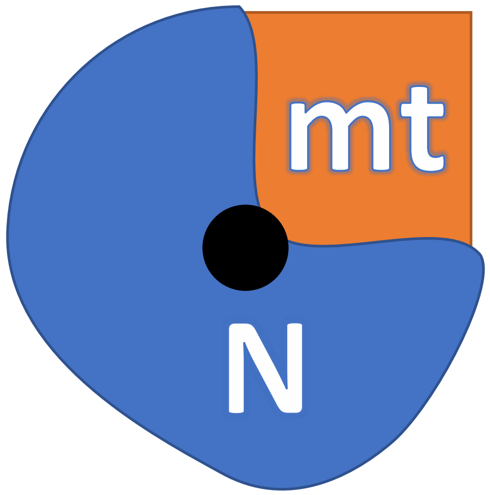
Co-evolution maintains co-adaption of co-functioning products

evolutionary time



Co- Co- Co- Co-transmission

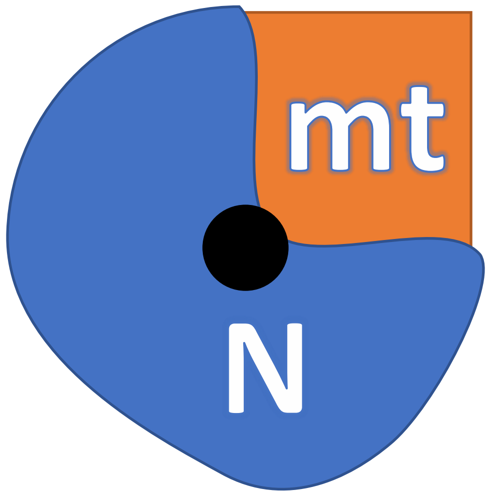
If it works well, why not inherit together?



A central principle of Mitonuclear Ecology

"co-transmission of mt and N-mt genes thwarts the coevolution of mt and N-mt genes"

Co- Co- Co- Co-transmission



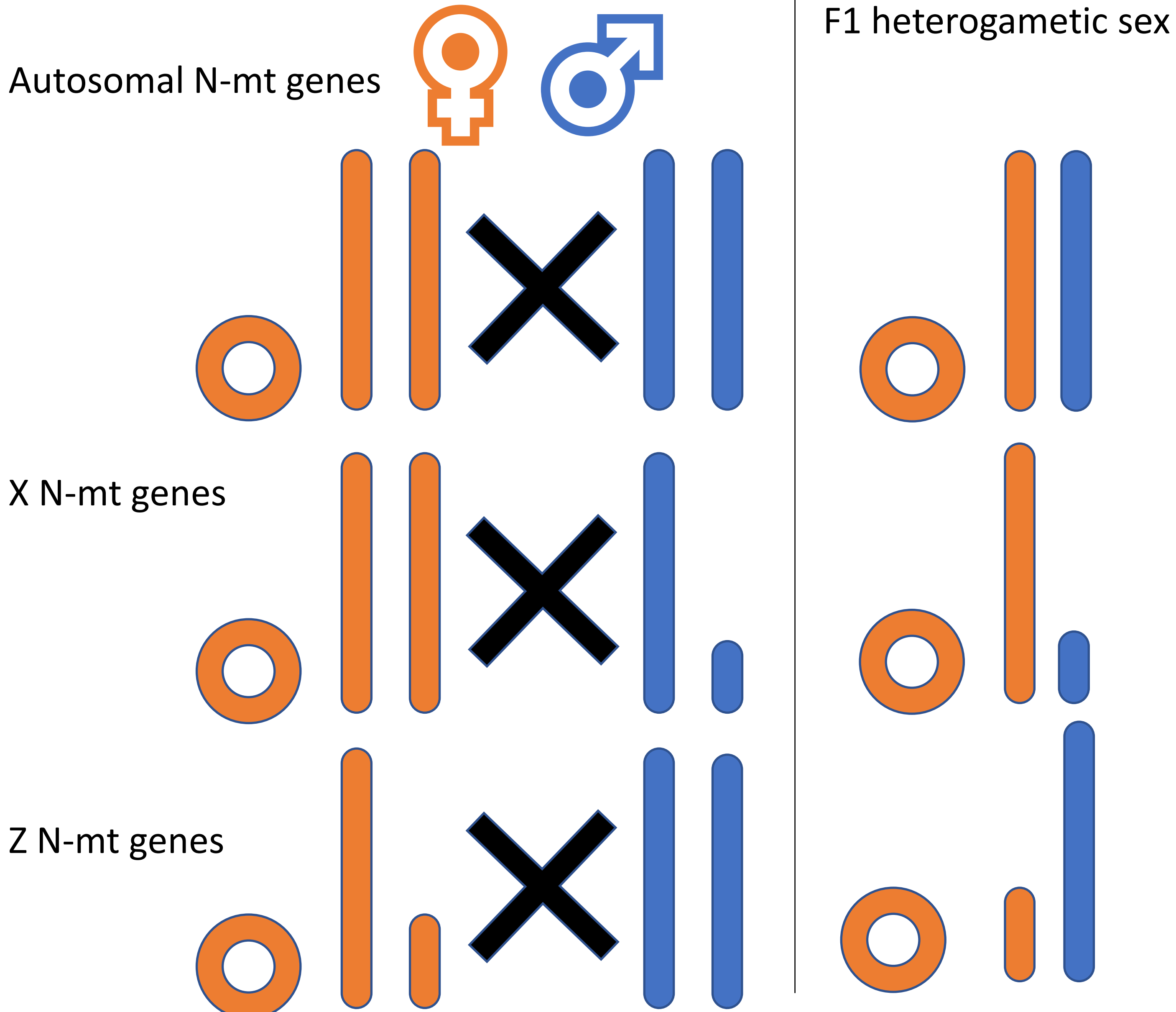
If it works well, why not inherit together?

Asexual vs sexual reproduction

Other ways to co-transmit?

Sex linkage and N-mt genes?

- N-mt genes on Y or W would be problematic



Sex – linkage of Nmt genes will co-transmit with mt genome?

TABLE 1 Patterns of chromosomal transmission

	Chromosomes					
Sex	**mtDNA**[a]	**Y**	**X**	**Autosomes**	W	Z
Female	1	0	2	2	1	1
Male	0	1	1	2	0	2
Total copies	1	1	3	4	1	3
Proportion cotransmitted with mtDNA		0	0.66	0.50	0	0.33

a Assuming strict maternal transmission of mtDNA.

Rand et al 2001, *Genetics*

A central tenant of Mitonuclear Ecology

“co-transmission of mt and N-mt genes thwarts the coevolution of mt and N-mt genes”

Co-transmission ≠ Co-evolution

- Hill-Robertson effect
  - Co-transmission via gene linkage creates larger units of selection
- Are Nmt genes sex-linked?
- If so, what are some predictions we can derive to explain broader patterns of behaviors / phenotypes in animals?

