SEXUAL SELECTION

What I have called Sexual Selection…depends not on a struggle for existence in relation to other organic beings or to external conditions, but on a struggle between individuals of one sex, generally the males for the possession of the other sex… When the males and females…have the same general habits but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection.

Darwin, *The Origin Of Species*

SEXUAL SELECTION

- **A special form of selection that accounts for many elaborated traits and behaviors in organisms.**
- **Arises from differences in the ability to find and mate with members of the opposite sex.**
- **Only occurs when access to one or the other sex is limiting, i. e., when there is competition for mates or offspring.**

Sexual selection is non-random variance in reproductive success.

- Two forms of sexual selection:
- Intrasexual selection: direct competition for mates between members of the same sex, *usually* male-male competition.
- Intersexual selection: differences in attractiveness to the opposite sex, *usually* non-random mate choice by females.

The form of Sexual Selection is directly related to the relative investment in offspring production.

The sex that invests more in offspring production has fewer reproductive opportunities.

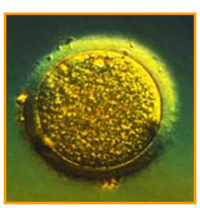
As a result they,

- Should be more discriminating (choosier).
- Become a limiting resource for the opposite sex.

ANISOGAMY-

Differential investment in reproduction

FEMALES: Sex that produces few, well-provisioned gametes (eggs)

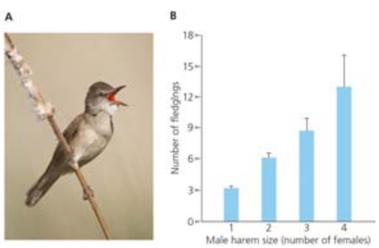


MALES: Sex that produces many, "cheap" gametes (sperm)

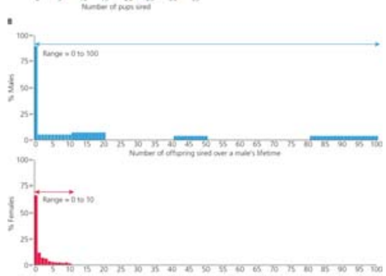
Figure 11.7 Z&E

Limitations on reproductive success differ for the sexes

- Females are limited by **fecundity**
- Males are limited by the number of mates they can obtain



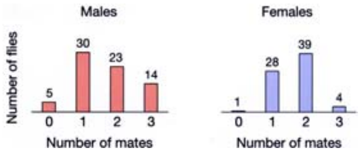
Elephant Seals



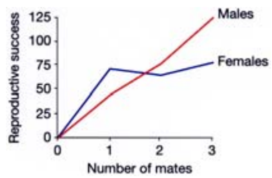
- Variance in reproductive success is MUCH greater in males

Figure 11.1 Z&E

Bateman's Principle: greater variance in reproductive success among males than females



- Since male gametes are not (as) limiting, male reproductive success increases linearly with increasing number of mates.
- When this is true, sexual selection is higher on males.

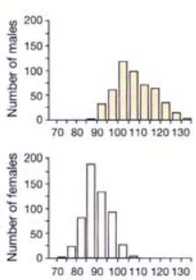


The asymmetric nature of sexual selection often leads to dramatic **sexual dimorphism** in characters directly related to male-male competition and/or female choice.

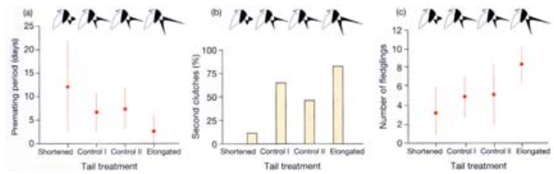
Peacock

Peahen

SEXUAL DIMORPHISM IN TAIL LENGTH IN BARN SWALLOWS

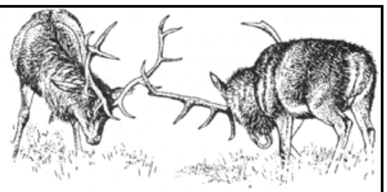


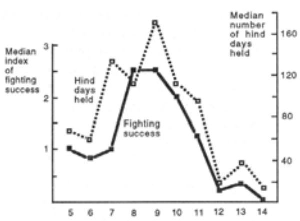
NON-RANDOM VARIANCE IN MATING SUCCESS RELATED TO TAIL LENGTH



	Male Tail Treatment				
Extra-pair copulations	Shortened tails	Control I	Control II	Lengthened tails	P
By males	0	0	0	0.040	< 0.001
By their social pair-mates	0.036	0.014	0.017	0	< 0.01

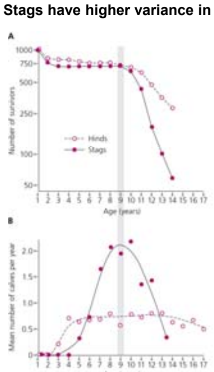
MALE-MALE COMPETITION





Male Red Deer with the greatest success in combat are able to retain females for longer periods.

- Male Red Deer who retain females longer have higher reproductive success.
- Stags have higher variance in reproductive success than Hinds.



High reproductive success is costly

Figure 11.13 Z&E

- Sexual selection can be very strong and often *opposes* natural selection.
- This can lead to exaggerated and sometimes *maladaptive* development of male traits.

- Male-male competition can explain the evolution of many morphological and behavioral traits

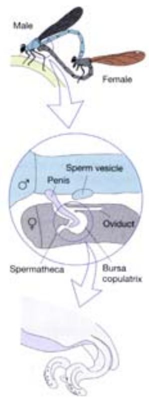
- Hercules beetles engage in titanic jousting matches using their elaborate horns to displace rival males.
- This competition has lead to an exaggeration of body size and horn size…

Beetle Fight

- Male-Male competition often does not stop with successful mating. There is often post-copulatory competition.
- This type of intrasexual competition is called,

SPERM COMPETITION

DAMSELFLY



Polyandry selects for male traits that increase paternity

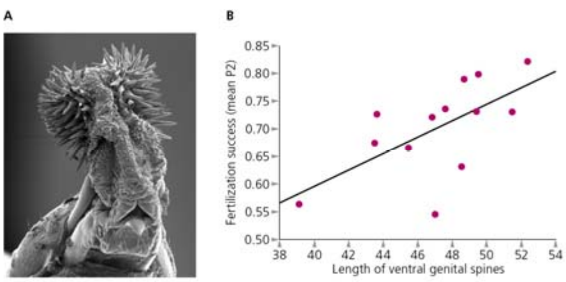


Figure 11.26 Z&E

EVIDENCE FOR SPERM COMPETITION IN PRIMATES

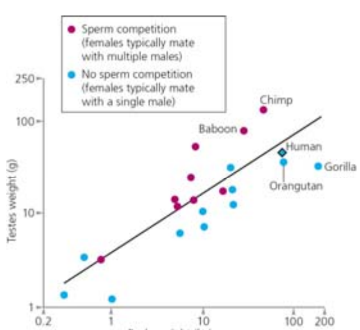


Figure 11.27 Z&E

AFTER: Harcourt et al. 1981

Competition drives cooperation among closely related sperm of deer mice

Heidi S. Fisher[1,2] & Hopi E. Hoekstra[1,2]

