Lect. 19. Natural Selection I

4 April 2017

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Last Time …

- Gene flow reduces among population variability, reduces structure
- Interaction of climate, ecology, bottlenecks, drift, and gene flow
- Genetic drift revisited
- Neutral theory
- How molecules evolve

Neutral theory

- Does not argue that “morphological, physiological and behavioral features of organisms evolved by random drift.”
- Adaptive features certainly evolve by natural selection, but…
- They constitute the minority of DNA sequence changes.
- **Most substitutions do not change amino acids and many of the ones that do, do not affect the function of the protein**.

How molecules evolve

- Natural selection at the molecular level preserves sites that are important in structure and function.
- Most substitutions take place at sites that are selectively “neutral”, i.e., a substitution that will have little or no effect on structure and function.

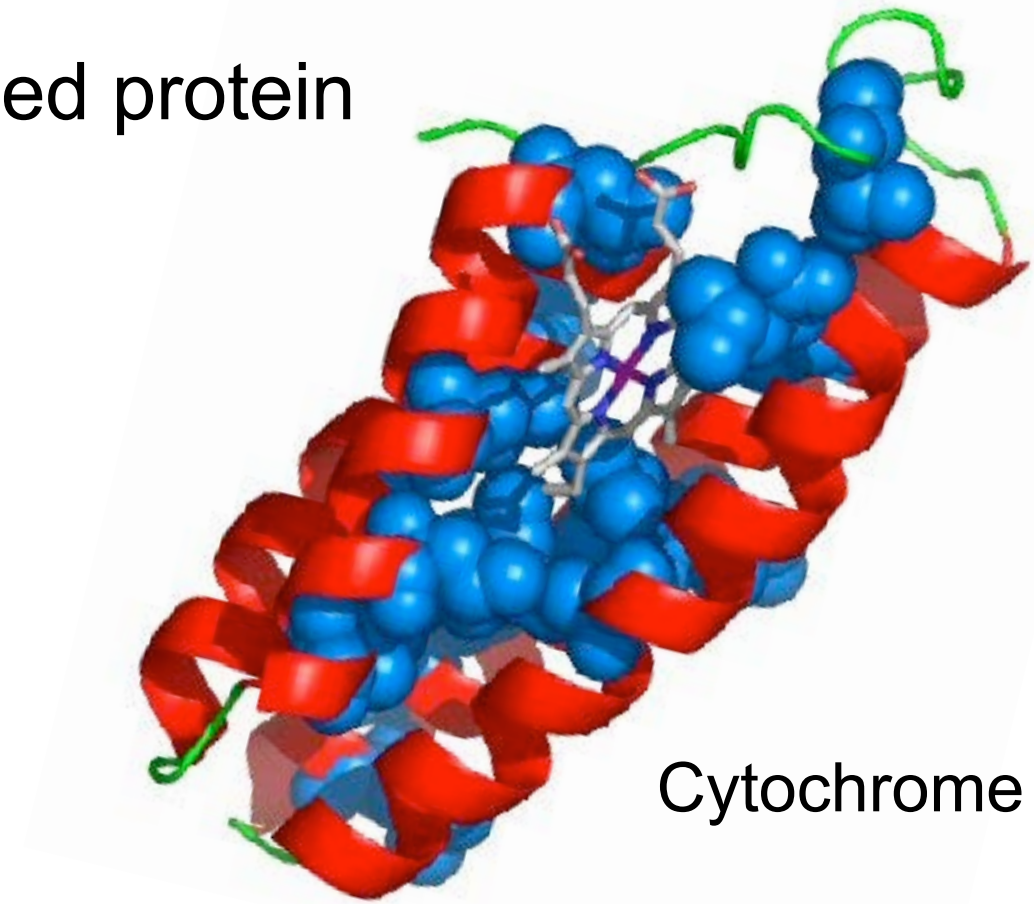
First example

- Protein coding genes- structure, function, and patterns of nucleotide substitution

Primary structure = DNA sequence

Secondary structure = AA sequence

Tertiary structure = folded protein



Cytochrome b

http://chemistry.umeche.maine.edu/CHY431/Proteins9.html

Protein coding genes- Primary structure.
DNA sequence- changes most common at "silent" (synonymous) 3rd positions vs "replacement" (nonsynonymous) 2nd positions

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                50                                  60
       T   G   L   F   L   A   M   H   Y   S   P   D   A   S   T   A   F   S   S   I   A
HUMAN ACA GGA CTA TTC CTA GCC ATG CAC TAC TCA CCA GAC GCC TCA ACC GCC TTT TCA TCA ATC GCC
  R1  T.. ..C ... ..T ... ..T ..A ..T ..T A.. ... ... A.. CTC ..G ..A ... ... ... G.T A..
  R2  T.. ..C ... ..T ... ..T ..A ..T ..T A.. ... ... A.. CTC ..G ..A ... ... ... G.T A..
  R3  T.. ..C ... ... ..G ..T ..A ..T ... A.. ... ... A.. ATC ..G ..A ... ... ... G.T A..
  R4  T.. ..C ... ..T ... ... ..A ... ... A.. ... ..T A.. CTC ..A ..A ..C ... ... G.T ...
  R5  T.T ..C ... ... ... ... ..A ... ..T A.. T.. ..T AG. ..T .A. AG. ... ... ... G.A A..

  B1  ... ..C ... C.. T.. ... GCA ..T ..T A.. G.T ..T A.T ..C CTA ... ..C G.T ..C G.A ...
  B2  ... ..C ... C.. ... ... GCA ... ... A.. G.T ..T A.T ..C CTA ... ..C G.T ..C G.A A..
  B3  ... ..C ..G C.. ... ..T GCA ... ... A.. G.T ... A.. ..C CTA ... ... G.C ..C G.A ...
  B4  ... ..C ... ... ... ... GCA ..T ... A.. G.C ... A.. ..C CT. ... ..C AAC ..C G.. ...
  B5  ... ..C ... C.A ... ... ... ... ... A.. G.C ... A.. ..C CTA ... ..C A.C ... G.A ...
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Substitutions influenced by triplet code of the amino acids

