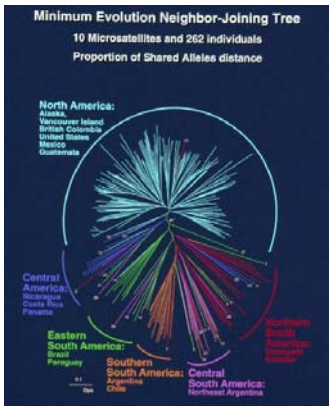
Lecture 18, 19 Oct 2006
CH5 Paradigms, CH6 Genetics, CH7 Populations

Conservation Biology
ECOL 406R/506R
University of Arizona
Fall 2006

Kevin Bonine
Kathy Gerst

Conservation Genetics



Lab this week:

sewage treatment plant on 20 October (web for readings)
27-29 October = ORPI, Pinacate, CEDO (Mexico)
($, food, see website for lab readings)

Housekeeping, 19 October 2006

506 Topic and References please

Upcoming Readings
today: Text Ch.6 (Ch 5 and 7), PVA, *Puma concolor*

Tues 24 Oct: Global Climate Change (web for readings)
Thurs 26 Oct: Guy McPherson
Tues 31 Oct: Ed Moll (long web reading)
Thurs 02 Nov: Exam Two
Tues 07 Nov: Don Falk (web reading)

Short oral presentations :
19 Oct Rachel Smith and Shea Cogswell
24 Oct Cori Dolan and Robert Johnson
26 Oct, 31 Oct, 02 Nov, 07 Nov, 16 Nov, 21 Nov: none
Move Jon and Laura to 09 Nov
Move Dan and Lane to 14 Nov

Thursday, October 19th, at 7:30 pm. Update on Mexican Gray Wolf, Jaguar, and other T&E species.

The Center for Biological Diversity invites the public to an illustrated presentation on the Endangered Species Act, Thursday, October 19th, at 7:30 pm. The event is free and will take place at Anjali, 330 East 7th Street, 1/2 block west of 4th Ave. Michael Robinson, the Center's Predator Conservation Coordinator, will give a slideshow about the Act, the species that are protected by this important law, the success stories of plants and animals that have persisted because of the Act's protection, as well as the current political threats to this law. We will also provide information on how to become an effective advocate for endangered species.
(Ed. note: Michael is a very good speaker and you are guaranteed to see great pictures and get good information)

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3

The Arid Lands Resource Sciences
Graduate Interdisciplinary Program
invites you to the
dissertation defense of
doctoral candidate

Maeveen Behan

who will present her dissertation entitled

"Science and Lore in Animal Law"

on Monday, October 23rd
at 9:00 o'clock in the morning
in room 113 of the
Office of Arid Land Studies
located at
1955 East Sixth Street

All are encouraged to attend
Visitor parking available along the back (north) fence

4

Global Climate Change Lecture Series

All lectures will take place at UA Centennial Hall.

All lectures begin at 7pm and are free to the public. Call 520.621.4090 for more information.

Tuesday, October 17
Global Climate Change: The Evidence
Malcolm Hughes, Professor of Dendrochronology

http://cos.arizona.edu/climate/

Tuesday, October 24
Global Climate Change: What's Ahead
Jonathan Overpeck, Director of the Institute for the Study of Planet Earth and Professor of Geosciences

Tuesday, October 31
Global Climate Change: The Role of Living Things
Travis Huxman, Assistant Professor of Ecology and Evolutionary Biology

Tuesday, November 7
Global Climate Change: Ocean Impacts and Feedbacks
Julia Cole, Associate Professor of Geosciences

Tuesday, November 14
Global Climate Change: Disease and Society
Andrew Comrie, Dean of the Graduate College and Professor of Geography and Regional Development

Tuesday, November 21
Global Climate Change: Could Geoengineering Reverse It?
Roger Angel, Regents' Professor of Astronomy

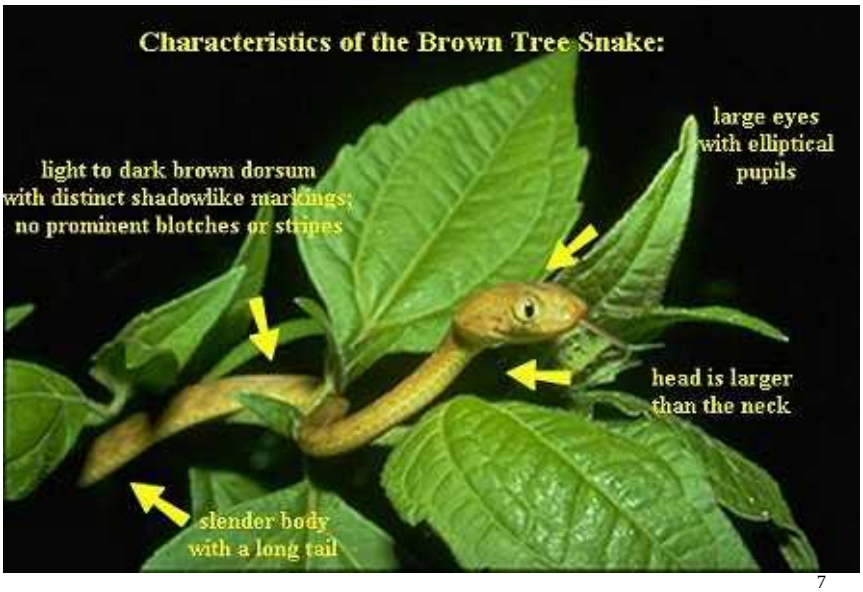
Tuesday, November 28
Global Climate Change: Designing Policy Responses
Paul Portney, Dean of the Eller College of Management and Professor of Economics