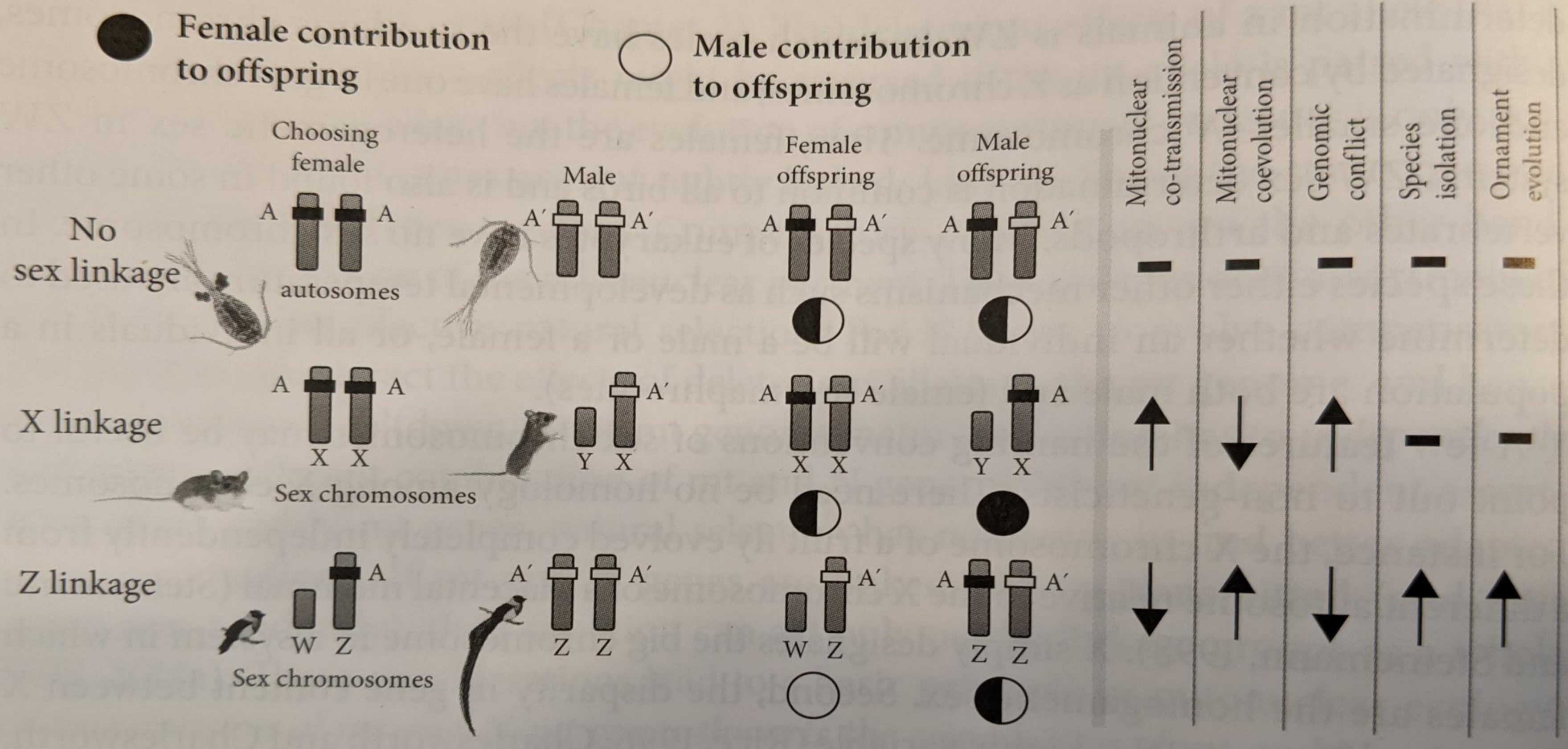


Figure 4.2 The effects of chromosomal position on patterns of inheritance of N genes. Allele A from the female is shaded black; Allele A′ from the male is shaded white. The proportion of the pie chart that is black or white indicates relative contribution of paternal and maternal alleles at that locus in the F1 generation. For autosomal genes, males and female each contribute one allele. In the XY system, females have a larger contribution at sex-linked loci. In ZW systems, males have a larger contribution at sex-linked loci. Adapted from Hill and Johnson (2013).

Some insight into the motivation for this chapter

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Research

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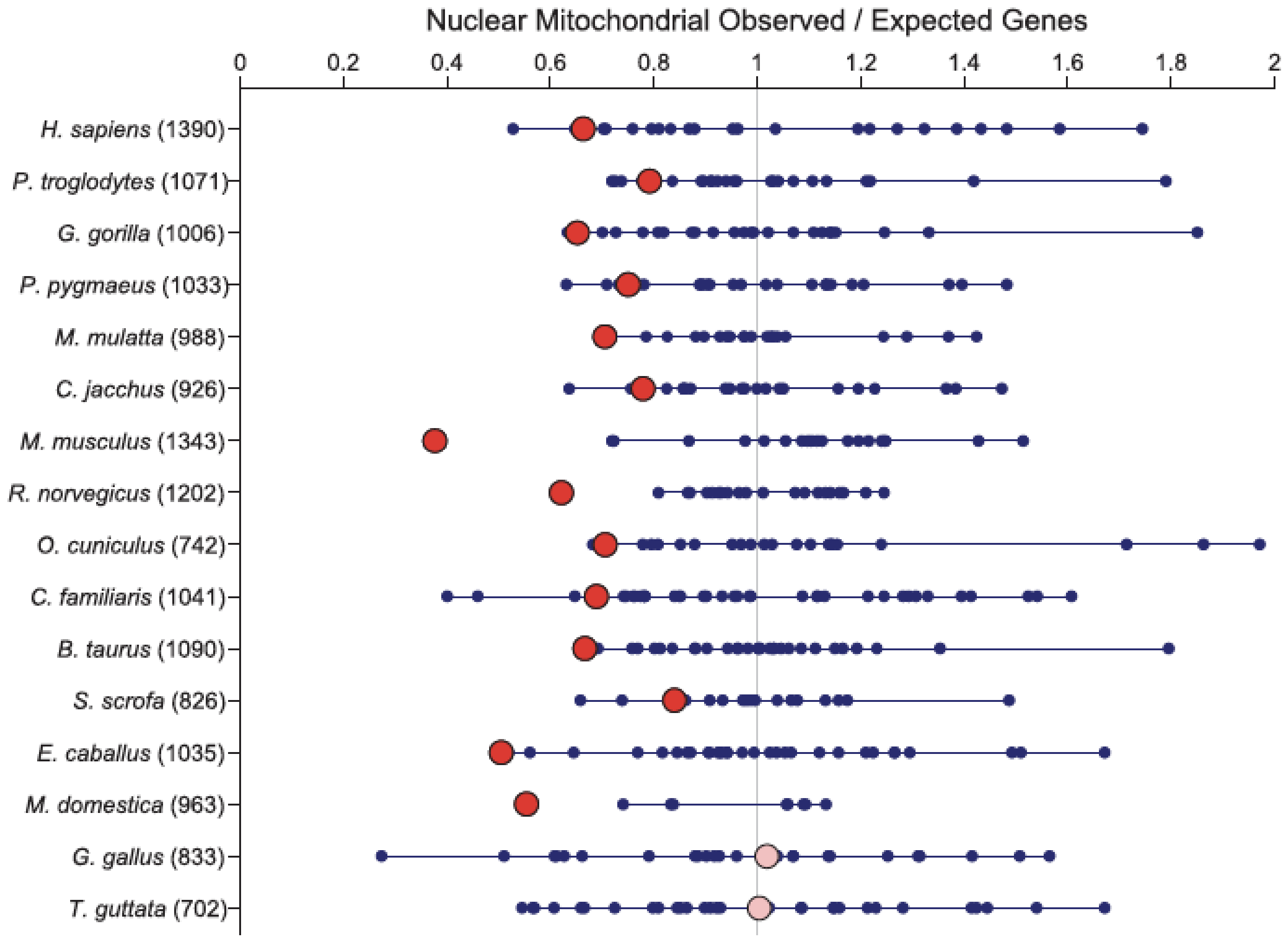
The mitonuclear compatibility hypothesis of sexual selection **(by female mate choice)**

Geoffrey E. Hill and James D. Johnson

Department of Biological Sciences, Auburn University, 331 Funchess Hall, Auburn, AL 36849-5414, USA

Why females assess ornaments when choosing mates remains a central question in evolutionary biology. We hypothesize that the imperative for a choosing female to find a mate with nuclear oxidative phosphorylation (OXPHOS) genes that are compatible with her mitochondrial OXPHOS genes drives the evolution of ornaments. Indicator traits are proposed to