R = Rodents, B = Birds

Kocher et al. 1989. PNAS 86:6196

More complicated than that……

Four-codon family

Six-codon family

Two-codon family

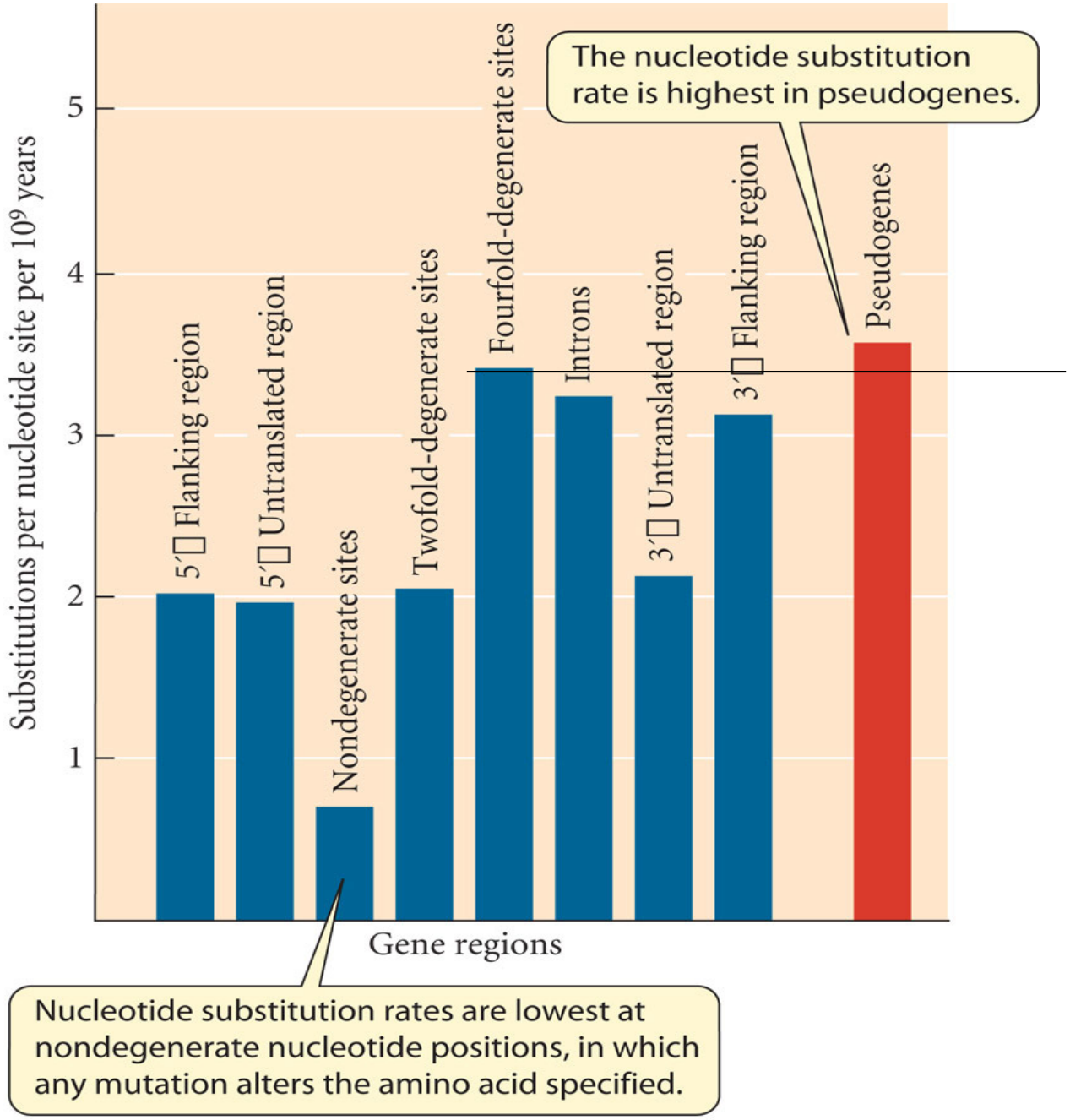
	AGA									UUA	
	AGG									UUG	
GCA	CGA						GGA			CUA	
GCC	CGC						GGC		AUA	CUC	
GCG	CGG	GAC	AAC	UGC	GAA	CAA	GGG	CAC	AUC	CUG	AAA
GCU	CGU	GAU	AAU	UGU	GAG	CAG	GGU	CAU	AUU	CUU	AAG
Ala	Arg	Asp	Asn	Cys	Glu	Gln	Gly	His	Ile	Leu	Lys

Three-codon family

One codon

			AGC								
			AGU								
			UCA	ACA			UA				
		CCC	UCC	ACC			GUC	UAA			
	UUC	CCG	UCG	ACG		UAC	GUG	UAG			
AUG	UUU	CCU	UCU	ACU	UGG	UAU	GUU	UGA			
Met	Phe	Pro	Ser	Thr	Trp	Tyr	Val	Stop			

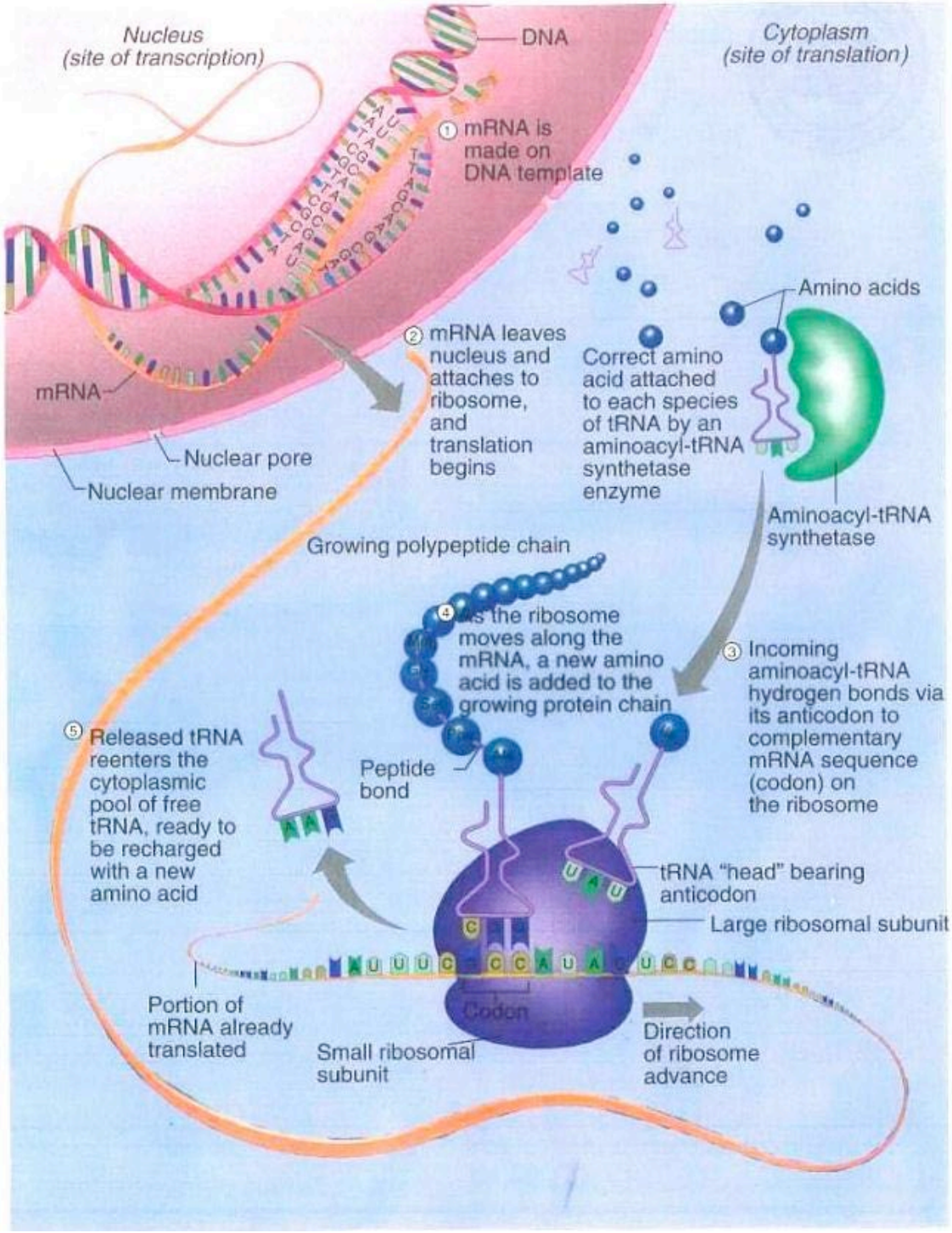
Note: changing the second position always changes the AA, except in Serine where it can be C or G iff the third position is C or U.