5

Shea and Rachel
will speak for 10 minutes on Elasmobranchs

6

http://www.fort.usgs.gov/resources/education/bts/bts_home.asp



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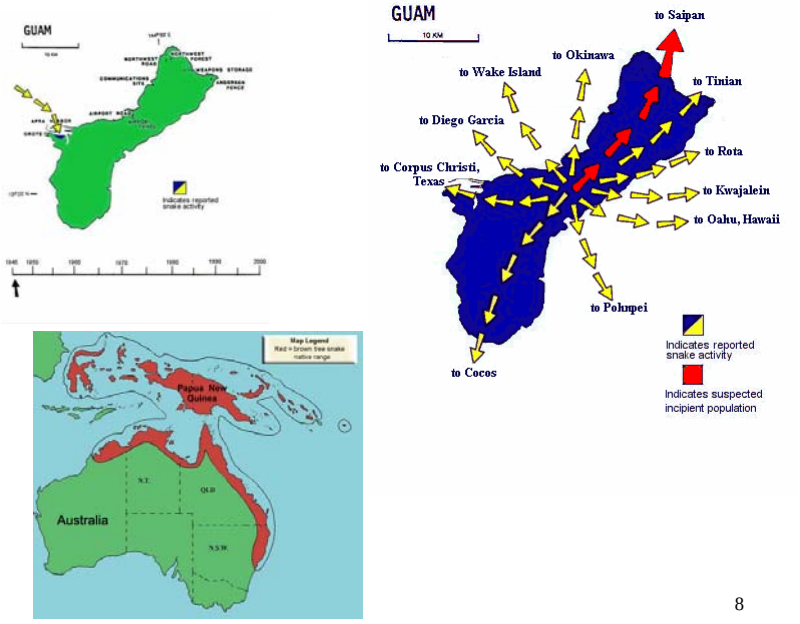

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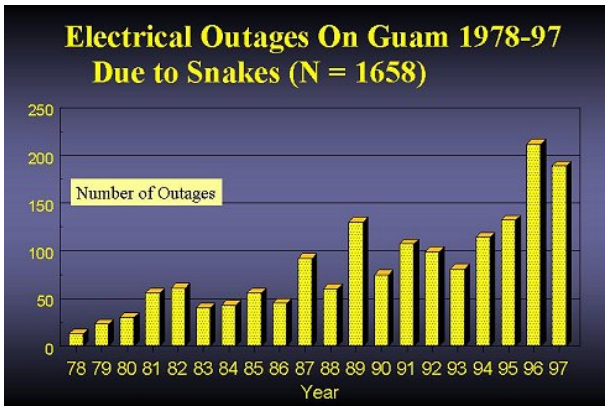

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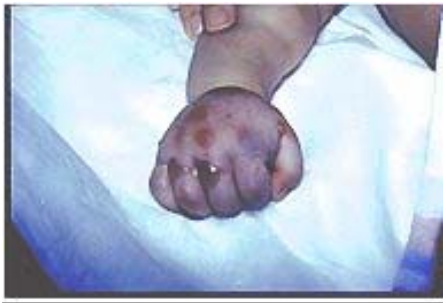


The hand of an infant with swelling, discoloration, and bleb formation.

Results of one night's captures by hand.

Chapter 5 (Paradigms...)

- Genetic Diversity (MVP, PVA)
- Island Biogeography
- Metapopulations
- Habitat Heterogeneity
- Disturbance

Chap 6 – Genetics of Conservation Biology

11

Habitat Heterogeneity

Conserve Bigger Area?

Conserve More Diverse Habitats?

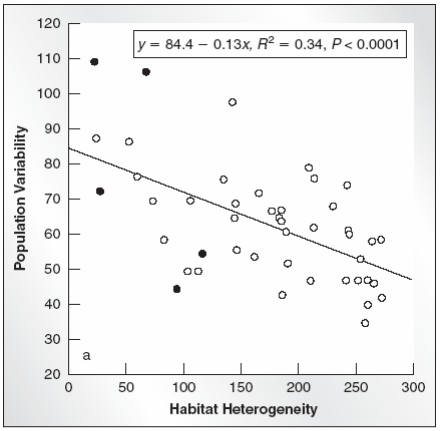


Figure 5.23
Populations of bush cricket (*Metrioptera bicolor*) subunits exemplify that population size is less variable as heterogeneity increases. Dark circles indicate patches where local extinctions occurred. White circles indicate patches with extant populations. Population variability was measured by the coefficient of variance (cv) of local population size, and habitat heterogeneity was measured using digitized infrared aerial photographs. Each patch was assigned values according to how much the patch deviated from the standard level of gray in the photographs (SD-hue).

After Kindvall (1996).

Disturbances

-Endogenous
-Exogenous

- Tree Fall in Forest
- Beaver Dam on Stream

An SUV is seen covered by sand as residents walk to their homes to inspect the damage by hurricane Ivan Wednesday, Sept. 22, 2004 in Pensacola Beach, Fla. Beach residents were allowed to see their homes for the first time since the hurricane. (AP Photo/Alan Diaz)

Conservation Genetics

(e.g., >20 MHC alleles)

(coadapted gene complexes?)