Sex linkage/determination

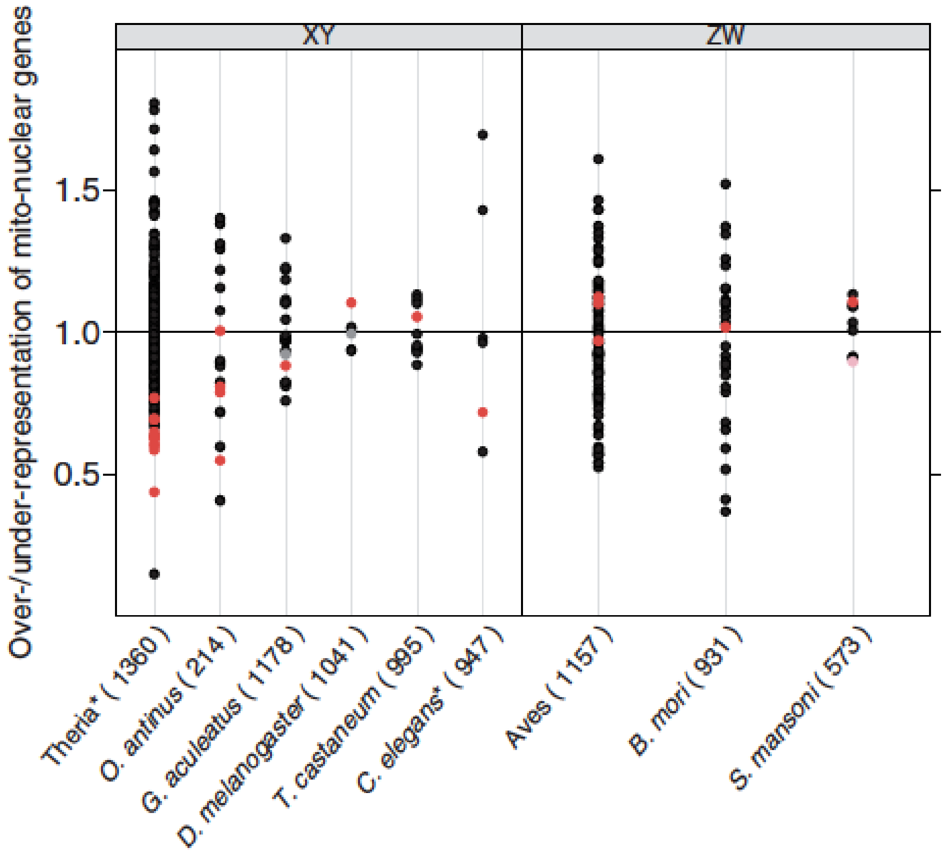


Drown et al. 2012

- Evidence for under-representation of N-mt on sex chromosomes in mammals

But…

- Doesn’t hold for other XY systems
- Not seen in ZW
- Predates evolution of sex chromosomes
- “Intimate” N-mt genes?



Dean et al. 2014

Deficit of Mitonuclear Genes on the Human X Chromosome Predates Sex Chromosome Formation

Rebecca Dean*, Fabian Zimmer, and Judith E. Mank

Department of Genetics, Evolution and Environment, University College London, United Kingdom

*Corresponding author: E-mail: r.dean@ucl.ac.uk.

Accepted: January 22, 2015

Haldane, Mitonuclear Breakdown, and Sex Chromosomes

- Haldane’s rule: box 4.1

Haldane, Mitonuclear Breakdown, and Sex Chromosomes

- Haldane’s rule: box 4.1
- XY systems, males should suffer greater breakdown
- ZW systems, females should suffer greater breakdown

- What is the source of breakdown? What genes?

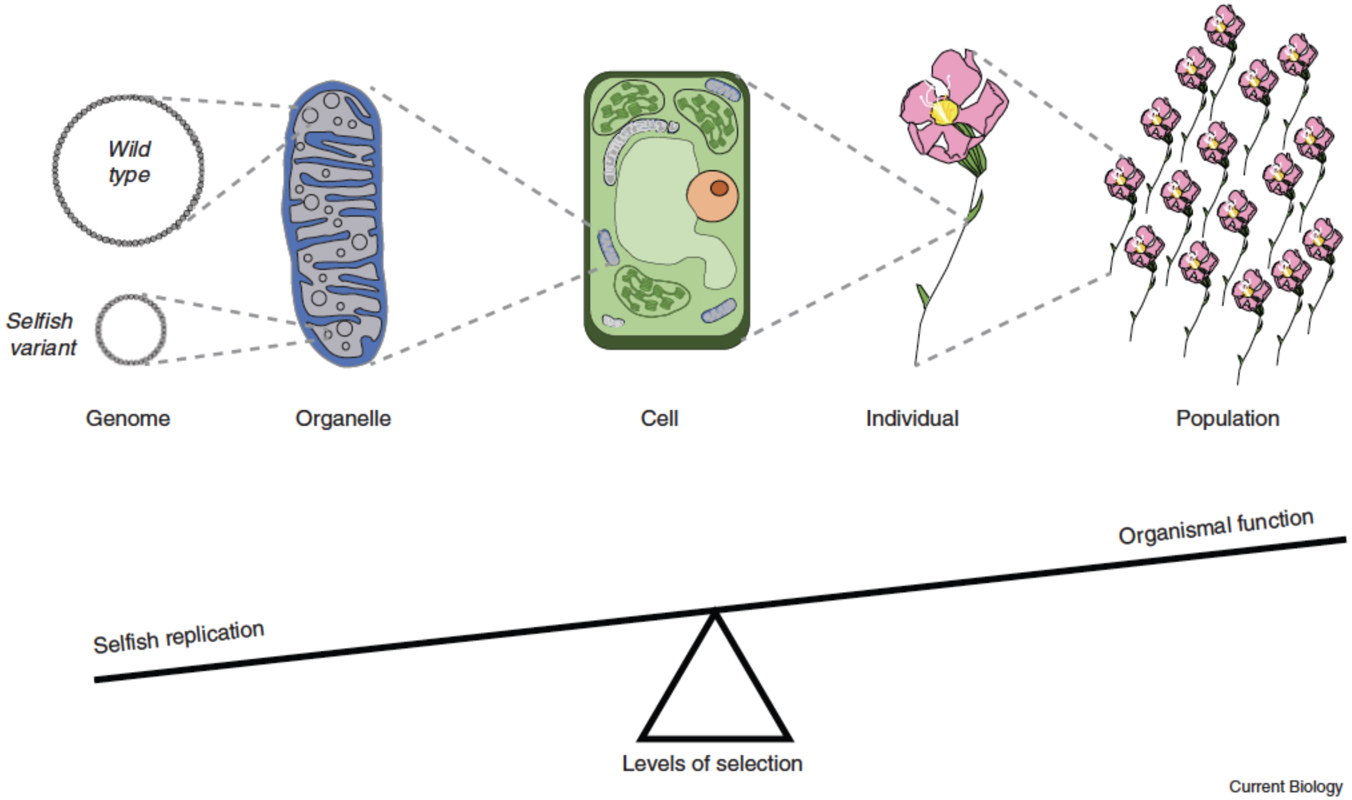
Haldane, Mitonuclear Breakdown, and Sex Chromosomes

- Haldane's rule: box 4.1
- XY systems, males should suffer greater breakdown
- ZW systems, females should suffer greater breakdown

- What genes contribute to Haldane-type hybrid breakdown?
- XY? Males get X and mito from mom
- ZW? Females get Z from dad, mito from mom