***EVOLUTION 3e*, Figure 10.14**

Second example

- Ribosomal RNA molecules- structure, function, and patterns of nucleotide substitution



Remembering from Introductory Biology… Protein synthesis

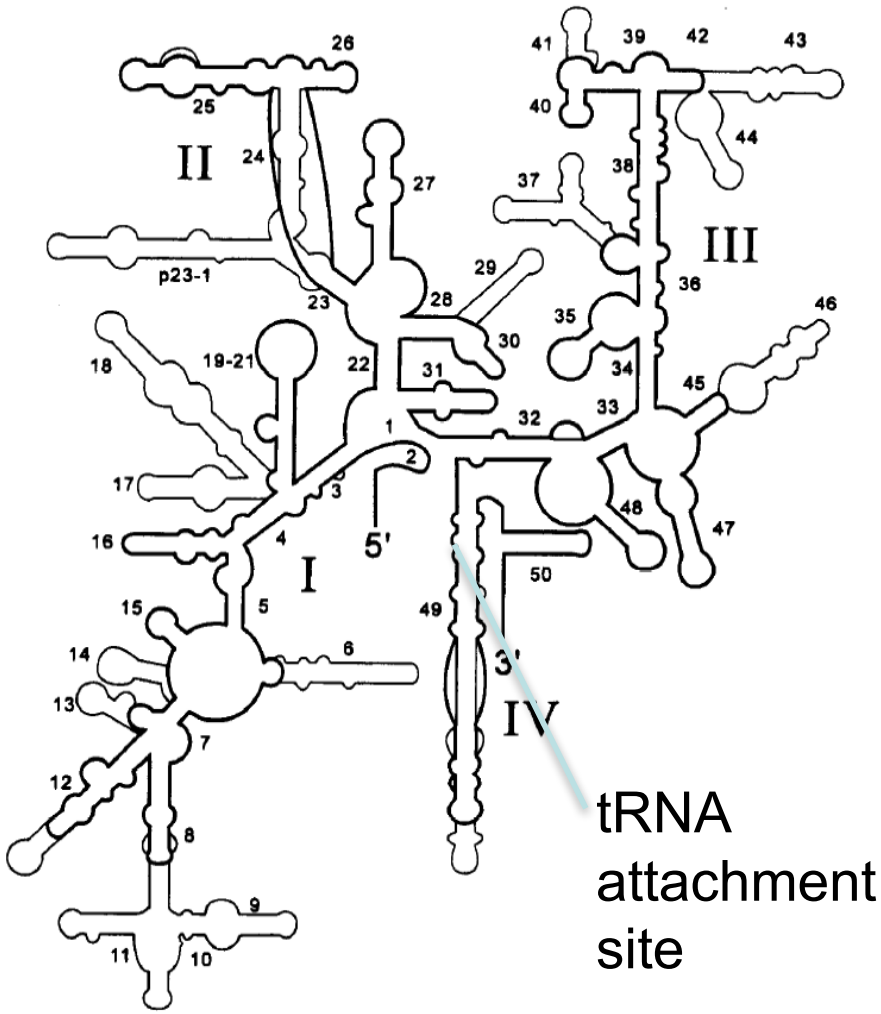
Ribosomes- site of protein synthesis

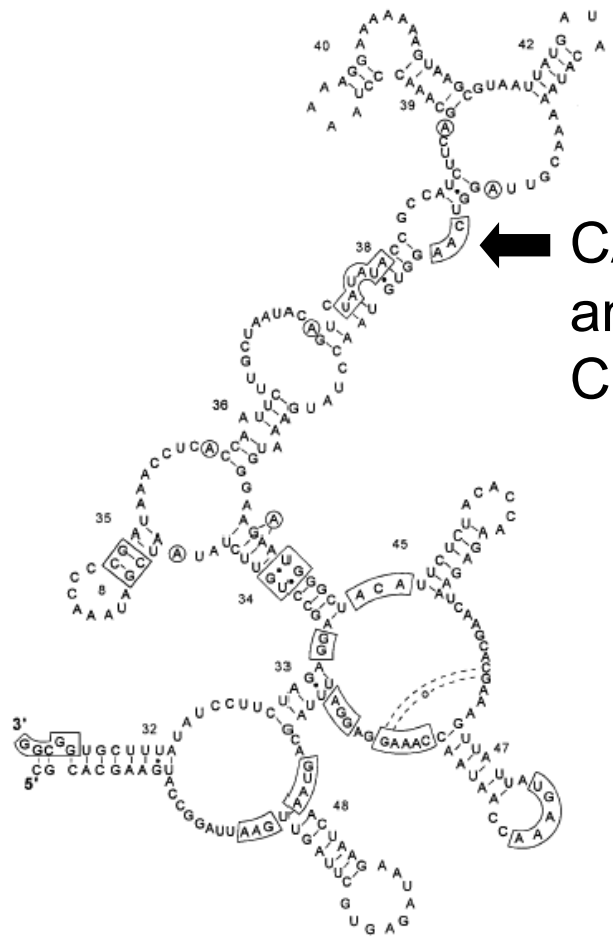
Large subunit
Small subunit

What are ribosomes made of?

Conservative Characters; Mosaic Evolution

e.g., rRNA secondary structure highly conserved. Primary sequence conserved to various degrees.



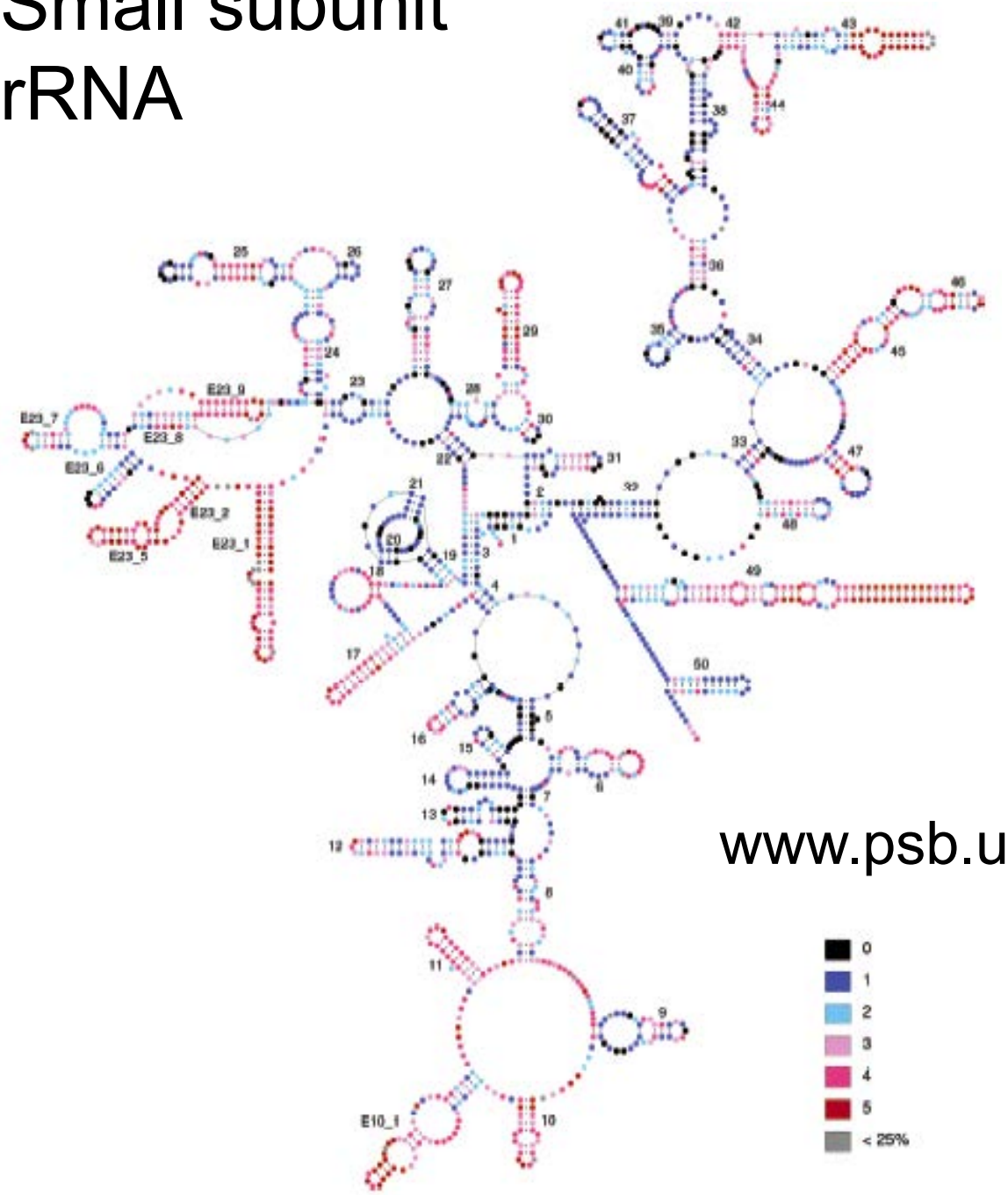


CAA in most animals, CGA in fish!