Among the extr
is the **coopera**
cooperative gro
and thereby ga
Accordingly, se
closely related
sperm of deer r
then we use thi
We find that sp
heterospecific s
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These results
deer mice dis
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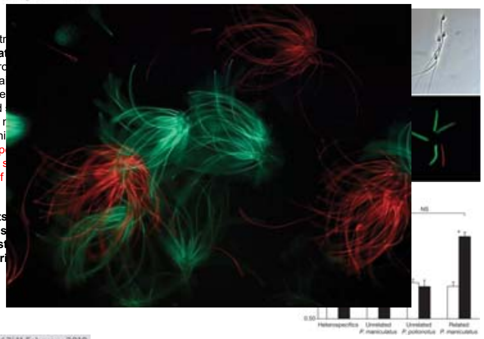


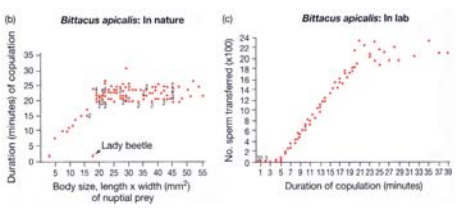
NATURE | Vol 463 | 11 February 2010

See Figure 11.28 Z&E

Nuptial Gifts:

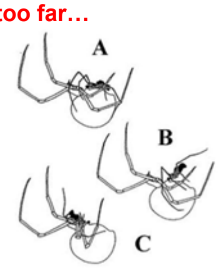
Male Hanging Flies present their female partners with insect food items. The size of the gift is correlated with the duration of copulation and the number of sperm transferred.

HANGING FLIES



Some times mate provisioning can go a little too far…

Australian Red-backed Spider



- Males are unlikely to mate more than once
- Transmit sperm *while being eaten*. More likely to mate successfully

See Figure 11.18 Z&E

FROM: M. C. B. Andrade. 2001.

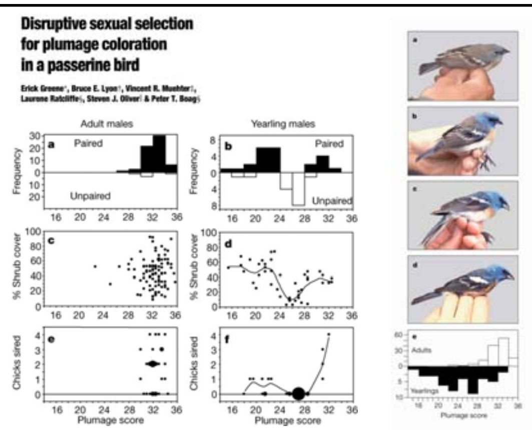
ALTERNATIVE REPRODUCTIVE STRATEGIES

If you can't beat them… Fool them!

- Many species have polymorphic male mating strategies.
- Sneakers: males not directly engaging in competition for mates may gain extra-pair copulations. (e.g., small "Jack" salmon)

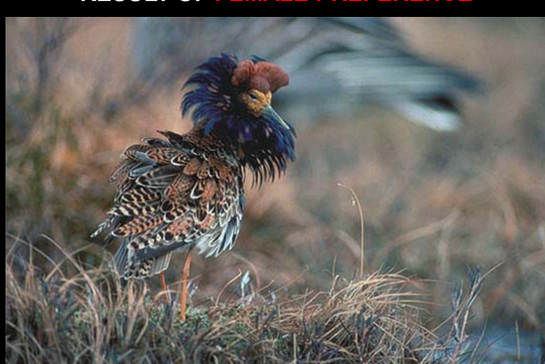
- Female mimicry: one way to distract or interrupt a competitor.

Plethodontid salamanders

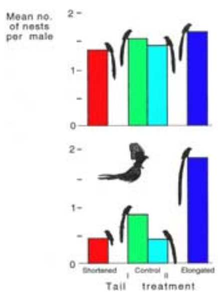


Nature (2000) 407:1000-1003

ELABORATE TRAITS CAN ALSO BE THE RESULT OF FEMALE PREFERENCE



FEMALE PREFERENCE FOR TAIL LENGTH IN WIDOWBIRDS



- Nesting success before experimental manipulation
- Nesting success after experimental manipulation

REASONS FOR FEMALE CHOICE OR PREFERENCE

Direct Benefits:

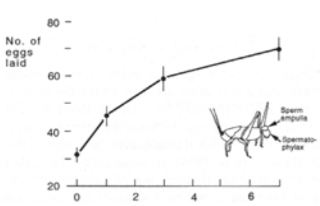
- Females may benefit from increased nutrition, provisioning, or paternal care that increases their reproductive output or the quality of their offspring.

Indirect benefits:

- Good Genes Hypothesis: Genetically superior mates produce fitter offspring.
- Sexy Son Hypothesis: Females that mate with preferred fathers produce sons that will have high mating success.

- **Many female insects gain *direct benefits* by consuming a portion of the spermatophore presented to them by males.**

Female Bush Cricket



Male Bush Cricket

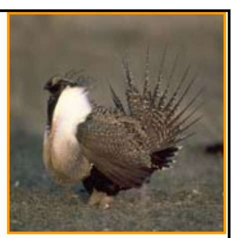
REGAL BOWER BIRD

- How can we explain female preferences when there are no direct benefits?

Birds of Paradise

GOOD GENES MODEL

ELABORATED MALE TRAITS MAY BE INDICATORS OF HERITABLE GENETIC QUALITY (I.E. FITNESS).