(heterozygosity)

(polymorphic vs. monomorphic)

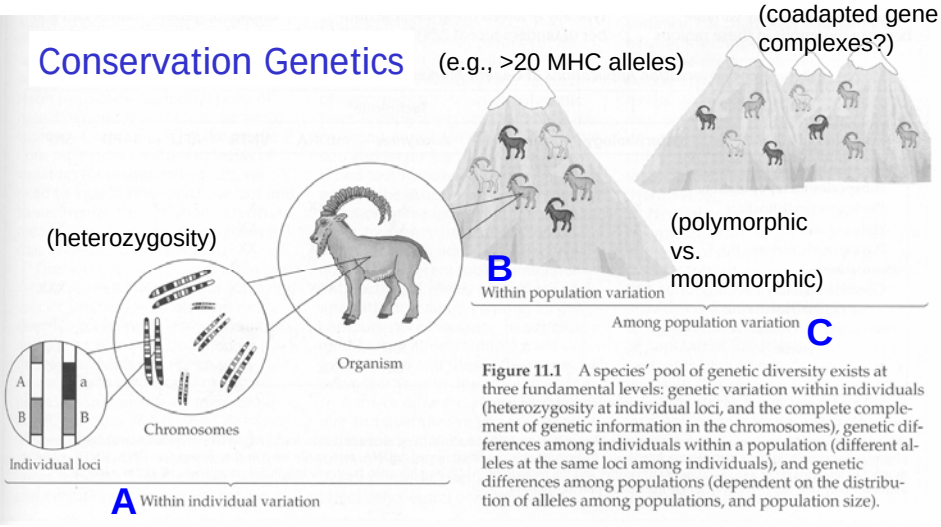


Figure 11.1 A species' pool of genetic diversity exists at three fundamental levels: genetic variation within individuals (heterozygosity at individual loci, and the complete complement of genetic information in the chromosomes), genetic differences among individuals within a population (different alleles at the same loci among individuals), and genetic differences among populations (dependent on the distribution of alleles among populations, and population size).

Groom, Meffe, & Carroll 2006

How do we keep the gene pool from becoming a gene puddle? (Foose 1983)

Allelic Variation Within and Among Populations

TABLE 11.2 *Gene Frequencies at Five Polymorphic Loci in the Club Moss* Lycopodium lucidulum

Locus	Allele	Woodridge, CT	Litchfield, CT	Binghamton, NY	New Lebanon, NY
PGM					
	a	0.00	0.00	0.50	0.00
	b	0.86	1.00	0.50	1.00
	c	0.14	0.00	0.00	0.00
PGI-2					
	a	0.68	1.00	1.00	0.75
	b	0.32	0.00	0.00	0.25
G6PD-1					
	a	0.93	1.00	0.82	0.91
	b	0.07	0.00	0.18	0.09
G6PD-2					
	a	1.00	1.00	0.50	1.00
	b	0.00	0.00	0.50	0.00
LGGP-1					
	a	0.50	0.50	1.00	1.00
	b	0.50	0.50	0.00	0.00

Source: Levin and Crepet 1973.

Groom, Meffe, & Carroll 2006

15

Heterozygosity

TABLE 11.3 *Ecological and Life History Correlates with Heterozygosity*

Occupancy of different life zones
Cosmopolitan and temperate + tropical > tropical > temperate > arctic
Degree of endemism
Species with broad geographic distribution > endemic species
General habitat requirements
Overground > arboreal or aquatic > underground
Degree of specialization
Generalists > specialists
Climatic conditions
Species inhabiting ecological extremes > regions of broader climatic variation
Degree of territoriality
Nonterritorial > territorial
Body size
Small > medium > large > very large

Note: Organisms sharing a given life history trait to the left of the > symbol tend to have greater heterozygosity than organisms with a different life history to the right of the > symbol.
Source: After Nevo et al. 1984.

Groom, Meffe, & Carroll 2006

16

TABLE 11.4 *Mean Total Heterozygosity (H_T) and Proportion Due to Among-Population Differentiation (D_{PT}) in Several Major Taxonomic Groups*

Taxon	H_T	Number of species	D_{PT}	Number of species
Vertebrates				
Fishes	5.1%	195	0.135	79
Amphibians	10.9%	116	0.315	33
Reptiles	7.8%	85	0.258	22
Mammals	6.7%	172	0.242	57
Birds	6.8%	80	0.076	16
Invertebrates				
Insects	13.7%	170	0.097	46
Crustaceans	5.2%	80	0.169	19
Molluscs	14.5%	105	0.263	44
Others	16.0%	15	0.060	5

Source: Ward et al. 1992.

Groom, Meffe, & Carroll 2006 17

Allelic Variation Among Populations

TABLE 11.5 *General Correlates of Genetic Variation among Population*

1. Genetic variation within species will be positively correlated with population size.
2. Genetic variation will be positively correlated with habitat area.
3. Genetic variation will be greater in species with wider ranges.
4. Genetic variation in animals will be negatively correlated with body size.
5. Genetic variation will be negatively correlated with rate of chromosomal evolution.
6. Genetic variation will be positively correlated with population size across species.
7. Genetic variation will be lower in vertebrates that in invertebrates or plants.
8. Genetic variation should be lower in island populations than mainland populations.
9. Genetic variation will be lower in endangered species than nonendangered species.

Source: After Frankham 1996.

Groom, Meffe, & Carroll 2006

18

Conservation Genetics

1. Maintain genetic diversity
   - Future response to environmental change
   - Speciation

2. Tools for population monitoring and assessment
   - Conservation Planning

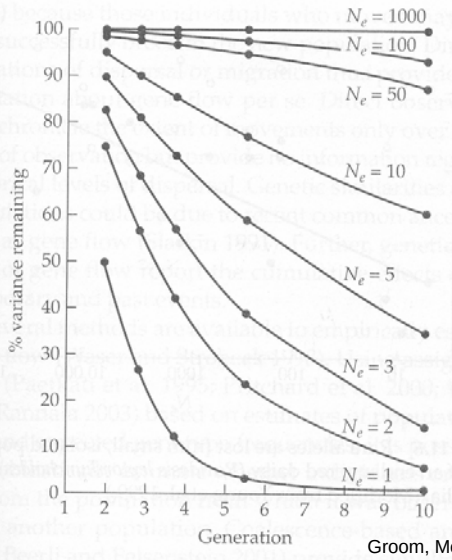
19

Genetic Issues:

-Inbreeding depression
-Loss of genetic diversity; can't respond to change
-Fragmentation, loss of gene flow
-Genetic drift > natural selection
-Mutational meltdown
-Genetic adaptation to captivity (reintroduction?)
-Taxonomic uncertainties
-Define management units (MUs)
-Forensics
-Understand species biology
-Outbreeding depression

20

Effective Population Size and Genetic Variance



Groom, Meffe, & Carroll 2006

Figure 11.3 Average percentage of genetic variance remaining over 10 generations in a theoretical, idealized population at various genetically effective population sizes (N_e). Variation is lost randomly through genetic drift.