E. coli compared to mitochondria

Hickson et al. 1996. MBE

Small subunit rRNA



Substitution probabilities vary along a molecule in relation to structural and functional constraints

Red = most variable
Blue = least
Invariable = black

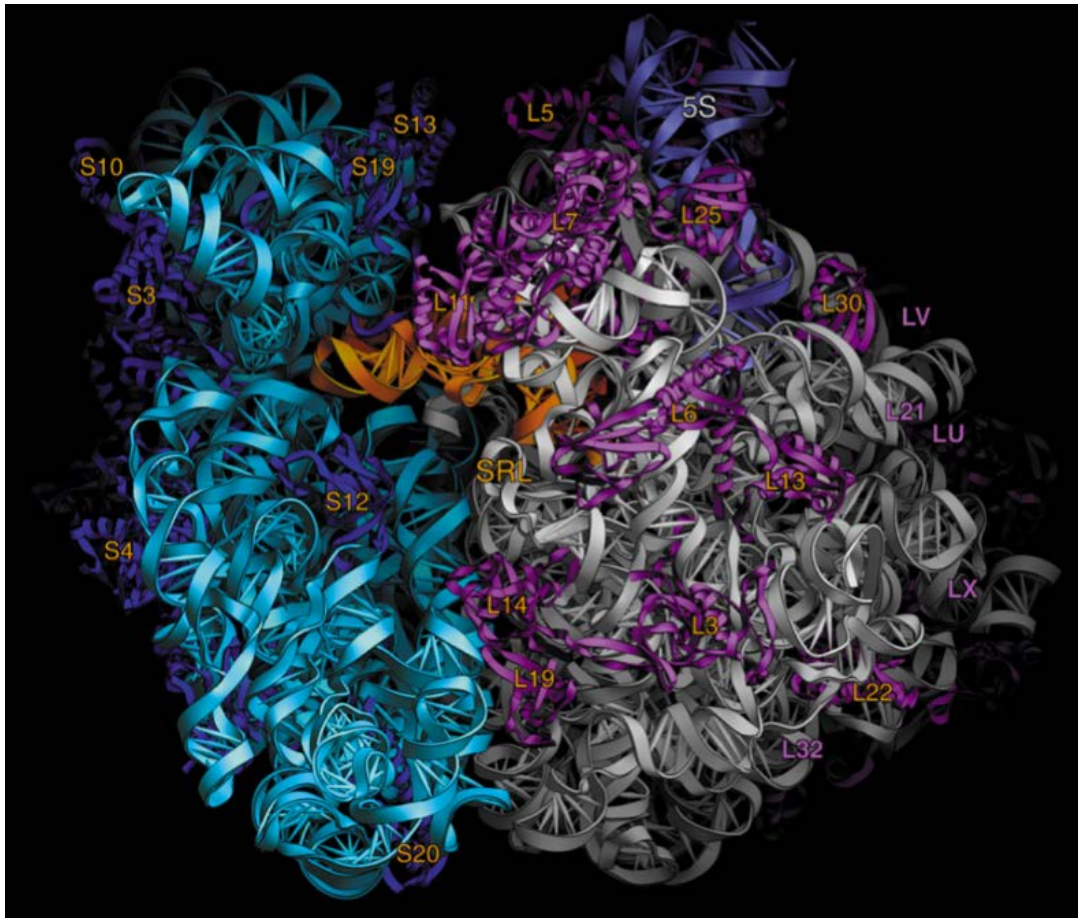
www.psb.ugent.be/rRNA/varmaps

500 eukaryotes mapped onto yeast structure, Yves Van de Peer

Simon et al. 2006. Annual Review of Ecology, Evolution & Systematics

Ribosome tertiary structure plus ribosomal proteins (dark blue & purple)

Small subunit turquoise



Large subunit gray

http://rna.ucsc.edu/rnacenter/ribosome_images.html

This time …

- Adaptive mutations are random
- No such thing as directed mutations
- Directional Selection wipes out variability unless…
- Competitive character displacement (finches & sticklebacks)
- Sexual selection

Next time …

- Conflicting selection pressures (sexual selection and predation)
- Importance of heritability
- Multiple niche polymorphisms (directional selection re-set each generation)
- Speed of directional selection

Adaptive mutations occur at random: Lenski et al. 1999

- 12 identical populations of *E. coli* were started from the same flask, fed glucose (adequate not preferred)
- Population sizes were always large and grown in culture for 11 years (24,000 generations, 1 generation every 3.5 hours)
- At end of experiment, all 12 descendant populations grew faster on glucose than initially.
- DNA sequences and substitutions were different among lineages.
- What does this illustrate?

No such thing as directed or anticipatory mutations

- Mutations are random with respect to the environment and the needs of the organism
- Random but favorable mutations increase in the population because the individuals carrying them survive better and leave more offspring.

Random Mutations

- Does not mean that environmental factors do not influence mutation (e.g., radiation and toxins can be mutagens)
- Mutation rates can be elevated by stressful environments,
- But they will be random with respect to the environmental stressors.

Strength of selection

- If predation is high, selection for camouflage or warning coloration can be strong
- Pesticide or antibiotic resistance – extremely strong natural selection.

Strong natural selection imposed by antibiotics

http://www.theatlantic.com/science/archive/2016/09/stunning-videos-of-evolution-in-action/499136/

Three conditions for evolution by natural selection:

- Phenotypic variation
- Phenotypes differ in fitness.
- The fitness differences are heritable