The Handicap Principle (Zahavi 1975)

- Some males may have a heritable trait that reduces viability.
- Only males with “Good Genes” can survive despite the handicap.
- Females that mate with these males will have offspring with higher fitness

HANDICAP PRINCIPLE

- **The bigger the handicap, the higher the genetic quality of the male carrying the trait.**
- **Female choice evolves and the handicap spreads and becomes elaborated.**
- **This is an example of an *honest signal* since there is a true cost to the elaborated trait that prevents "cheaters".**

FISHERIAN RUNAWAY SEXUAL SELECTION

An alternative to the "Good Genes" Hypothesis:

- **Assortative mating within a population between males with the most exaggerated trait and females with the strongest preference can lead to a genetic correlation between trait genes and preference genes. *The female preference genes will "hitchhike" onto the successful male genes*.**

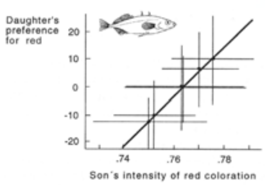
FISHERIAN RUNAWAY SEXUAL SELECTION

- **Suppose that males with longer tails are preferred at first because they have higher viability (Good Genes).**
- **The increased reproductive success of these males increases the frequency of trait and preference genes and reinforces assortative mating since offspring carry genes for both exaggerated tail length and strong preference.**
- **When there is a genetic correlation between the male trait and female preference then the process becomes self-reinforcing.**

FISHERIAN RUNAWAY CAN LEAD TO MALADAPTIVE TRAITS

- **When the trait and the preference are genetically correlated, then the trait can evolve way beyond the point where it indicates overall genetic quality.**
- **Runaway of the male trait can proceed to a point of exaggeration where it actually decreases male fitness.**
- **The runaway process leads to a situation where the only benefit to female choice is that her sons inherit the most attractive state of the trait. This is in direct contrast to the "Good Genes" Hypothesis and has been referred to as the "Sexy-son" Hypothesis.**

- **Evidence for a genetic correlation between trait and preference from Three-spine Sticklebacks.**



EXPERIMENTAL EVIDENCE FOR FISHER'S RUNAWAY PROCESS

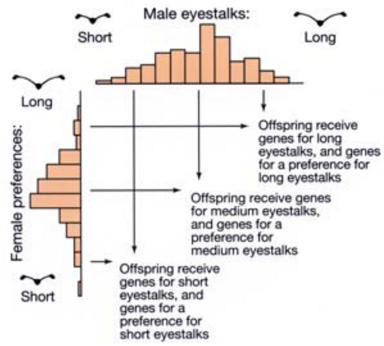
- **Stalk-eyed Flies have heritable variation for the distance between eyes in males and for female preference for stalk length**

AFTER: Wilkinson et al.

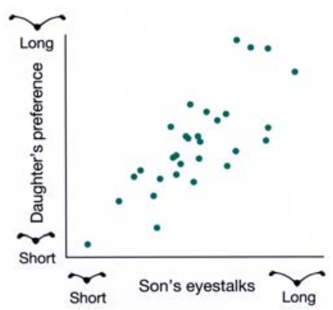
Short Stalk →

Long Stalk →

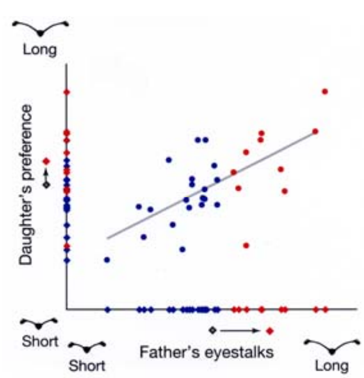
ASSORTATIVE MATING AND THE DEVELOPMENT OF A GENETIC CORRELATION BETWEEN TRAIT AND PREFERENCE



EVIDENCE FOR A GENETIC CORRELATION BEWEEN TRAIT AND PREFERENCE

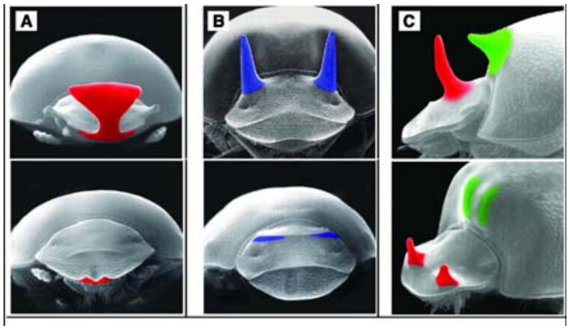


RESULTS OF SELECTION EXPERIMENTS



EVIDENCE THAT MALE TRAITS ARE LIMITED BY NATURAL SELECTION

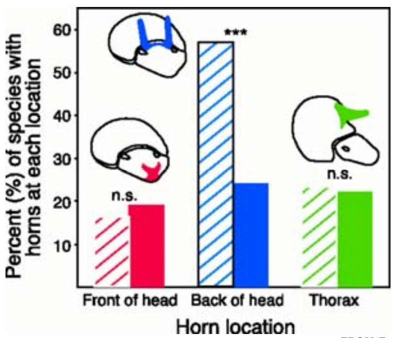
MALE HORNS



FEMALE HORNS

FROM:Emlen *Science* 2001

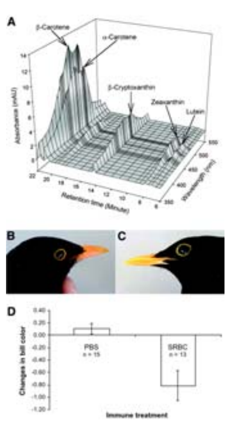
DEVELOPMENT OF MALE TRAITS CAN BE ECOLOGICALLY DEPENDENT



FROM:Emlen *Science* 2001

Immune Activation Rapidly Mirrored in a Secondary Sexual Trait

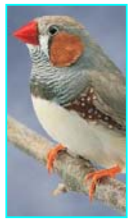
A crucial assumption underlying most models of sexual selection is that sexual advertisements honestly reflect the phenotypic and/or genetic quality of their bearers (1). Here we show that experimental activation of the immune system is rapidly mirrored in the expression of a carotenoid-based secondary sexual trait in male blackbirds (*Turdus merula*).



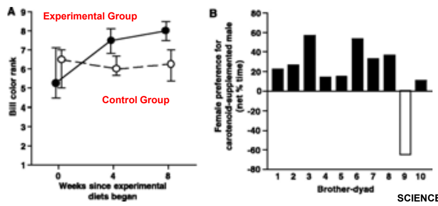
FROM: Faivre et al. Science. April 4, 2003

Carotenoid Modulation of Immune Function and Sexual Attractiveness in Zebra Finches

Blount et al.



One hypothesis for why females in many animal species frequently prefer to mate with the most elaborately ornamented males predicts that availability of carotenoid pigments is a potentially limiting factor for both ornament expression and immune function. An implicit assumption of this hypothesis is that males that can afford to produce more elaborate carotenoid-dependent displays must be healthier individuals with superior immunocompetence… In this study, we show that manipulation of dietary carotenoid supply invokes parallel changes in cell-mediated immune function and sexual attractiveness in male zebra finches (*Taeniopygia guttata*).