21

-Bottleneck (size)
-Growth Rate (r)
-Recovery of Variation

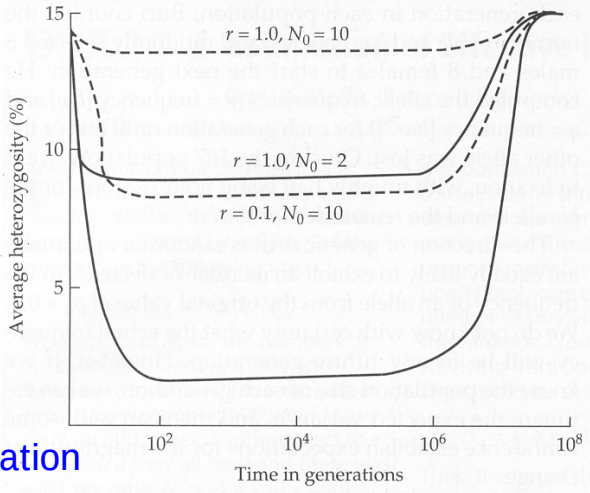
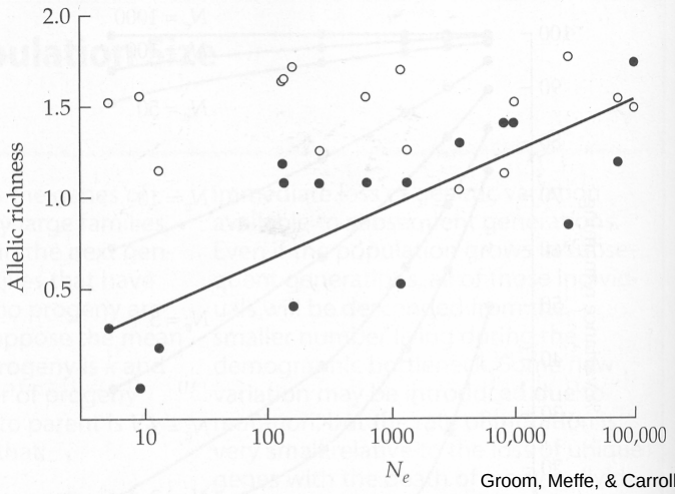


Figure 11.5 After a bottleneck, genetic variation (as measured by average heterozygosity) very slowly recovers. Recovery is quickest when populations have a high growth rate ($r = 1.0$), and when the bottleneck is less severe (founding number $N_0 = 10$ or greater). (Modified from Nei 1975.)

Groom, Meffe, & Carroll 2006

Rare Alleles and N_e



Groom, Meffe, & Carroll 2006

Figure 11.6 Rare alleles are lost from small, isolated populations of an endangered daisy (*Rutidosis leptorrhynchoides*) in Australia. (Modified from Young et al. 1999.)

23

Inbreeding ←→ Outbreeding Depression

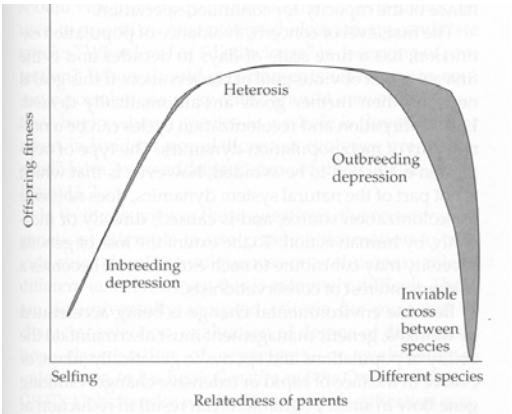


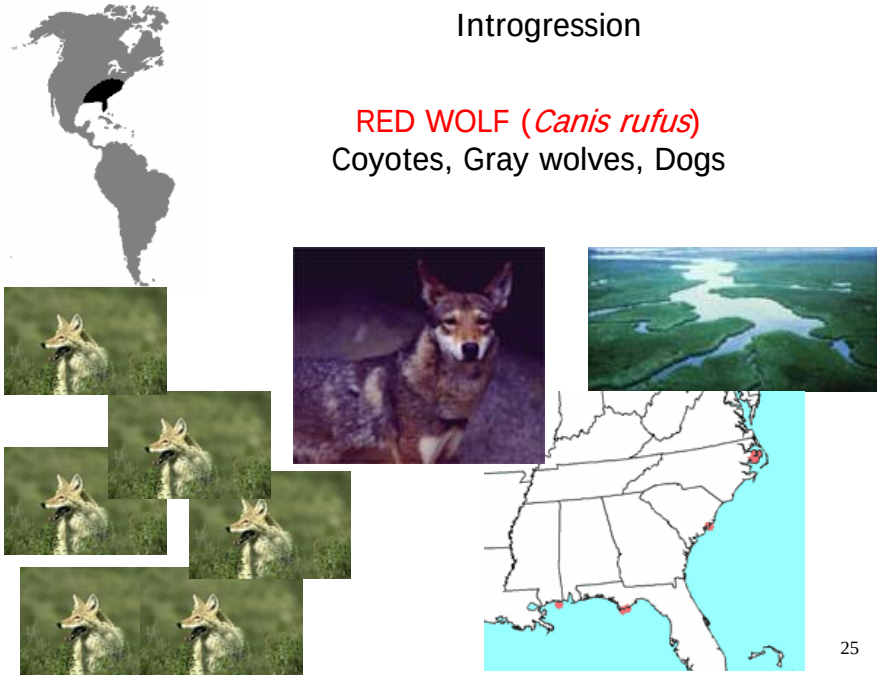
Figure 11.9 Offspring fitness is influenced by the degree of relatedness of parents. Closely related parents produce inbred young that are less fit than those of unrelated parents of the same species, leading to "inbreeding depression." When parents are unrelated, fitness rises yielding hybrid vigor or "heterosis." As parents are more distantly related, some decline in fitness may occur (outbreeding depression) and usually at some point, offspring from crosses between species are far less fit, even to the point of inviability.