Modes of Selection

Three major categories of natural selection

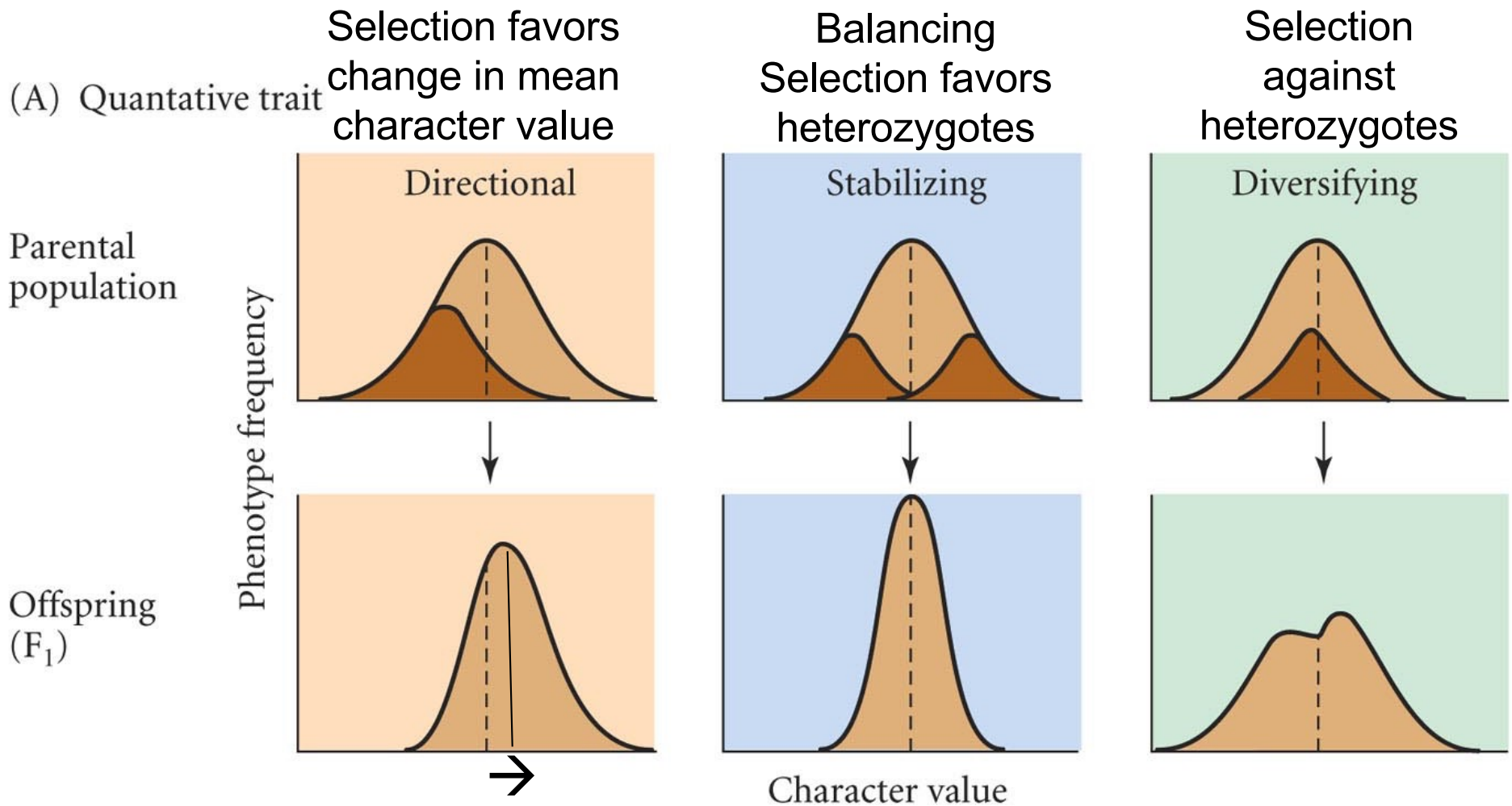


Fig. 12.1 Futuyma. Dark brown areas = lower fitness, selected against

Selection for mimicry: wasps mimics

Wasp
model

Wasp-mimicing
sharpshooter

Typical
sharpshooter

http://www.photographersdirect.com/bu
rs/stockphoto.asp?imageid=1747674

Wasp leafhopper (Lissoscarta sp) and its wasp model (Angiopolybia sp), Peru Flickr Artour_A

Some other insects that mimic wasps

Spiders that mimic ants

Camouflage

W. W. Lamar, P. Carmichael & G. Shumway. 1997. World publications

Yellow-crested weed fish, photo @strange_animals

Camouflaged Lichen Geckos

Giant Leaftail Gecko *Uroplatus fimbriatus* (above)

Frilled Leaftail Gecko *Uroplatus henkeli* (above, and below

William W. Lamar, P. Carmichael & G. Shumway. 1997. World publications

Camouflaged adult and juvenile tree hoppers

http://www.animalpicturesarchive.com/animal/a1/Camouflage_J01-HornedCicada_s_caterpillars.jpg

Questions About Directional Selection

- What is the effect of directional selection on variability?

- Directional selection will tend to wipe out variability unless….?

Directional Selection (cont.)

If organisms are perfectly adapted to their environments then variation would make individuals less adapted and less able to compete. Selfing would be favored.

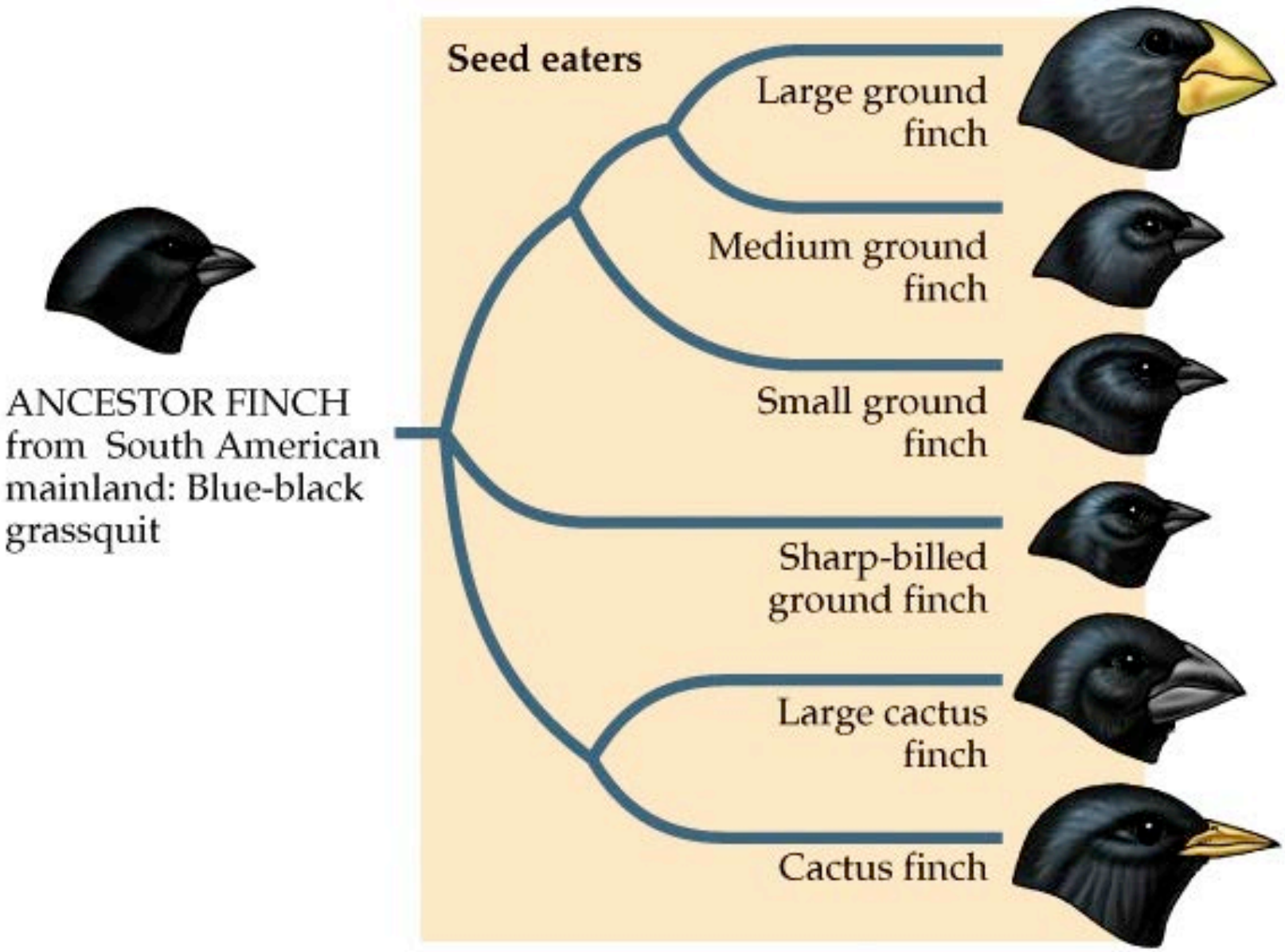
So why is there so much sexual reproduction and so much variation?