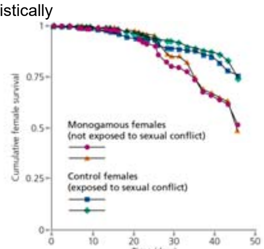


SCIENCE, April 4, 2003

SEXUAL CONFLICT CAN LEAD TO ANTAGONISTIC COEVOLUTION

- **Sexual conflict:** traits that confer a fitness benefit on one sex but cost to the other
  - Traits coevolve antagonistically

- Female *Drosophila* reared in competitive and non-competitive environments show different costs to mating with males from a competitive environment



See section 11.6 Z&E

Figure 11.32 Z&E

ALTERNATIVE HYPOTHESIS FOR THE ORIGIN OF FEMALE PREFERENCE

Sensory Bias (Ryan)

- **Preexisting preferences for certain traits may be hardwired in females and lead to the development of exaggerated traits in males.**

EXAMPLE OF SENSORY BIAS IN TRINIDAD GUPPIES

- Female guppies are attracted to ORANGE. This response may be due to feeding behavior selecting for the ability to locate ripe fruit.

- Sexual selection then favors males with lots of orange working on a preference that is already in place.

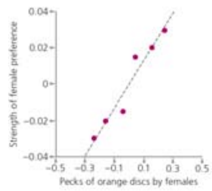
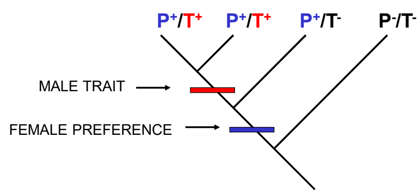


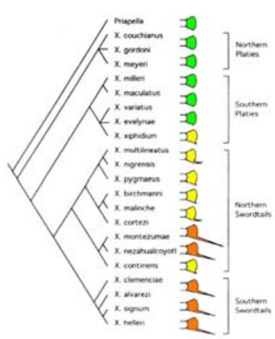
Figure 11.22 Z&E

PHYLOGENETIC PREDICTIONS OF THE OF SENSORY BIAS HYPOTHESIS



- Female preference should evolve first, followed by the evolution of the male trait.

Phylogeny of Species in the genus *Xiphoporus*



FROM: Meyer et al. 1994 *Nature*

EVIDENCE FOR SENSORY BIAS


Swordtail

- Females of species in the genus *Xiphoporus* in which males do not have swords PREFER males with swords.
- The primitive condition is for male to have no swords.

MALE PARENTAL CARE INCREASES MALE INVESTMENT IN OFFSPRING PRODUCTION

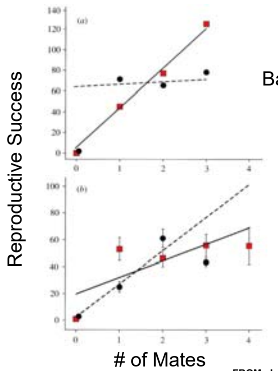

Male Dendrobatid Frog carrying a tadpole


Male Giant Water Bug guarding a clutch of eggs

MALE "PREGNANCY" IN SEAHORSES AND PIPEFISH CAN LEAD TO SEXUAL DIMORPHISM:

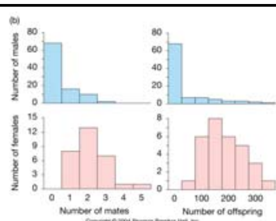
- Stronger sexual selection on females leads to the expression of secondary sexual characters in females NOT males.

BATEMAN'S GRADIENT AND SEX-ROLE REVERSAL

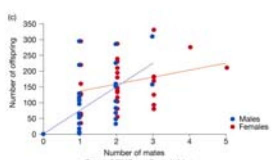


Pipefish

FROM: Jones et al. 2000. *Proc. R. Soc. Lond.* B 267:677-680



- Jones et al. (2002) used highly polymorphic microsatellite loci to genotype an entire population of rough-skinned newts to get a direct estimate of mating success and offspring production. From these data they were able to assess the relative strength of sexual selection on males and females.



FACTORS THAT CONTRIBUTE TO THE STRENGTH OF SEXUAL SELECTION

Mating systems:

- **Monogamy: Pair fidelity**
- **Polygyny: Male promiscuity**
- **Polyandry: Female promiscuity**

Monogamy ⟷ Polygyny/Polyandry

Increasing intensity of sexual selection →

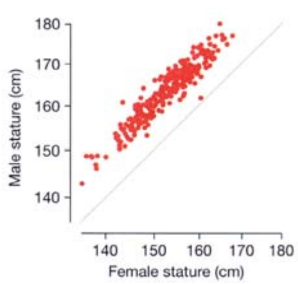
POLYANDRY IS MORE COMMON THAN WE THOUGHT

- Recent advances in molecular techniques (e.g.,DNA fingerprinting and Microsatellites) allow the direct assessment of paternity.
- The emerging evidence suggests that polyandry (females mating with more than one male) is far more common in nature than was assumed based on behavioral observations.
- For example, in apparently monogamous birds 15 – 20% of offspring are sired through extra-pair copulations.
- This observation indicates that sexual selection may operate even in monogamous species.

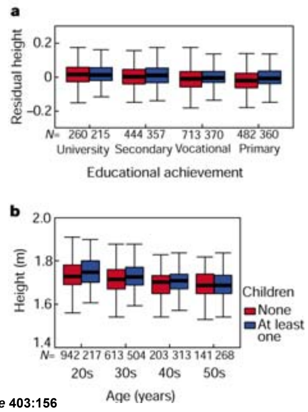
ECOLOGICAL DETERMINANTS OF THE INTENSITY OF SEXUAL SELECTION

- The opportunity for sexual selection is influenced by the Breeding Sex Ratio (BSR), ratio of receptive females to sexually active males which varies with the particular ecological setting.
- Intensity can vary between closely related species, among populations, or within a population over time.