Groom, Meffe, & Carroll 2006

24

Introgression

RED WOLF (*Canis rufus*)
Coyotes, Gray wolves, Dogs



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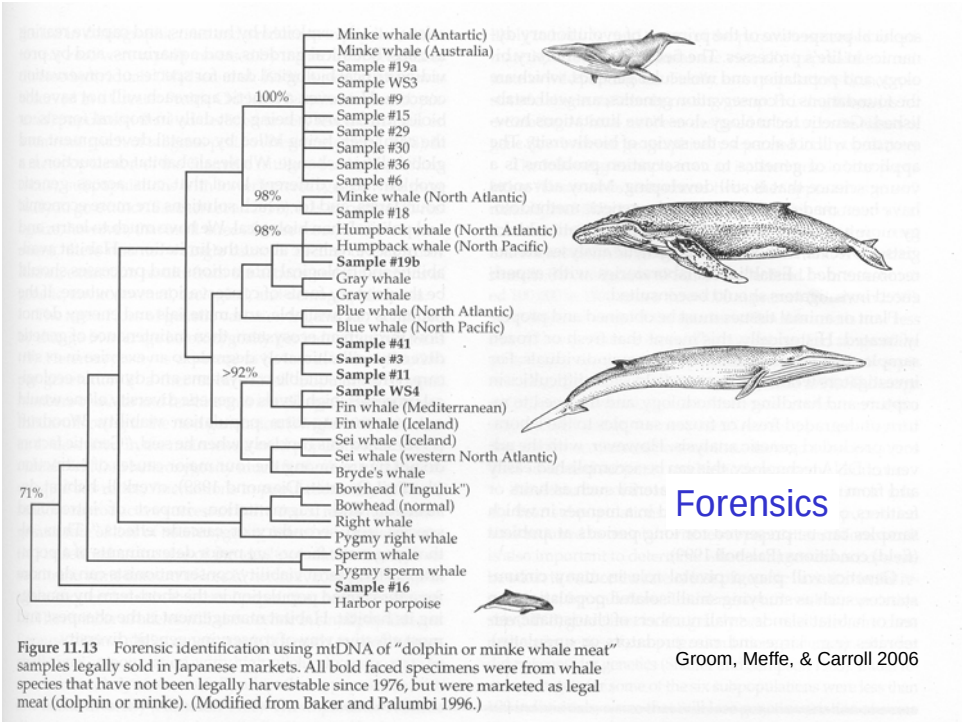


Figure 11.13 Forensic identification using mtDNA of "dolphin or minke whale meat" samples legally sold in Japanese markets. All bold faced specimens were from whale species that have not been legally harvestable since 1976, but were marketed as legal meat (dolphin or minke). (Modified from Baker and Palumbi 1996.)

Groom, Meffe, & Carroll 2006

Applications of Genetics to Conservation Biology

-Molecular Taxonomy
-Populations, Gene Flow, Phylogeography
-Relatedness, Paternity, Individual ID

Dr. Melanie Culver
SNR, UA

Molecular Taxonomy: Molecules versus Morphology

- Cryptic species (sibling species)
- Morphological variation without genetic variation

28

Relatedness
(Kinship, Paternity and Individual ID)

Application of molecular genetic techniques, using hypervariable, repetitive DNA

(ie. microsatellites, minisatellites)

to questions of kinship, paternity or individual ID

29

Populations, Gene Flow, Phylogeography

-Compare genetic traits among populations

-Resolve substructure among populations

-Infer movement patterns among individuals

-Infer historical events for species

30

Non-Invasive Sampling

- Allows sampling without disturbance to individual
- Rare or hard to capture species
- Examples (hair, scat, feathers, saliva/cheek swab, regurgitated pellets, dried blood, biopsy dart, museum tissues)

31

Subspecies Taxonomy, Phylogeography, Gene Flow:
Puma (cougar, mountain lion)

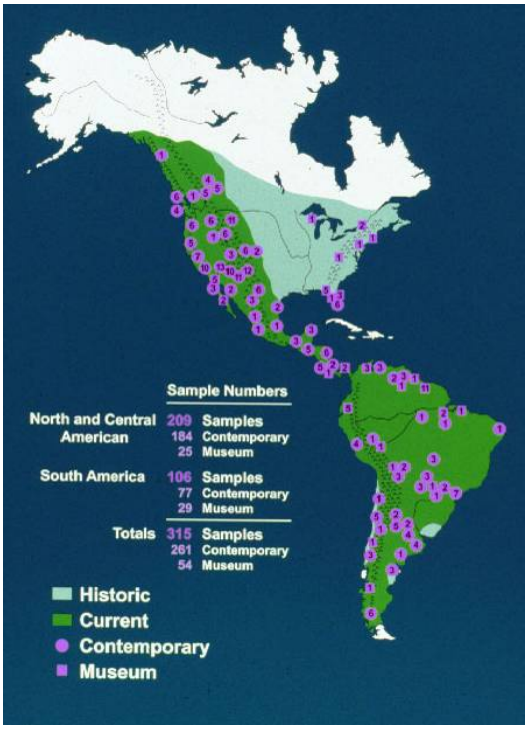
32 Puma subspecies, as of the early 1900s