Temporal variation may be unpredictable

- El Niño Southern Oscillation (ENSO)
- Climate change- not only warming but unpredictable shifts in rainfall or unusually warm periods in winter or spring.
- Human caused habitat modification is usually too fast for adaptation to take place

Importance of long term studies

- Peter and Rosemary Grant began studying Galapagos finches in 1977.
- Found correlation between beak size and seed size; recorded competition between different finch species with different sized beaks.
- 1977-1981. Drought caused a small-seeded plant species favored by small finches to disappear



Importance of long term studies

- Only large seeds available after drought
- Severe mortality among *Geospiza fortis* finches, strong directional selection for larger beak size and larger birds.
- 1982-83 El Niño brought heavy rain
- Plant species with large hard seeds replaced by plant species with small soft seeds; these persisted through 1991

Importance of long term studies

- 1984-1991 many birds died (strong selection), bills became narrower. Only 37% of the 1983 large-billed birds reproduced in 1987 and the ones that did had narrower bills.
- demonstrated that bill shape and size were heritable.
- used quantitative genetics to predict the bill size would decrease to 0.13 mm and then observed avg. bill sizes very close to that.

Galapagos Is.

Competitive Character Displacement

Grant, P. & R. Grant. 1982. Niche shifts and competition in Darwin's finches: *Geospiza conirostris* and congeners. Evolution 36: 637-657.

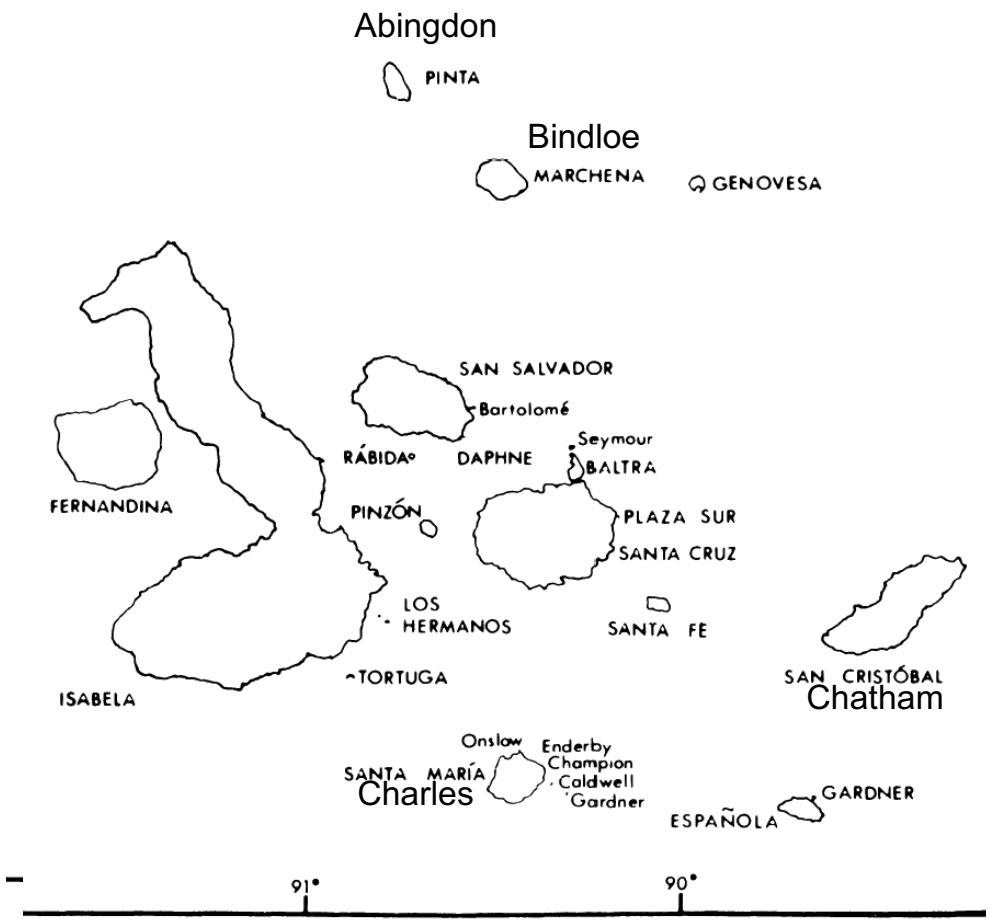


FIG. 1. The Galápagos Islands.

13 Spp. Darwin's Finches

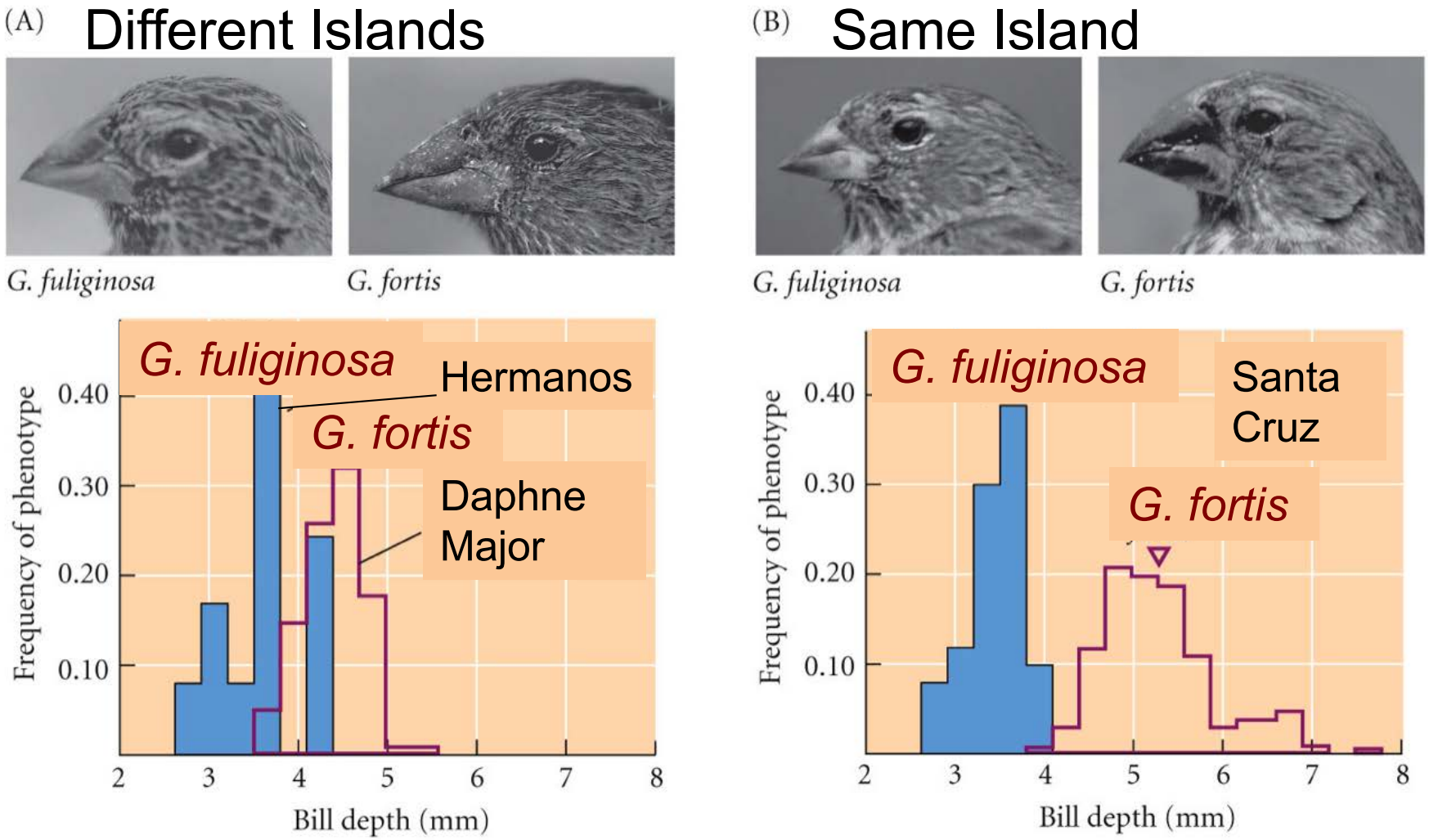
Ground finches, genus *Geospiza*, feed on seeds

Photo: Peter Grant, *G. fortis,* the medium ground finch

Galapagos Is.