SEXUAL DIMORPHISM IN HUMANS



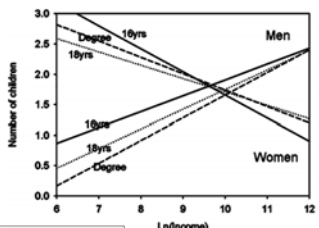
TALL MEN HAVE HIGHER REPRODUCTIVE SUCCESS

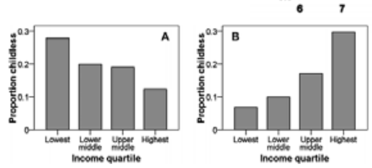


FROM: Pawlowski et al. 2000. *Nature* 403:156

Natural Selection on Male Wealth in Humans

Nettle & Pollet

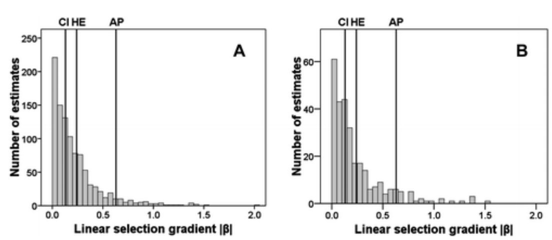




Men Women

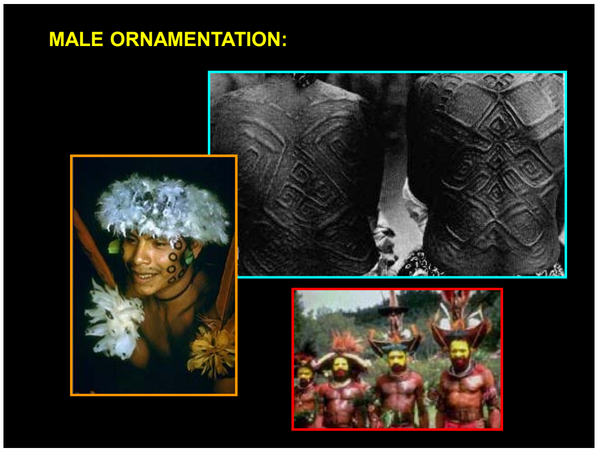
Am Nat 2008. 172:658–666

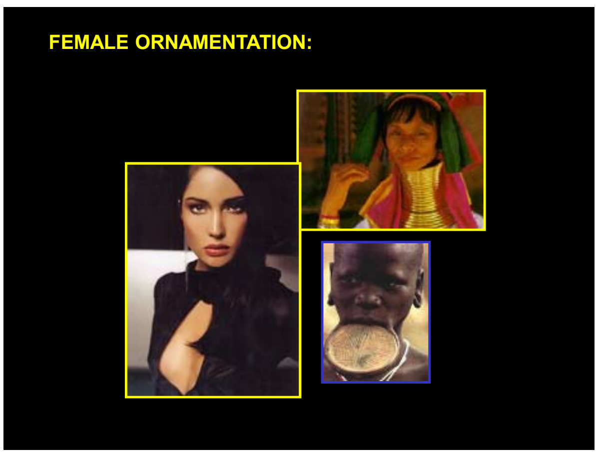
Selection Gradients on Wealth

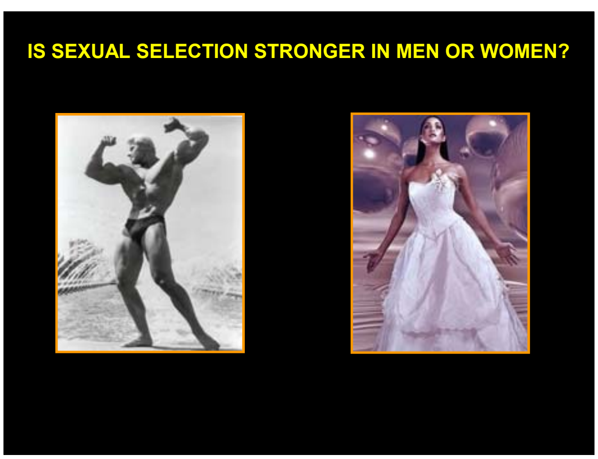


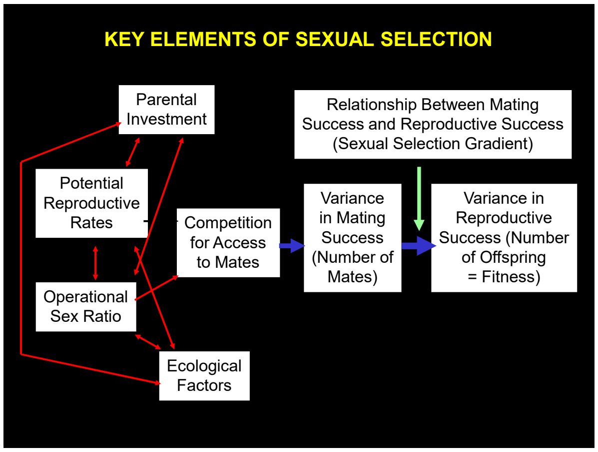
A, Position in the cross-taxa distribution of linear selection gradients (|β|) of selection on male wealth in contemporary industrial (CI), historical European (HE), and African polygynous (AP) human societies. B, Comparison restricted to |β| values where the component of fitness measured is fecundity. Cross-taxa data are from Kingsolver et al. (2001).

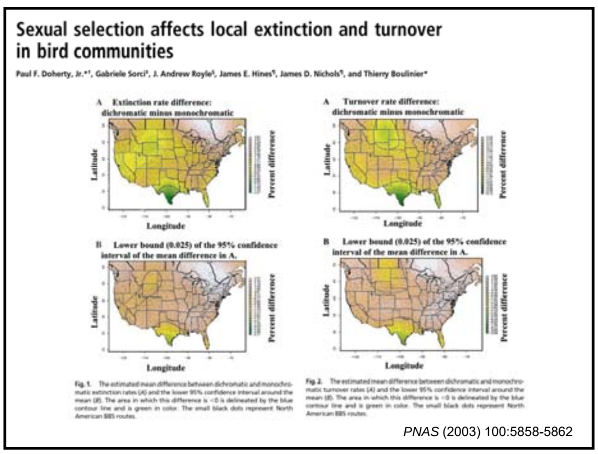
Am Nat 2008. 172:658–666


MALE ORNAMENTATION:


FEMALE ORNAMENTATION:


IS SEXUAL SELECTION STRONGER IN MEN OR WOMEN?





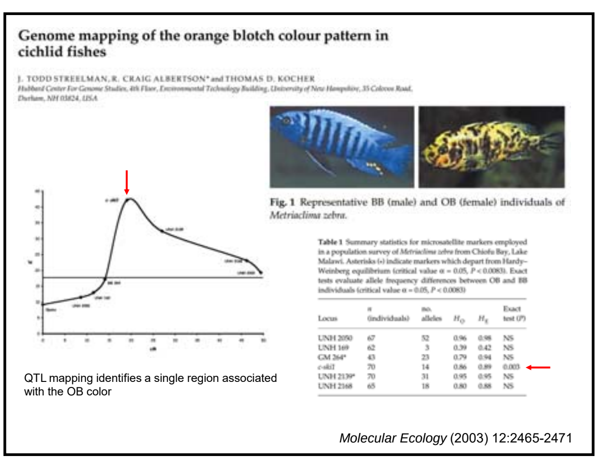
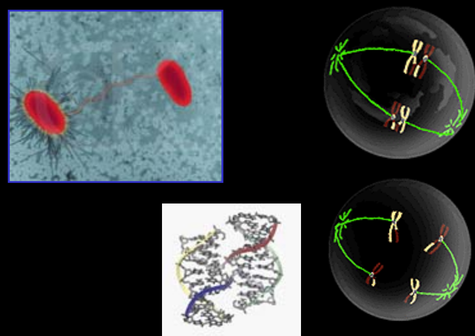