Objectives

- Does current population differentiation reflect
  - Trinomial descriptions?
  - Physical or ecological barriers?
  - Isolation by distance?
- Are current levels of genetic variation the same within each population?
- Does population structure and genetic variation reflect
  - Historic migrations?
  - Historic dispersals?
  - Historic bottlenecks?

34

Modern and museum puma samples collected, total of 315



Molecular Methods Used

- Mitochondrial gene sequencing
  - 16SrRNA
  - NADH-5
  - ATPase8
- Nuclear microsatellite length determination
  - 10 domestic cat microsatellite loci

36

Neutral Markers often studied.

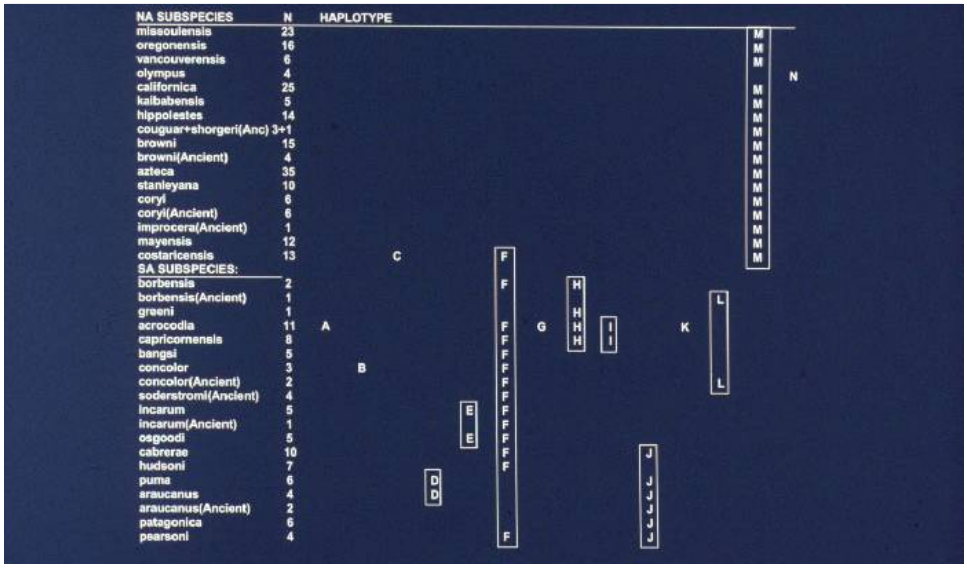
Relevance to natural selection and adaptation?

Ultimately, source of all variation is mutation.

mutation rate = 10^{-4} – 10^{-6}

37

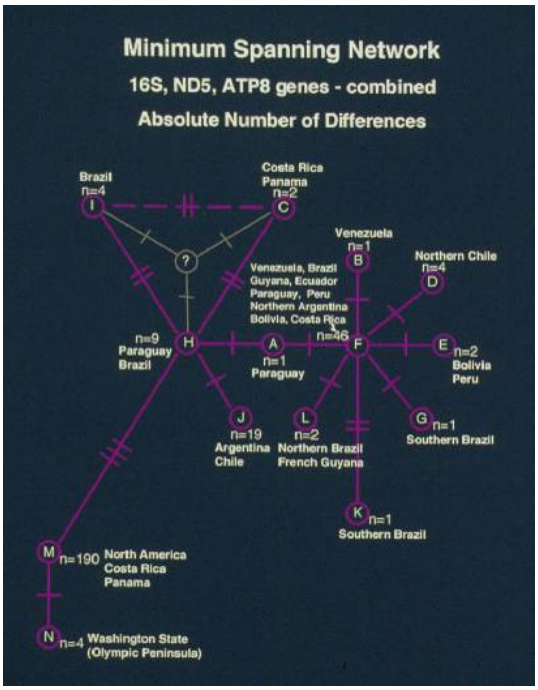
Mitochondrial DNA Haplotypes (in a geographical cline)