Competitive Character Displacement among small, medium and large ground finches

Grant, P. 1986.



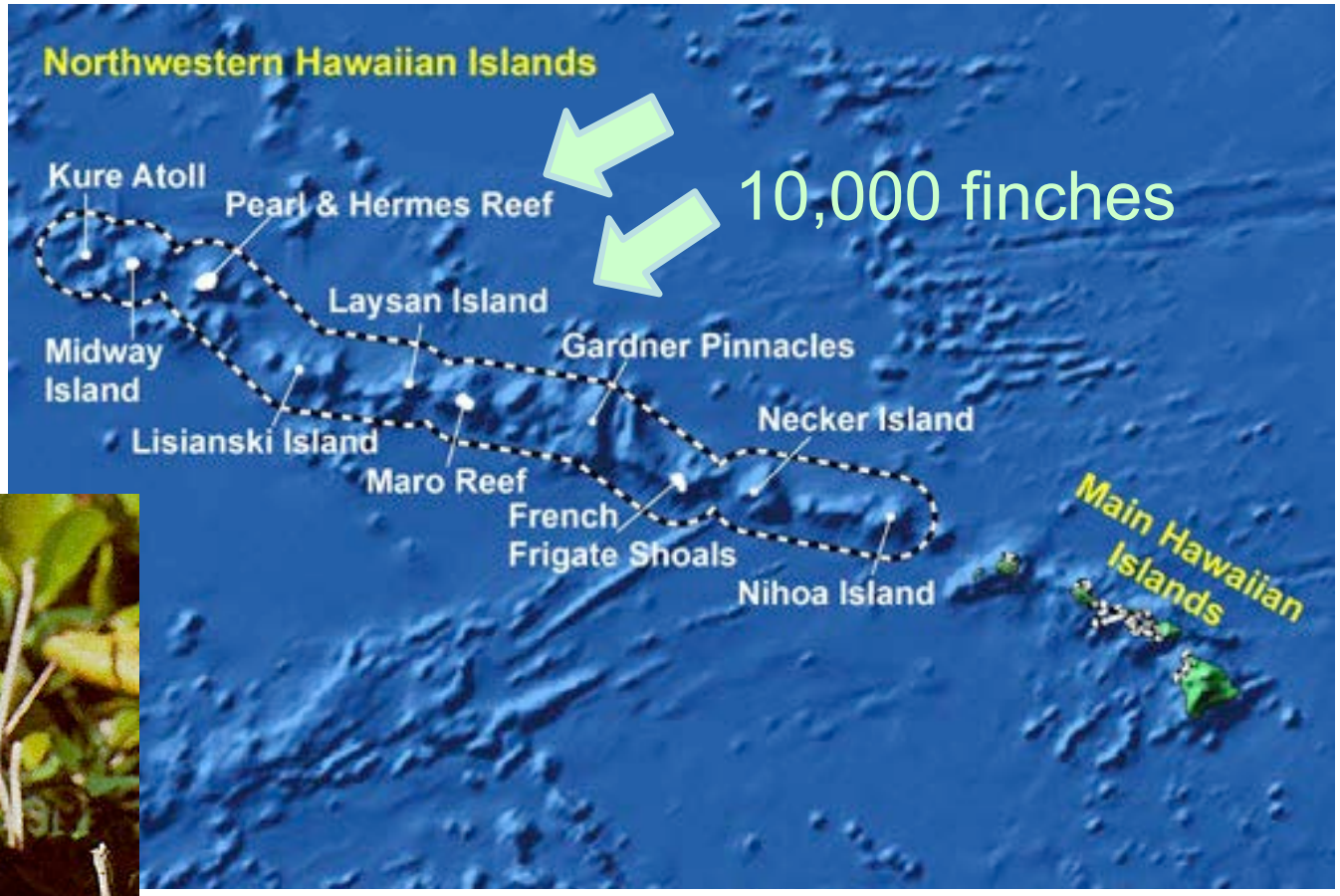
***EVOLUTION 2e*, Figure 19.20**

Laysan Finch

Conant, S. 1988. Evol. Ecol.

Parallel variation in beak size & seed size

Tribulus cistoides



http://www.mcbi.org/shining_sea/place_wpacific_nwhi.htm

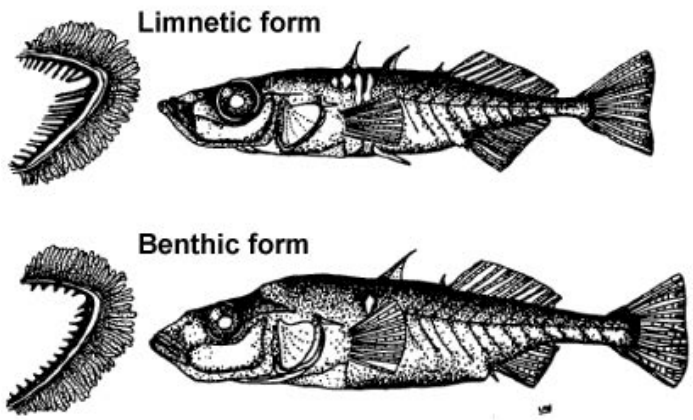
http://hbs.bishopmuseum.org/endangered/laysfinch.html

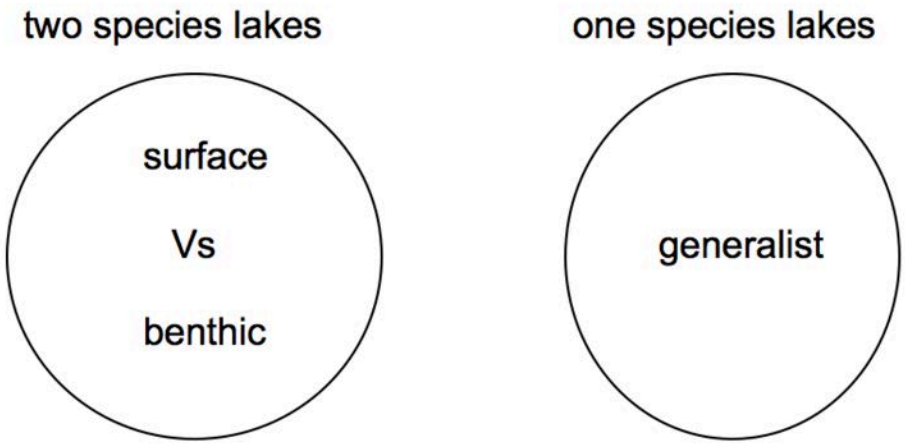
Laysan finches parallel story to Galapagos finches

- 1967- A population of 11 Laysan finches translocated to Pearl & Hermes Reef in 1967.
- Laysan- large hard seeds only 5% of vegetation
- Pearl & Hermes Reef, large hard seeds 78% of the vegetation.
- 1984- (15 years later) Conant measured bill shape and size differences between the two islands not due to body size or sex ratio.