Table 1 Summary statistics for microsatellite markers employed in a population survey of *Metriaclima zebra* from Chiofu Bay, Lake Malawi. Asterisks (*) indicate markers which depart from Hardy–Weinberg equilibrium (critical value $\alpha = 0.05$, $P < 0.0083$). Exact tests evaluate allele frequency differences between OB and BB individuals (critical value $\alpha = 0.05$, $P < 0.0083$)

Locus	n (individuals)	no. alleles	H_O	H_E	Exact test (P)
UNH 2050	67	52	0.96	0.98	NS
UNH 169	62	3	0.39	0.42	NS
GM 264*	43	23	0.79	0.94	NS
c-ski1	70	14	0.86	0.89	0.003
UNH 2139*	70	31	0.95	0.95	NS
UNH 2168	65	18	0.80	0.88	NS

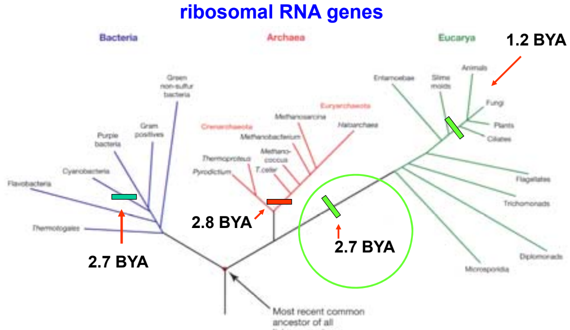
EVOLUTION OF SEXUAL REPRODUCTION



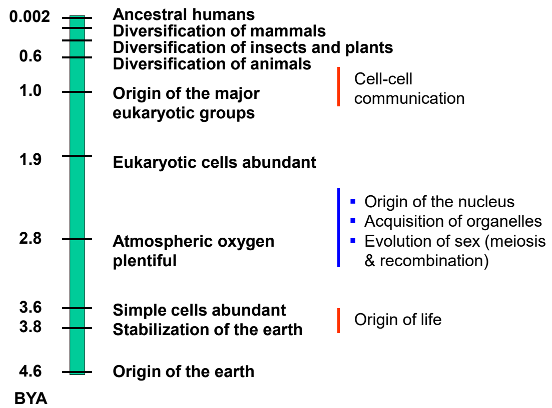
Three questions:

- **When did recombination evolve?**
- **Why did recombination evolve?**
- **How is recombination maintained in natural populations?**

Divergence dates of the 3 major domains based on ribosomal RNA genes



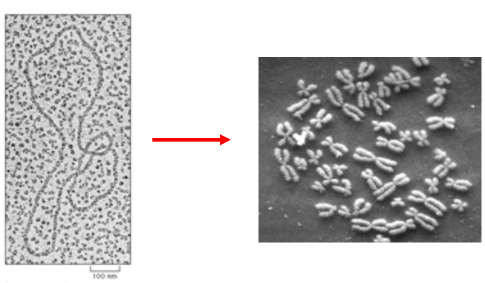
FROM: Knoll 1999 *Science*



EVOLUTION AND DIVERSIFICATION OF THE EUKARYOTES

- **What factors contributed to the rapid diversification of eukaryotic lineages?**
  - Increased atmospheric O_2 concentration – switch to aerobic respiration?
  - Global climate change – Major ice age around 2.7 BYA?
  - Evolution of sexual reproduction?

Haploid Circular Chromosome | **Diploid Linear Chromosomes**



Prokaryote | **Eukaryote**

Primitive Eukaryote: *Giardia lamblia*

- *Giardia* has two haploid nuclei
- No mitochondria (???)

GENOME SIZE IN PROKARYOTES

TABLE 13.1 Range of C values in bacteria

	Range in genome size (kb)	*Ratio (highest/lowest)*
Eubacteria	580–13,200	20
Mycoplasmas	580–1,800	3
Gram negative	650–7,800	12
Gram positive	1,600–11,600	7
Cyanobacteria	3,100–13,200	4
Archaebacteria	1,600–4,100	3

From Cavalier-Smith (1985), updated by knowledge of the *Mycoplasma genitalium* (Fraser et al. 1995).

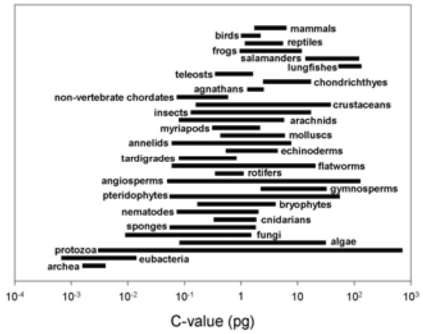
GENOME SIZE IN EUKARYOTES

TABLE 13.3 C values from eukaryotic organisms ranked by size

Species	*C value (kb)*
Navicola pelliculosa (diatom)	35,000
Drosophila melanogaster (fruitfly)	180,000
Paramecium aurelia (ciliate)	190,000
Gallus domesticus (chicken)	1,200,000
Erysiphe cichoracearum (fungus)	1,500,000
Cyprinus carpio (carp)	1,700,000
Lampreta planeri (lamprey)	1,900,000
Boa constrictor (snake)	2,100,000
Parascaris equorum (roundworm)	2,500,000
Carcarias obscurus (shark)	2,700,000
Rattus norvegicus (rat)	2,900,000
Xenopus laevis (toad)	3,100,000
→ ***Homo sapiens*** **(human)**	**3,400,000**
Nicotiana tabaccum (tobacco)	3,800,000
Paramecium caudatum (ciliate)	8,600,000
Schistocerca gregaria (locust)	9,300,000
Allium cepa (onion)	18,000,000
Coscinodiscus asteromphalus (diatom)	25,000,000
Lilium formosanum (lily)	36,000,000
Amphiuma means (newt)	84,000,000
Pinus resinosa (pine)	68,000,000
Protopterus aethiopicus (lungfish)	140,000,000
Ophioglossum petiolatum (fern)	160,000,000
Amoeba proteus (amoeba)	290,000,000
Amoeba dubia (amoeba)	670,000,000

Compiled by Li and Graur (1991) from Cavalier-Smith (1985), Sparrow et al. (1972), and other references. The C value for humans is highlighted for reference.

INCREASE IN GENOME SIZE



From: Gregory (2005) *The Evolution of the Genome*, Elsevier Press

COMPOSITION OF THE HUMAN GENOME

- ~1.5% of the genome consists of protein-coding sequences
- ~45% is composed of transposable elements
- ~15% is composed of repetitive elements
- ~24% is composed of introns

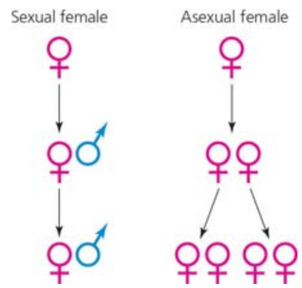
Data from the International Human Genome Sequencing consortium *Nature* (2001) 860-921

WHY SEXUAL REPRODUCTION???