Cytonuclear conflict

- Within individuals
- Mother's curse



Havird et al. 2019

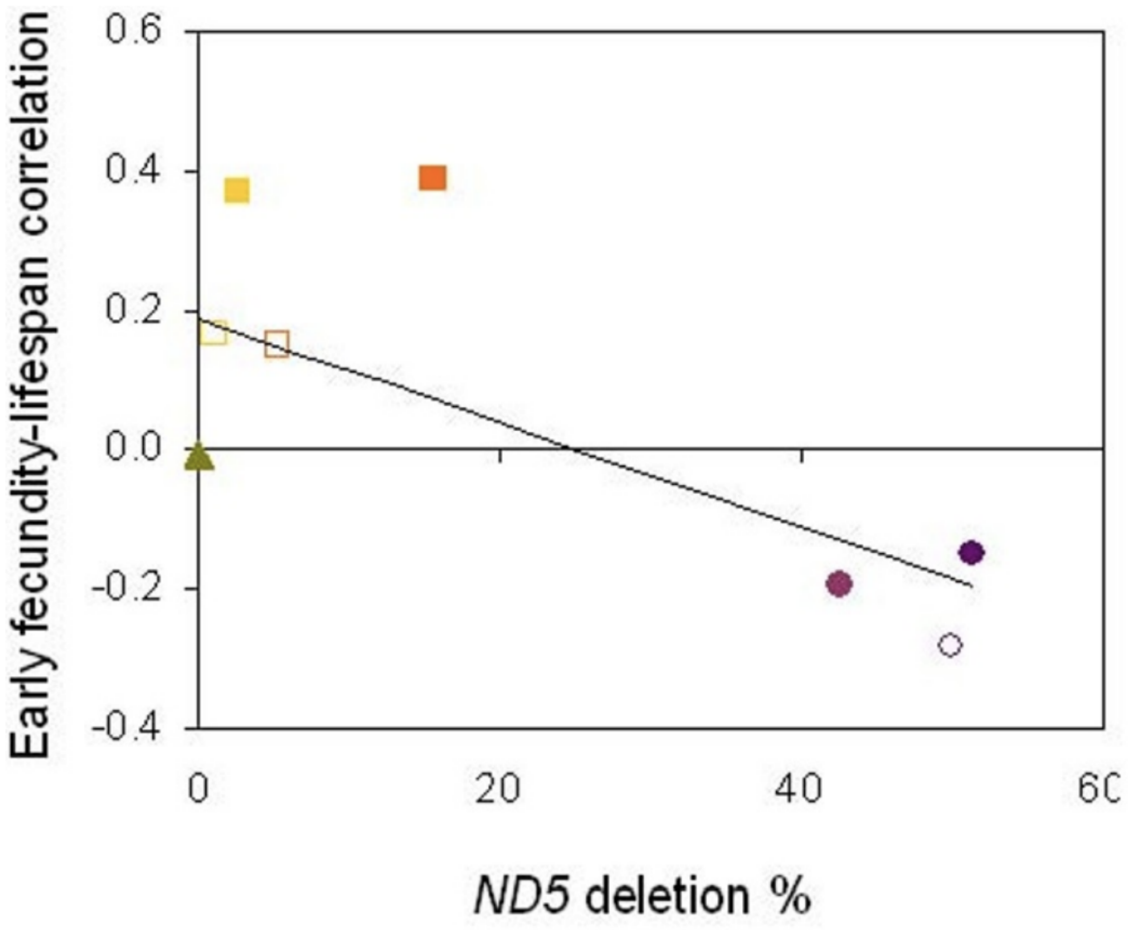
Selfish replication

Table 1. Six possible mechanisms of selfish mitochondrial replication and six possible nuclear responses.

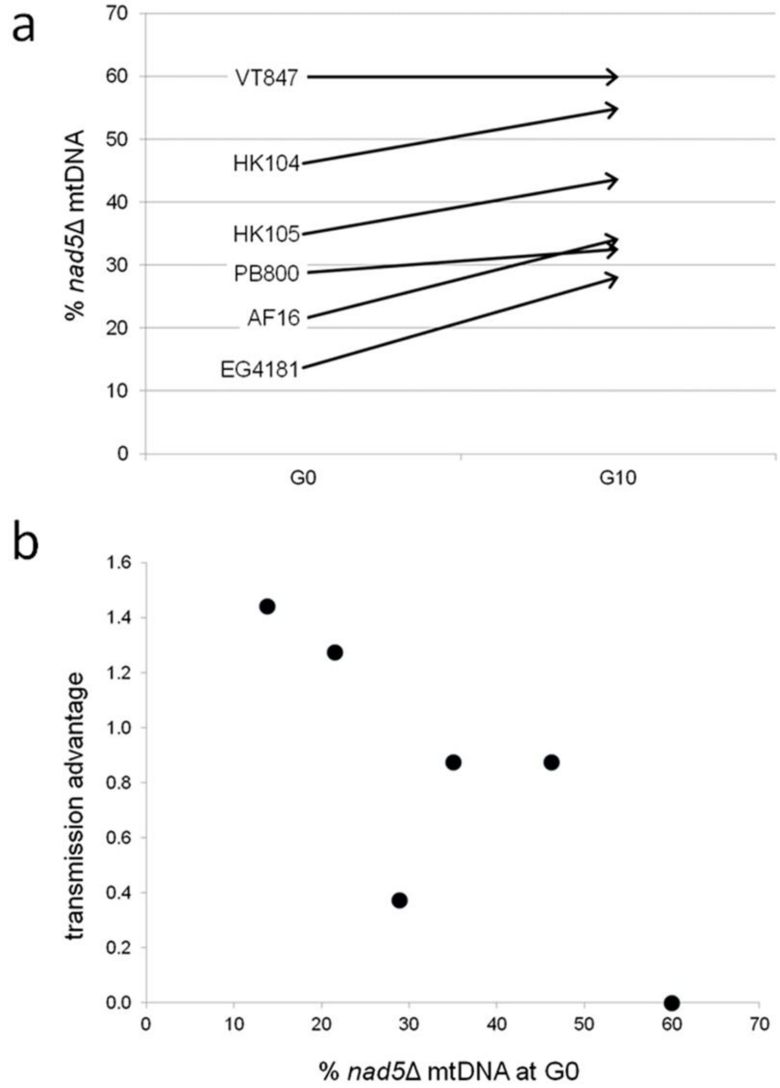
Mechanism	Details	Example taxa	Citations
Selfish replication			
1. Faster replication	Via deletions and preferential recruitment of replication machinery	Humans, nematodes, *Drosophila*, yeast	[40,51,53–55,57,59, 190,191]
2. Moral hazard hypothesis	Poor organelles result in increased DNA replication	Nematodes (and simulations)	[67–70]
3. Selfish organelle growth and division	Genome variation causes replication of organelles, not DNA	Plastids in evening primrose?	[72]
4. Epigenetic tagging	Replication and transcription may be mutually exclusive	Mammals, possibly in copepods	[73–75]
5. Organelle inheritance bias	Variants causing organelles to move into germline	None, relevant mechanisms proposed in bivalve molluscs	[76]
6. Warfare	Organelles producing toxins to disrupt competing organelles	None, relevant observations in heteroplasmic mice	[79]
Nuclear responses			
1. Gene transfer	Functional movement of genes from the mitochondrial to the nuclear genome	Mitochondrial replication — all eukaryotes; dNTP levels — yeast	[1,80]
2. Organelle selection	Selective mitophagy aided by mitochondrial fusion/fission cycles	Characterized most extensively in mammals	[6,70,81–83,87]
3. Cell selection	Mitochondrial function in germline selective sieves and apoptosis	Characterized most extensively in mammals	[89–91,93]
4. Sexual recombination	Sex may counteract the parasitic nature of selfish replication	None; modeling studies contrarily suggest sex evolved after mitochondrial control	[4,32,97–99]
5. Germline bottlenecks	Reduces heteroplasmy	Mammals; parallels in young endosymbionts	[100,101,105,106]
6. Uniparental inheritance	Reduces heteroplasmy	Figure 2	[96,107]