End of Lecture 19

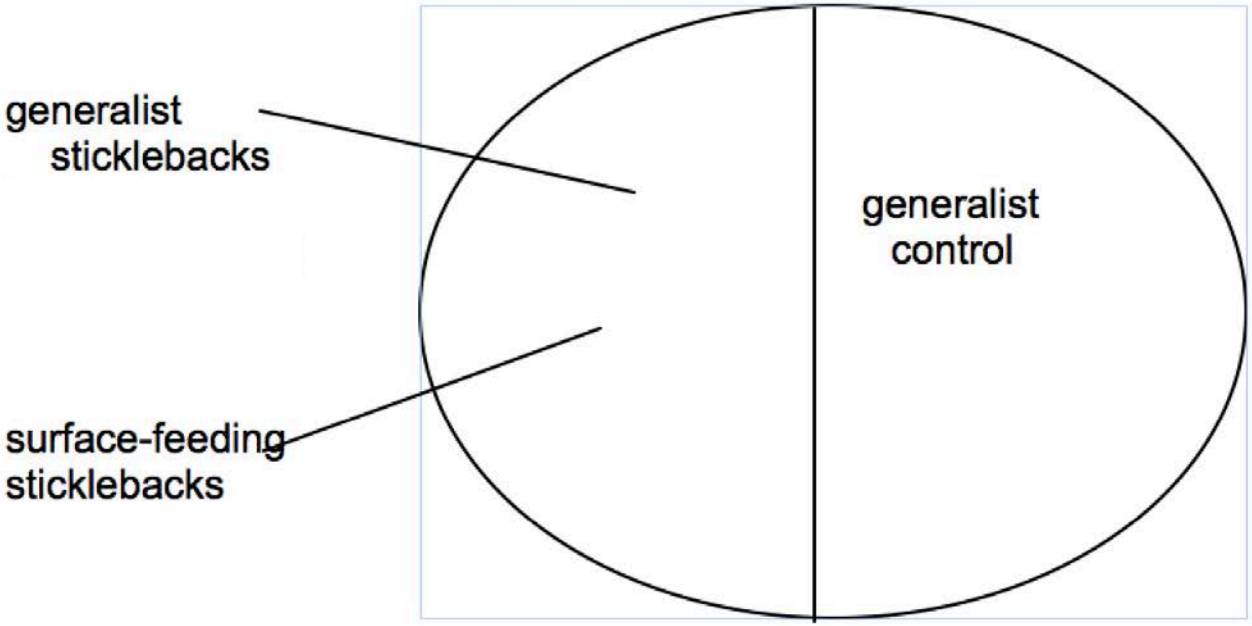
Competitive Character Displacement in Stickleback Fish, 12,000 year old glacial lakes in Canada, Dolph Schluter





Competitive Character Displacement in Stickleback Fish, 12,000 year old glacial lakes in Canada, Dolph Schluter

Experiment: Artificial ponds on UBC campus. Schluter experimentally introduced (and replicated w/ fish at different densities…



Sexual Selection: A special case of directional selection

- Traits are favored that enhance mating success
- Sexual selection exists because

  *females produce few, large gametes (eggs)

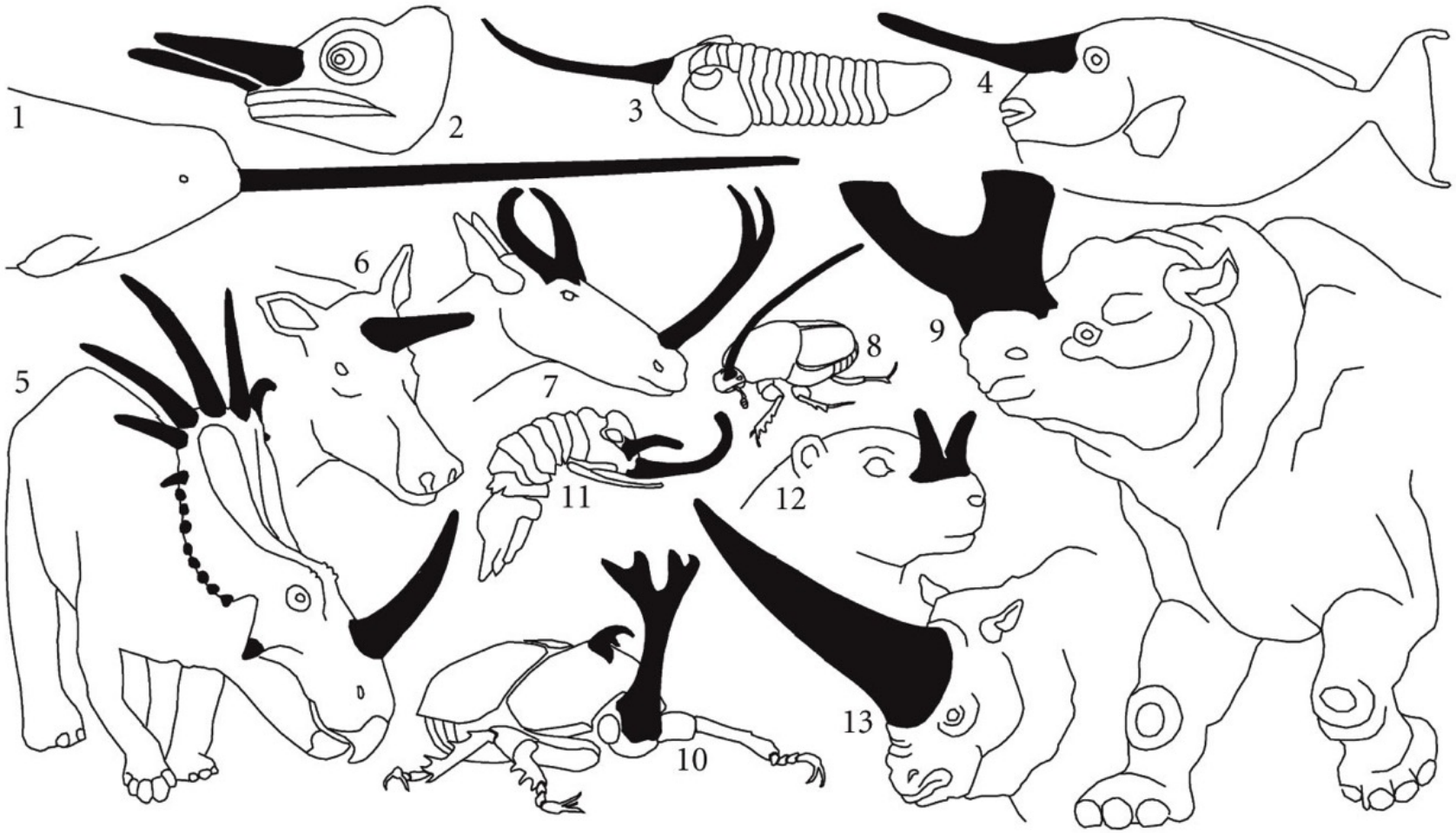
  *Thus, females are choosy

  *males many small gametes

  *males suffer much less reduction in fitness if they make a wrong choice.

Run-Away Sexual Selection

- Predicted by R.A. Fisher, 1930
- Attractiveness in males selected by females
- Females w/ best discrimination ability will leave more offspring
- Runaway process until counteracted by an opposing force (e.g., predation).
- Preference alleles do not directly influence fitness but
- Males w exaggerated male trait father more offspring
- The exaggerated male trait and the female preference become genetically correlated (linked, hitchhiking)



Horn-like structures have evolved in males of many species for intraspecific compete for females. Futuyma Evolution 3e, Fig. 15-18.

TABLE 15.1 Mechanisms of sexual selection and traits likely to be favored

	Mechanism	Traits favored
*	Same-sex contests	Traits improving success in confrontation (e.g., large size, strength, weapons, threat signals); avoidance of contests with superior rivals
*	Mate preference	Attractive and stimulatory features; offering of food, territory, by opposite sex or other resources that improve mate's reproductive success
	Scrambles	Early search and rapid location of mates; well-developed sensory and locomotory organs
	Endurance rivalry	Ability to remain reproductively active during much of season
*	Sperm competition	Ability to displace rival sperm; production of abundant sperm; mate guarding or other ways of preventing rivals from copulating with mate
	Coercion	Adaptations for forced copulation and other coercive behavior
	Infanticide	Similar traits as for same-sex contests
*	Antagonistic	Ability to counteract the other sex's resistance to mating (by, e.g., co-evolution hyperstimulation); egg's resistance to sperm entry

Source: After Andersson 1994; Andersson and Iwasa 1996.

***EVOLUTION 3e*, Table 15.1**

https://www.youtube.com/watch?v=OJgfcOd1R7E 16:16-22:10

Sexual selection - bowerbirds, pheasants, widowbirds