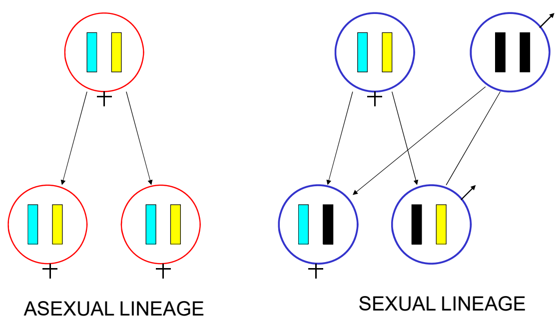
- **What factors favor the evolution and maintenance of sexual reproduction?**
- **Is there an advantage *or* cost to asexual reproduction?**

- The trade-offs, and the various advantages and disadvantages to sexual reproduction are described in **Table 11.1**

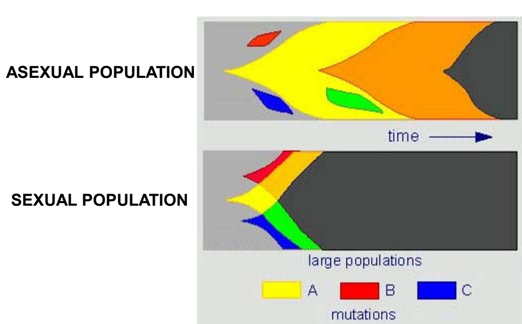
THE TWO-FOLD COST OF SEX
- Demographic



THE TWO-FOLD COST OF SEX
- Genetic



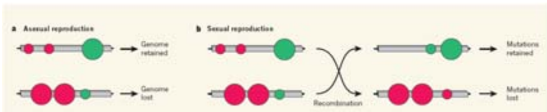
RECOMBINATION SPREADS BENEFICIAL GENES RAPIDLY THROUGH A POPULATION



Sex speeds adaptation by altering the dynamics of molecular evolution

Michael J. McDonald[1,2*], Daniel P. Rice[1,2*] & Michael M. Desai[1,2,3]

An analysis confirms the long-standing theory that sex increases the rate of adaptive evolution by accelerating the speed at which beneficial mutations sweep through sexual, as opposed to asexual, populations.



Picking rubies from the rubbish.

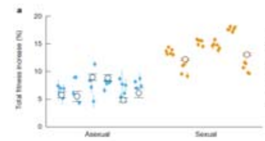


Figure 1 | The rate and molecular signatures of adaptation. a, Total fitness increase over ~1,000 generations of adaptation in asexual (blue) and sexual (orange) populations. Open circles represent the mean fitness of the population (for type a populations without frequency dependence); solid points represent the fitness of individual clones (mean of five replicate fitness assays, error bars ± s.e.m.). **b,** Classification of observed and fixed mutations in sequenced lines.

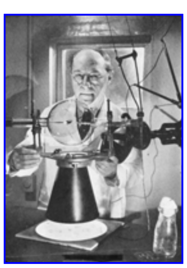
MOLECULAR EVOLUTION

McDonald et al. *Nature* (2016)

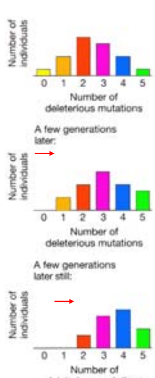
WHAT DO WE KNOW ABOUT INCOMING MUTATIONS?

- The spectrum of mutations is enormous, ranging from chromosomal rearrangements (translocations and inversions) and duplications to insertion and excisions of transposable elements to single base substitutions, insertions, and deletions.
- The vast majority of mutations appear to be deleterious. Slightly deleterious mutations are far more common than lethals.
- This input of slightly deleterious new mutation decreases population mean fitness by 1.0 -2.0% each generation.

MULLER'S RACHET AND MUTATIONAL MELTDOWN IN ASEXUAL POPULATIONS



H. J. Muller and the X-ray machine with which he did his Nobel Prize-winning experiments at the University of Texas



MULLER'S RACHET

- An asexual genome cannot produce offspring better than itself, except by rare back mutation.
- The ratchet advances when the best class leaves no offspring, or if all of its offspring have acquired new deleterious mutations.
- A mutational meltdown begins when the mutation load is so great that the populations is unable to replace itself.

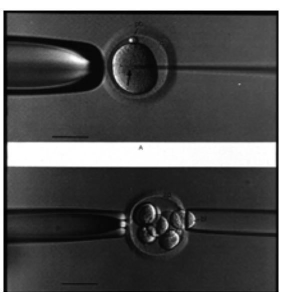
MUTATIONAL MELTDOWN OF THE HUMAN Y CHROMOSOME

- The original Y chromosome contained around 1,500 genes.
- All but about 50 have been inactivated or lost. This translates into a rate of loss of about 5 genes per million years.
- At the present rate of decay, the human Y chromosome will self-destruct in about 10 million years.

This process has already occurred in the mole vole which has completely lost the Y chromosome.

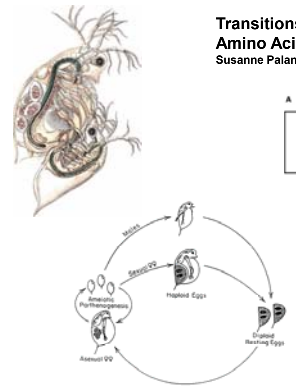
ARE WE ACCELERATING THE DECAY IN HUMAN Y CHROMOSOMES WITH MODERN *IN VITRO* FERTILIZATION TECHNIQUES?

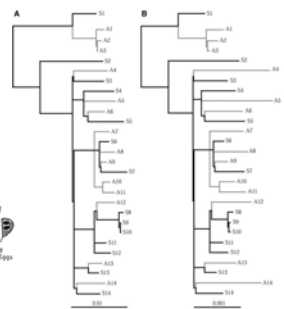
Many sperm abnormalities and infertility disorders are associated with defects on the Y chromosome.



Transitions to Asexuality Result in Excess Amino Acid Substitutions

Susanne Paland and Michael Lynch





Silent Replacement

Science 17 February 2006:
Vol. 311. no. 5763, pp. 990 - 992

THE BIG BENEFIT OF SEX

- **Recombination provides a mechanism for genomic repair, eliminating deleterious mutations (*).**

PARENT

A	*
B	*
*	C

GAMETES

A	A	*	*
B	*	*	B
C	*	C	*

Parents can produce offspring that have *higher fitness* genotypes than themselves.