Havird et al. 2019

Selfish *nad5*Δ mtDNA nematodes



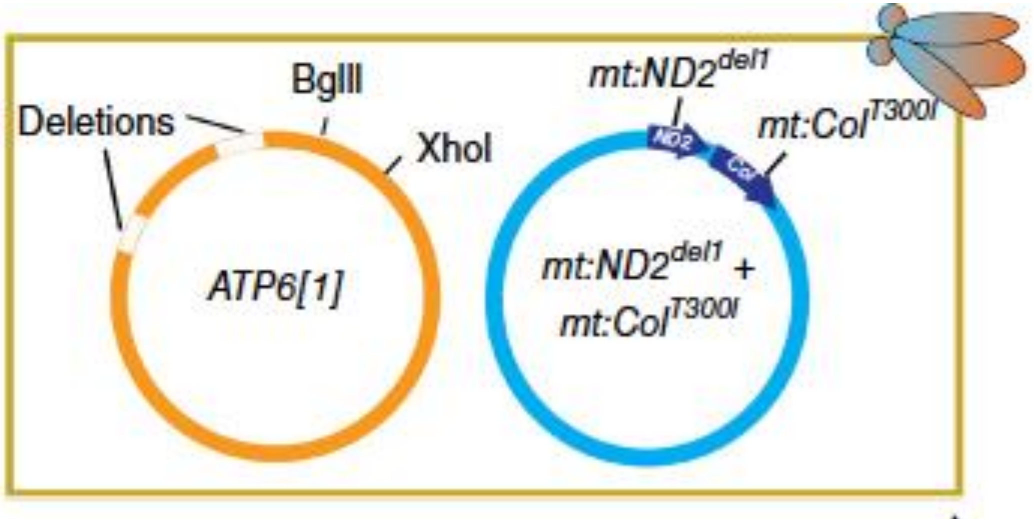
Estes et al. 2011

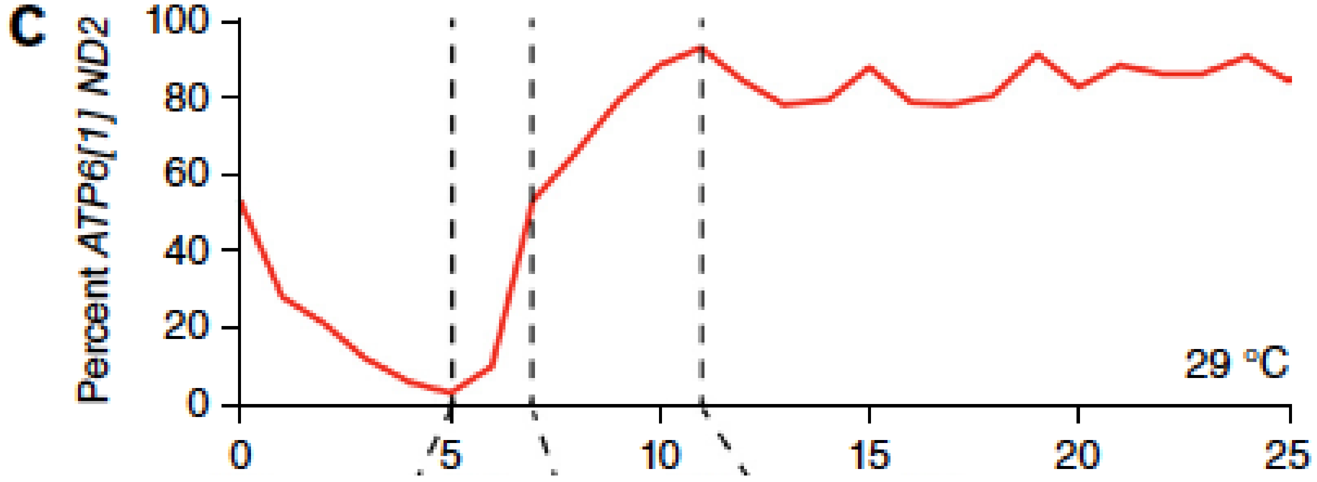


Clark et al. 2012

Selfish ATP6 mt Drosophila

- Close vs. distant competition

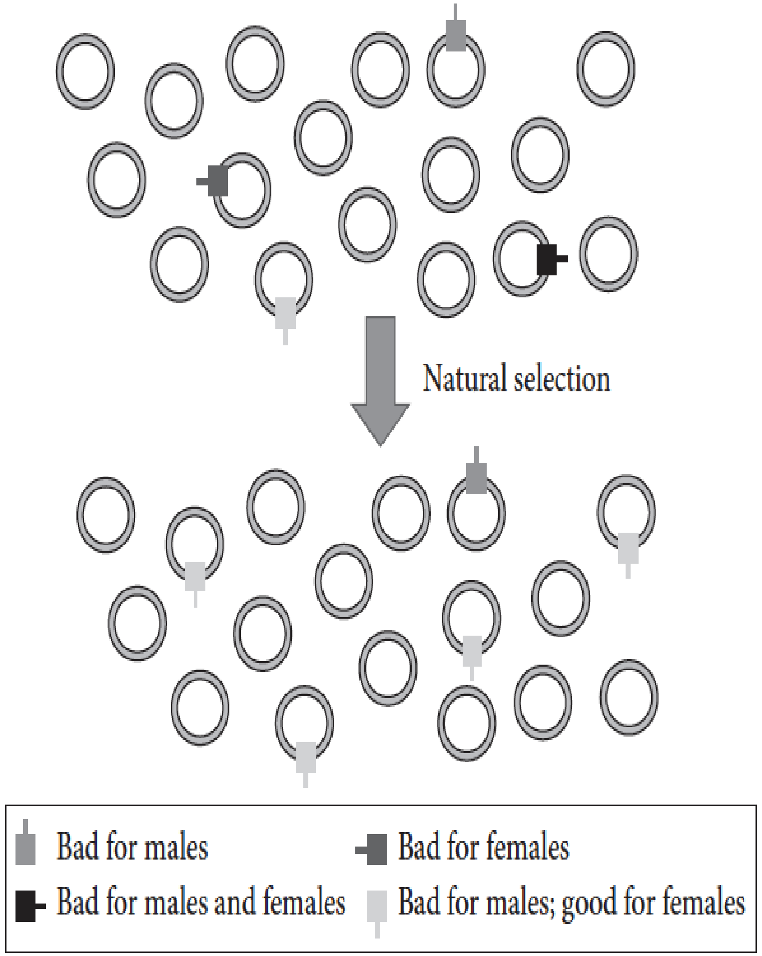




Ma and O'Farrell 2016

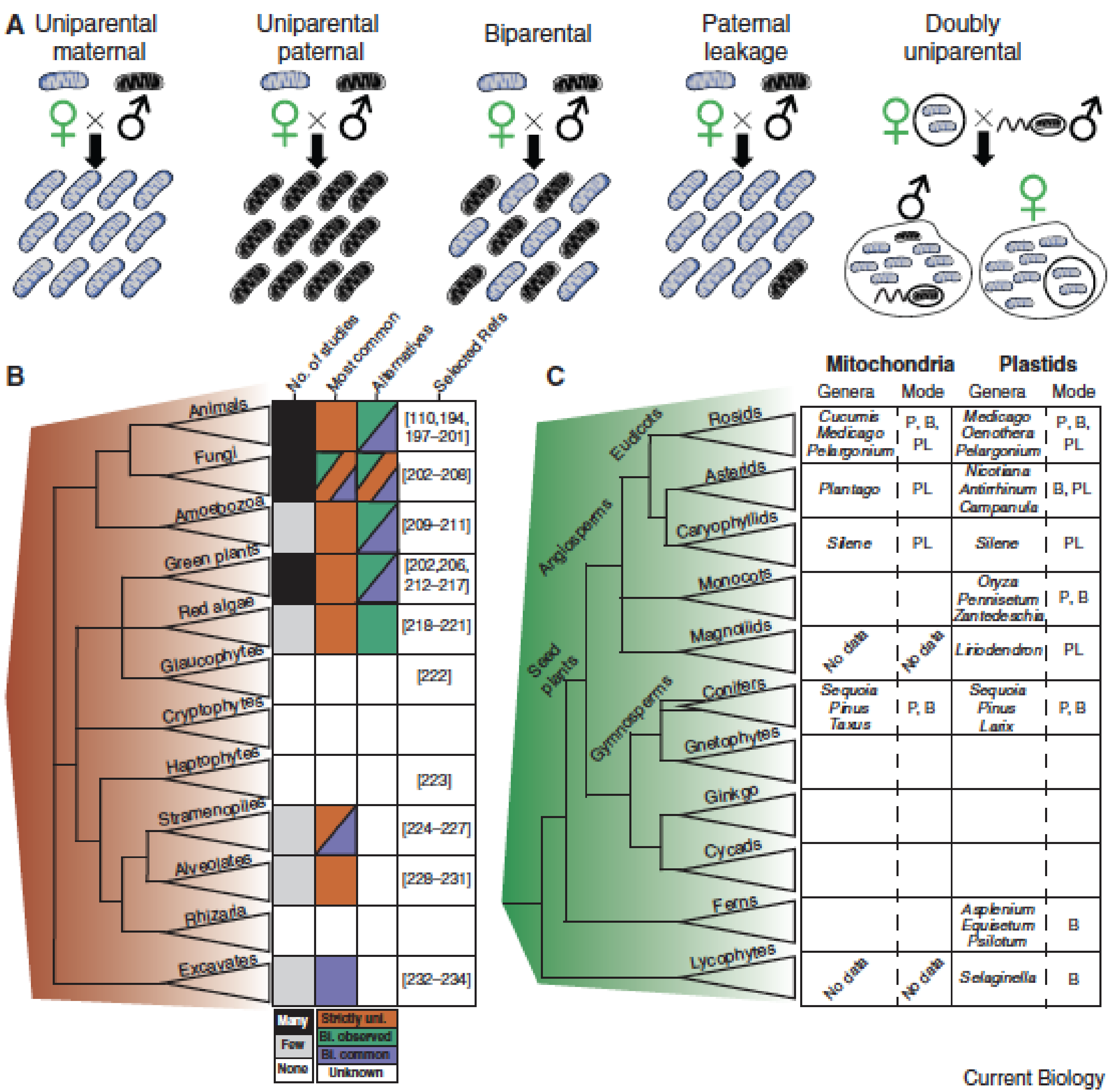
Uniparental inheritance and the mother's curse

- Uniparental inheritance is likely a response to prevent selfish replication and competition among distantly related genomes