-Ancestral haplotypes

-2 historical radiations

-NA is most recently founded population



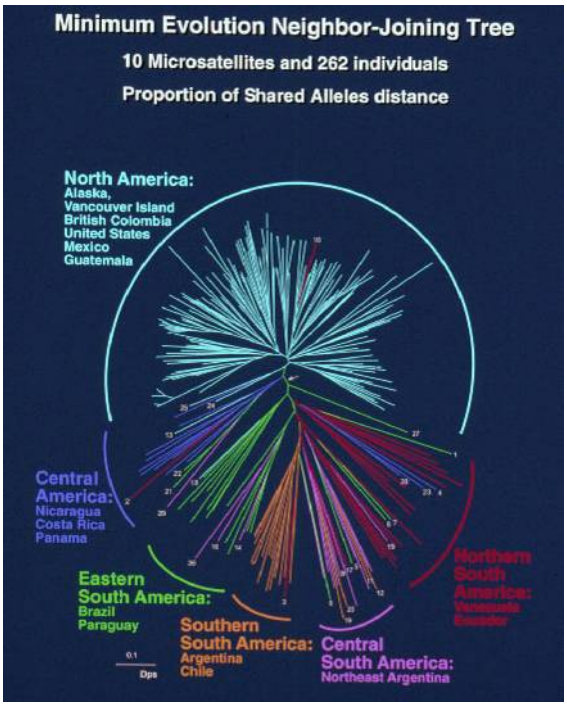
Microsatellite Alleles at FCA008

Group	Subspecies	Tot no individ	Allele size 134	136	138	140	142	*144	146	148	150	152	154	156	158	160	162	164	166	168	170	172	174	176
NA	missoulensis	21												25						18	1			
"	oregonensis	14												26						2				
"	vancouverensis	6												12										
"	olympus	4												8										
"	californica	23												43						3				
"	kaibabensis	3												5						1				
"	hippolestes	12												19						5				
"	couguar	1												2										
"	browni	17												30						4				
"	azteca	33												59	1					6				
"	stanleyana	10												20										
"	coryi	6												12										
"	mayensis	11	3											18						1				
CA	costaricensis	13	9										1	7						3	3	1	2	
ESA	borbensis	2												1				1				2		
"	greeni	1													1				1					
"	acrocodia	12	1		1	2	2			1	1			6	6	1			1			2		
"	capricornensis	8	3			1			1		1	1		2	5				1			1		
NSA	bangsi	5	2			1					1	3	2								1			
"	concolor	5	1	1						1			1	4	2									
"	soderstromi	2												3		1								
"	incarum	5		1										4	1		1		3					
"	osgoodi	5		4										2	1				1	1		1		
CSA	cabrerae	10	2	3	1									2	6				4			1		1
"	hudsoni	7		1											4				3	2		2	2	
SSA	puma	3												1	1				1		2	1		
"	araucanus	4												1					1		1	3	2	
"	patagonica	6	2											3						2			5	
"	pearsoni	4												1	1				3			1	2	

-Geographic clustering of individuals

~Six groups identified

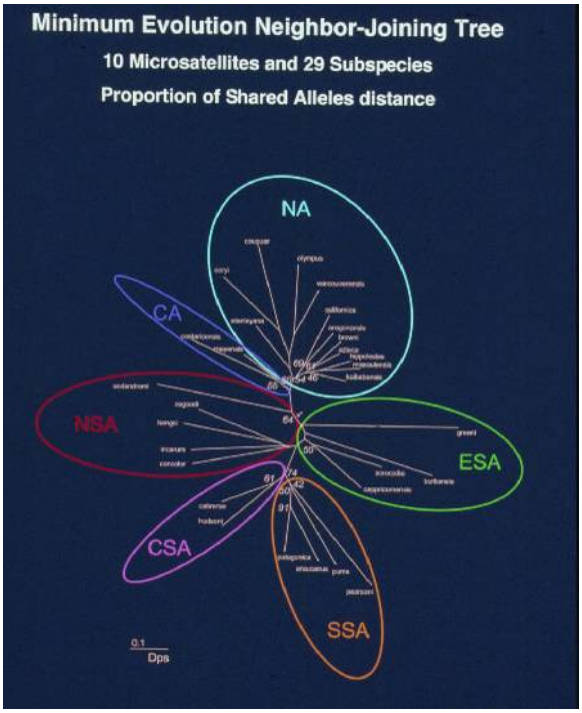
2 distance methods agree



-Subspecies associate into same 6 groups

-Statistical support from bootstrap values

-2 distance methods agree



BOX 11.3 Calculation of *F*-Statistics

Derrick W. Sugg, University of Georgia, Savannah River Ecology Laboratory

F_{IS}, F_{IT}, F_{ST}

Fixation indices, or *F*-Statistics, were developed by Sewall Wright (1922, 1965, 1969, 1978) as a means to describe how genetic diversity is partitioned in a population. By partitioning genetic diversity into different components one can determine the relative amounts residing within individuals, subpopulations, and the overall population. Because adaptive evolution requires genetic variation to proceed, it is important to understand how much of the total variation is available for selection acting on individuals. More recently, conservation biologists have shown renewed interest in fixation indices because they provide a means to determine how natural populations maintain genetic variation (beneficial for developing management strategies) and to determine levels of genetic variation in threatened or captive populations (beneficial for assessing the success of management strategies).

Typically when one calculates fixation indices it is for a structured population. The classical approach is to sample individuals from different subpopulations at fairly distinct geographic locations. Such a population is said to consist of three levels of structure: individuals (*I*), subpopulations (*S*), and the total population (*T*). One calculates the average individual heterozygosity by counting the number of heterozygous individuals in a subpopulation and dividing that sum by the total number of individuals in the subpopulation. This calculation is made for every subpopulation, and the average for all subpopulations is called the average individual heterozygosity:

$$\left(H_I = \frac{1}{k}\sum_{i=1}^{k}\frac{\#\,Heterozygotes_i}{N_i}\right)$$

where k is the number of subpopulations and N_i is the number of individuals in the ith subpopulation. At the same time one can use those individuals to determine the frequency of the genes. The gene frequencies are used to calculate the expectations for heterozygosity in the average subpopulation ($\bar{H}_S$) and the total population (H_T). The expectation for the average subpopulation is

$$\bar{H}_S = \frac{2}{k}\sum_{i=1}^{k} p_i - p_i^2$$

where p_i is the frequency of the gene in the ith subpopulation. The expected number of heterozygous individuals for the entire population is given by, $H_T = 2(\bar{p} - \bar{p}^2)$ where p is the frequency of the gene averaged over all individuals in the population without respect to the subpopulation they came from. $\bar{H}_S$ predicts the frequency of heterozygous individuals in subpopulations had they mated at random and H_T predicts the same frequency if individuals are mating at random without respect to subpopulations.