SEXUAL REPRODUCTION CONTRIBUTES TO VARIATION

Example – A Line Cross Experiment

- Consider 2 diploid individuals with 3 loci and 2 alleles,

Parents: aabbcc x AABBCC

F_1 progeny: AaBbCc

F_2 progeny:

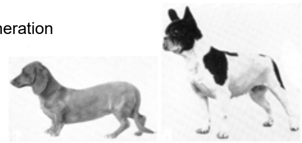
AABBCC	AABBCc	AABBcc
AABbCC	AABbCc	AABbcc
AAbbCC	AAbbCc	AAbbcc
AaBBCC	AaBBCc	AaBBcc
AaBbCC	AaBbCc	AaBbcc
AabbCC	AabbCc	Aabbcc
aaBBCC	aaBBCc	aaBBcc
aaBbCC	aaBbCc	aaBbcc
aabbCC	aabbCc	aabbcc

27 COMBINIATIONS

AN "OUTBREAK OF VARIATION"

Cross between a Dachshund and a French Bulldog

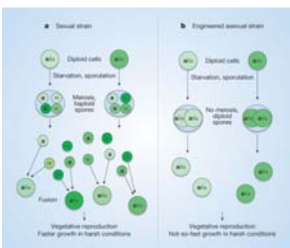
- Parental Generation

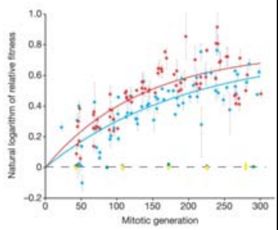


- F_1 Progeny

- F_2 Generation

FROM: C. R. Stockard. 1941. The Genetic and Endocrine Basis for Differences in Form and Behavior. Wistar Inst. Anat. Biol., Philadelphia, PA





- asexual strains in the benign environment
- sexual in the benign environment
- asexual in the harsh environment
- sexual in the harsh environment.

- **Many modern theories that provide an explanation for the advantage of sex incorporate an idea originally proposed by Weismann more than 100 years ago: *sex allows natural selection to proceed more effectively because it increases genetic variation.***

Sex increases the efficacy of natural selection in experimental yeast populations
Goddard et al. *Nature* 2005

SEXUAL REPRODUCTION ALLOWS POPULATIONS TO STAY ONE-STEP AHEAD OF THEIR PARASITES

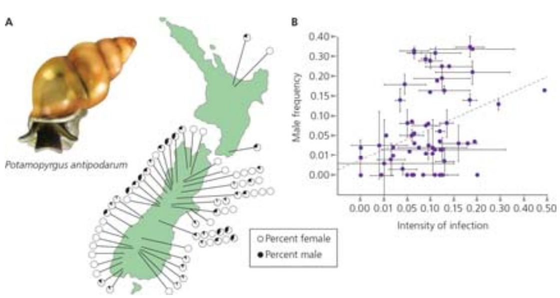


Figure 11.6 Z&E

FROM: Lively (1992)

The Red Queen Hypothesis for the Evolution of Sex

"A slow sort of country!" said the Queen. "Now, *here*, you see, it takes all the running *you* can do, to keep in the same place. If you want to get somewhere else you must run at least twice as fast as that"

From *Alice in Wonderland*
Lewis Carroll

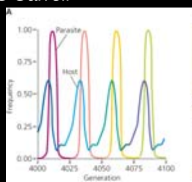


Figure 11.5 Z&E

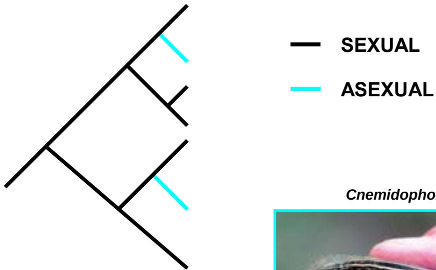
ADVANTAGES TO ASEXUALITY

- **Avoids the two-fold cost of producing males.**
- **No need to locate mates, an advantage at low density.**
- **Maintains *coadapted gene complexes*, an advantage in stable environments.**

DISADVANTAGES TO ASEXUALITY

- **Deleterious mutation accumulation (Muller's Ratchet) in small populations.**
- **Time delay in acquiring optimal multilocus genotypes in changing environments.**
- **Slow rate of evolution allows sexually reproducing antagonists (parasites, competitors, and predators) to get the upper hand.**
- **Selective sweeps can eradicate all variation from a population.**

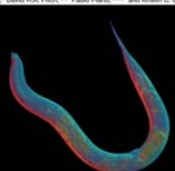
MOST ASEXUAL LINEAGES ARE EVOLUTIONARILY "YOUNG"



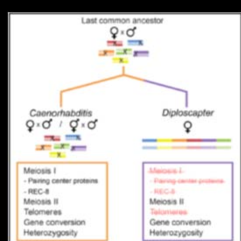
Cnemidophorus

Genome Architecture and Evolution of a Unichromosomal Asexual Nematode

Hélène Fradin, Karin Kiontke, Charles Zegar, Michelle Gutwein, Jessica Lucas, Mikhail Kovtun, David L. Corcoran, L. Ryan Baugh, David H.A. Fitch, Fabio Piano, and Kristin C. Gunsalus



~18 Million Year old Asexual Lineage



Why don't they "meltdown"?

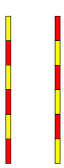
http://www.npr.org/sections/health-shots/2017/10/12/556246090/tiny-transparent-worm-challenges-notions-about-sex

Current Biology 27, 2928–2939, October 9, 2017

Bdelloid Rotifers: an ancient asexual lineage

One of the strongest candidates for ancient asexuals, bdelloid rotifers date back at least 40 million years. That's the age of the oldest bdelloid recovered from amber. Despite bdelloids' asexuality, they've diversified into ~360 species.

See Box 11.1 in Z&E



Bdelloid homologous chromosomes have diverged to the point that most genes have only one functional copy ( ). Now, they are *locked* into asexuality.

After Welsh & Meselson. Science 2000

SUMMARY OF THE EVOLUTION OF SEX

- Sexual reproduction (recombination) is a unique feature of eukaryotes and likely originated early in the history of this domain around ~2.7 BYA.
- Increases in genome size and the proliferation of genome “parasites” may have favored the early evolution of recombination.
- Asexuality avoids the “2-fold” cost of sex. Asexual lineages have both a genetic and demographic advantage over sexual lineages.
- The effects of mutation accumulation in asexual lineages may offset these costs.
- In stable environments, asexuality preserves well adapted genotypes and may be favored.
- In contrast, in variable environments, sexual lineages may be capable of rapid adaptation and sex may be favored.