- Opens up the door to another kind of conflict:
- ‘‘In males, cytoplasmic genes in outbreeding species will have no selection on them at all to function properly.’’ Cosmides and Tooby 1981



Frank and Hurst 1996; Gemmel et al. 2004

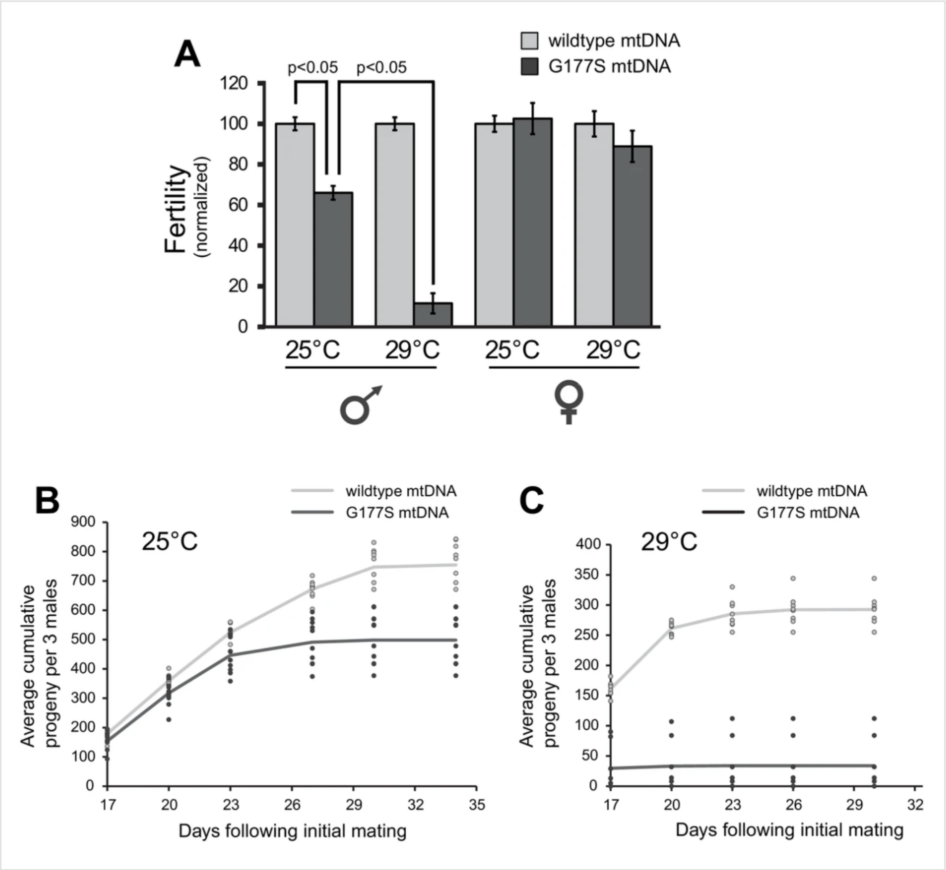
Uniparental inheritance isn't universal



Havird et al. 2019

Evidence of mother's curse

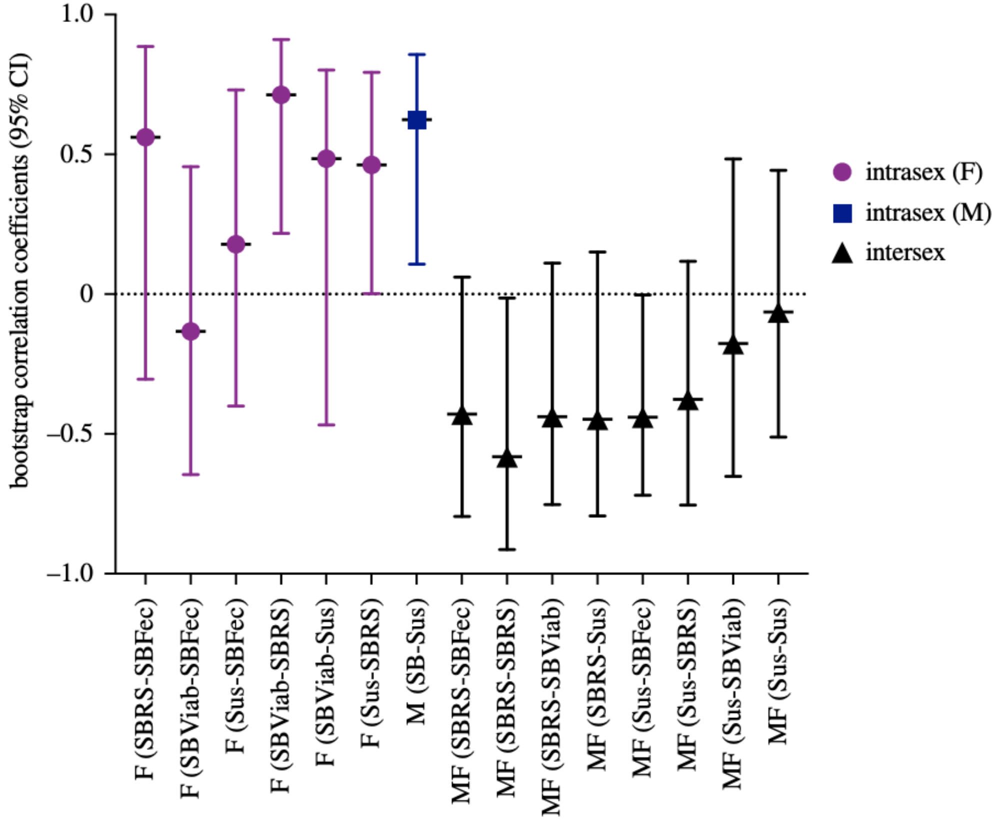
- Weak form – COX2 variant in *Drosophila*
  - *Not true sexually antagonistic conflict*