These estimates of the observed and expected frequency of heterozygous individuals can be used to calculate the fixation indices, F_{IS}, F_{IT}, and F_{ST}. Values for F_{IS} determine whether or not subpopulations have fewer or more heterozygous individuals than expected. It is calculated from:

$$F_{IS} = \frac{\bar{H}_S - H_I}{\bar{H}_S}$$

When there are fewer heterozygous individuals than expected ($\bar{H}_S > H_I$), F_{IS} will be positive. When $\bar{H}_S < H_I$ then F_{IS} will be negative. Therefore, negative values for F_{IS} indicate an excess of heterozygous individuals in subpopulations and positive values indicate the opposite condition. F_{IT} is calculated in a similar manner:

$$F_{IT} = \frac{H_T - H_I}{H_T}$$

and the interpretation of positive and negative values are the same except that they apply to the total population instead of the subpopulations. Finally, the degree of genetic differentiation among subpopulations (how unique they are) is given by:

$$F_{ST} = \frac{H_T - \bar{H}_S}{H_T}$$

which is always greater than or equal to zero. High values for F_{ST} indicate that subpopulations have very different gene frequencies, and when $F_{ST} = 1$ then subpopulations are said to be "fixed" for different genes; each subpopulation has a unique gene for each locus.

Models by Wright make simplifying assumptions including equal reproductive contributions among breeding adults and a large number of subpopulation of equal and constant size contributing dispersers to the pool of migrants. More recently, Wright's models have been recast using different methodologies or by emphasizing the importance of different evolutionary forces. Readers interested in this subject area are encouraged to read additional literature in this area including Slatkin (1991), Crow and Aoki (1984), Chesser (1991a,b), Wade and McCauley (1988), and Whitlock and McCauley (1999).

Groom, Meffe, & Carroll 2006

Wright's Fst Estimates and Slatkin's Migration Estimates

mtDNA

	NA	CA	ESA	NSA	CSA	SSA
NA	-	0.1	0.1	0.02	0.03	0.1
CA	*0.784	-	8.3	0.5	1.6	1.6
ESA	*0.815	0.057	-	0.8	2.3	2.2
NSA	*0.958	*0.492	0.384	-	4.2	0.5
CSA	*0.935	0.233	*0.177	*0.107	-	1.3
SSA	*0.835	0.240	*0.186	*0.526	*0.281	-

(Fst near 0 = little divergence) (Migrants/generation)

microsatellites

	NA	CA	ESA	NSA	CSA	SSA
NA	-	4.0	4.4	8.0	2.2	0.9
CA	*0.110	-	2.3	3.5	3.5	1.2
ESA	*0.103	*0.179	-	15.7	4.8	1.0
NSA	*0.059	*0.126	*0.031	-	6.0	1.1
CSA	*0.186	*0.126	*0.094	*0.077	-	2.4
SSA	*0.367	*0.288	*0.330	*0.316	*0.172	-

Summary:
-6 groups identified using microsatellites
-mtDNA haplotypes overlayed onto map, supports 6 groups
-Location of 2 ancestral haplotypes

Major restrictions to gene flow:
-Amazon River
-Rio Parana
-Rio Negro
-Andes?

Fossil Record versus Molecular Divergence Estimates

- Oldest fossils in North and South America date to 0.2-0.3 Mya
- From mtDNA mutation rate of 1.15%/My, divergence for extant puma lineages is 390,000 years ago
- From mutation rate of 5 x 10^{-9}/yr for microsatellite flanking regions, pumas are less than 230,000 years old

46

Historical Inferences

- Extant pumas originated in Brazillian Highlands (ancestral haplotypes)
- Fossil record suggests dispersal to NA soon after the common origin in Brazil
- 2 historical radiation events occurred

47

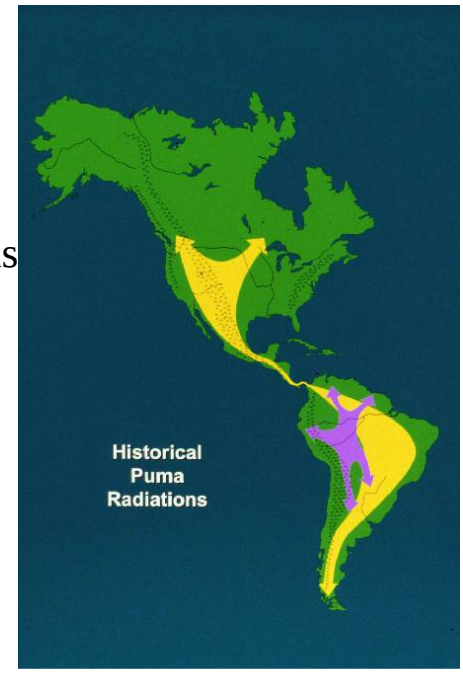
-Ancestor to puma crosses land-bridge ~2-3 Mya

-Puma origin in Brazilian Highlands ~300,000 ya

2 Major historical radiations

-One locally distributed

-One broad ranging



Puma Bottlenecks

- Subspecies-level
  - North America low overall genetic variation
- Population-level
  - Florida monomorphic at 8/10 microsatellite loci
  - Olympic Peninsula and Vancouver Island, monomorphic at 5/10 microsatellite loci

Puma Conclusions

- Pumas originated in Brazil approximately 300,000 years ago
- Possible extirpation and recolonization in North America (Pleistocene age?)
- Molecular data does not support 32 subdivisions, instead 6 groups
- Pumas are fairly panmictic within 6 groups

51

Conservation Implications

-Maintain habitat connectivity within 6 large groups

-Management should consider effects of bottlenecked populations

-Eastern cougar, Florida panther and Yuma puma management take into account revised subspecies

52