Patel et al. 2016

Evidence of mother's curse

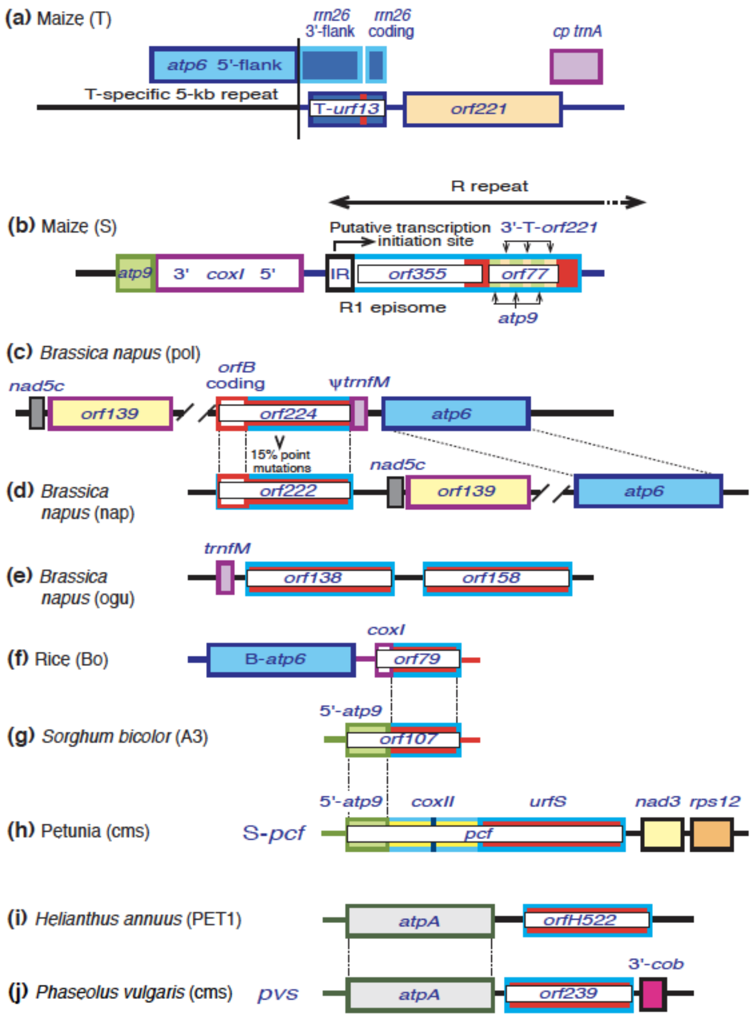
- Strong form – CYTB variant in *Drosophila*
  - *True sexually antagonistic conflict*



CAMUS AND DOWLING 2018

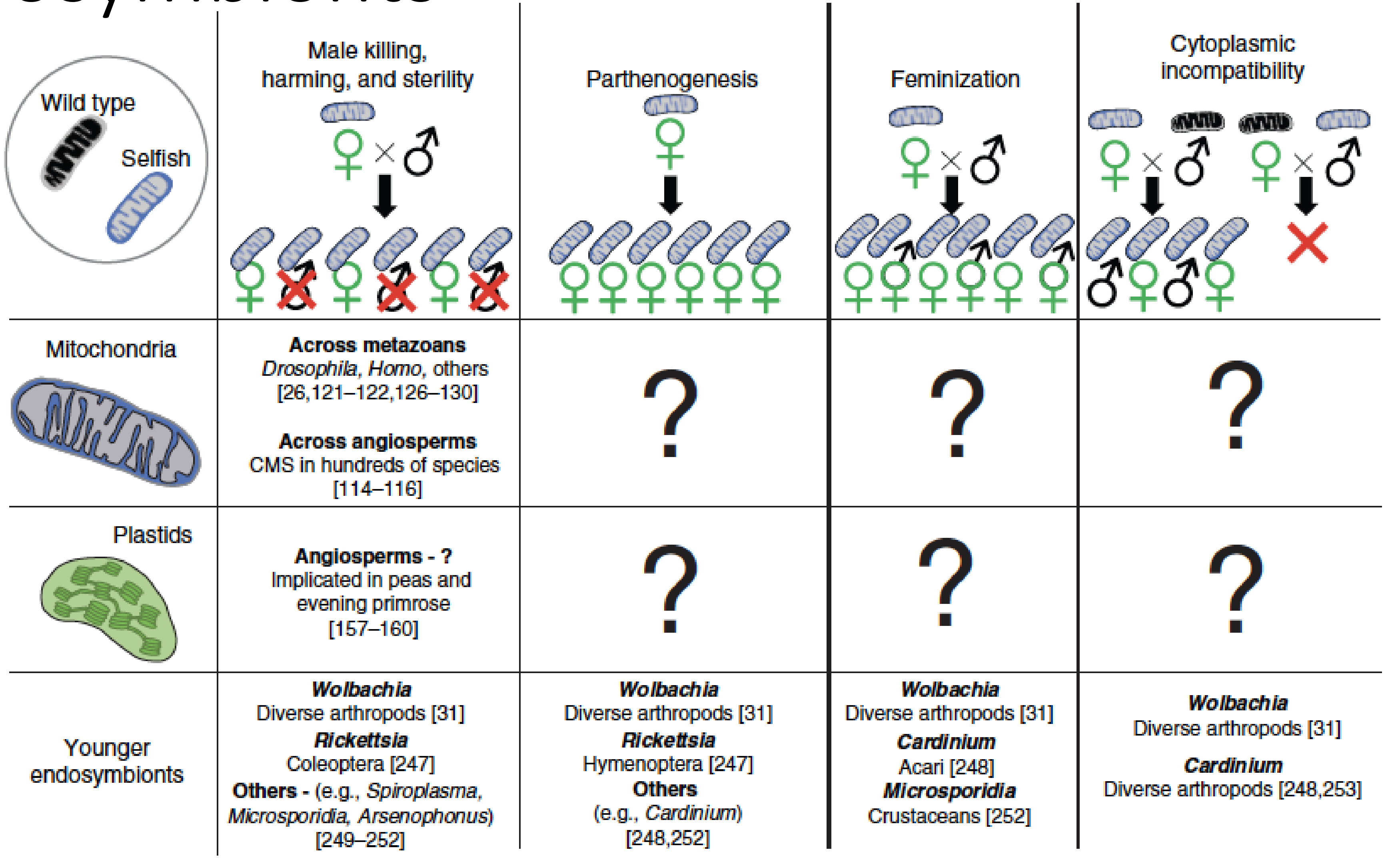
Cytoplasmic male sterility

- Chimeric mt ORFs
- Gynodioecy
- Nuclear RF genes
- True conflict
- Energy-limitation hypothesis



Schnable and Wise 1998

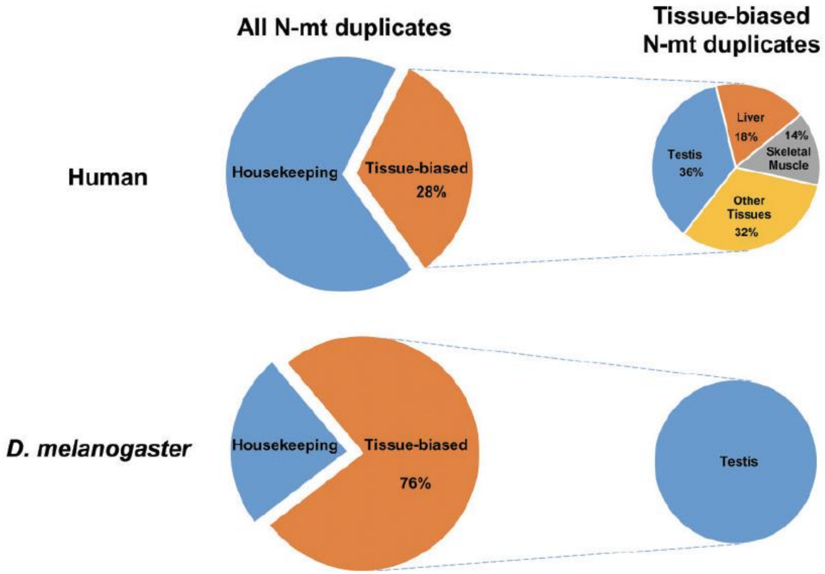
Limited repertoire in old vs. young endosymbionts

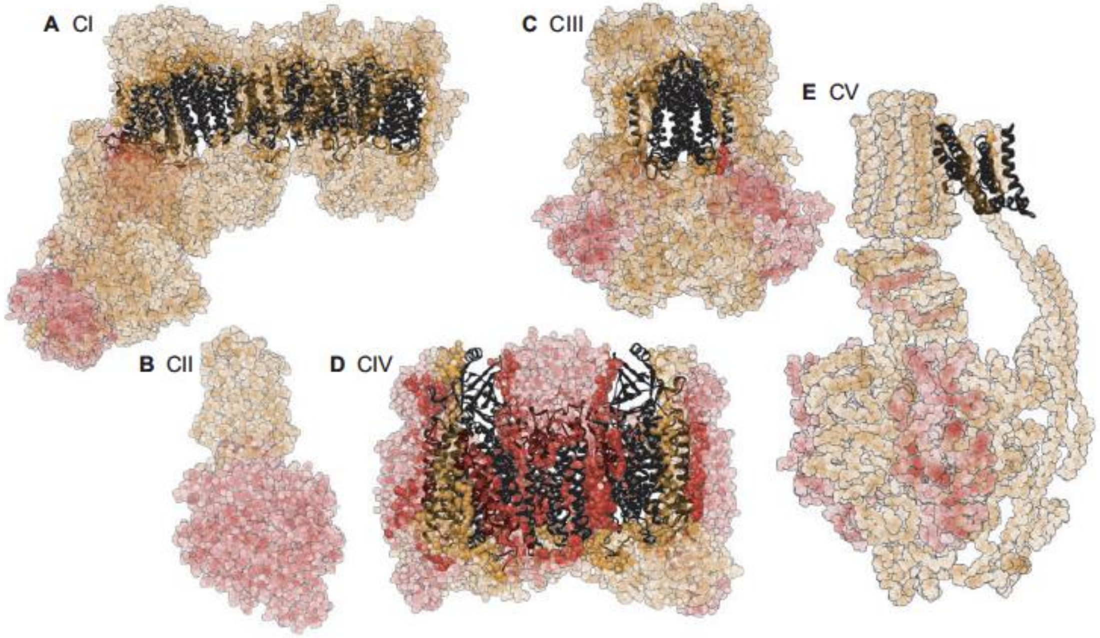


Havird et al. 2019 Current Biology

Nuclear responses to combat sex conflict

- RF genes, coevolution, etc.
- Sex-specific N-mt paralogs





Mt subunits

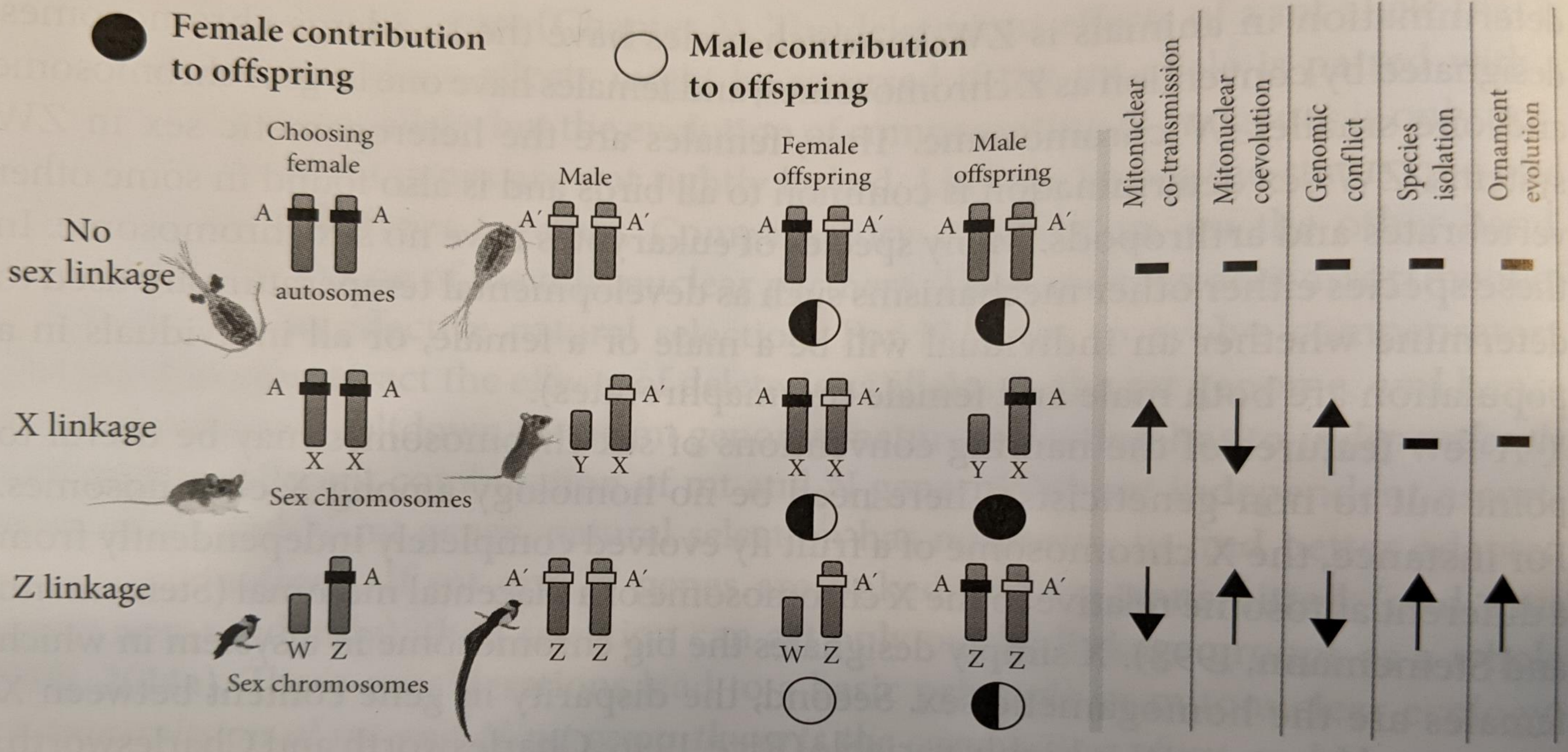
Nuc singleton subunits

Nuc duplicate subunits

Gallach et al. 2010, Eslamieh et al. 2018, Havird and McConie 2019

Conflict vs. coevolution

- Hill favors coevolution
- All the hypotheses put forward in light of coevolution could also be interpreted in light of conflict
- E.g., speciation and CMS



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