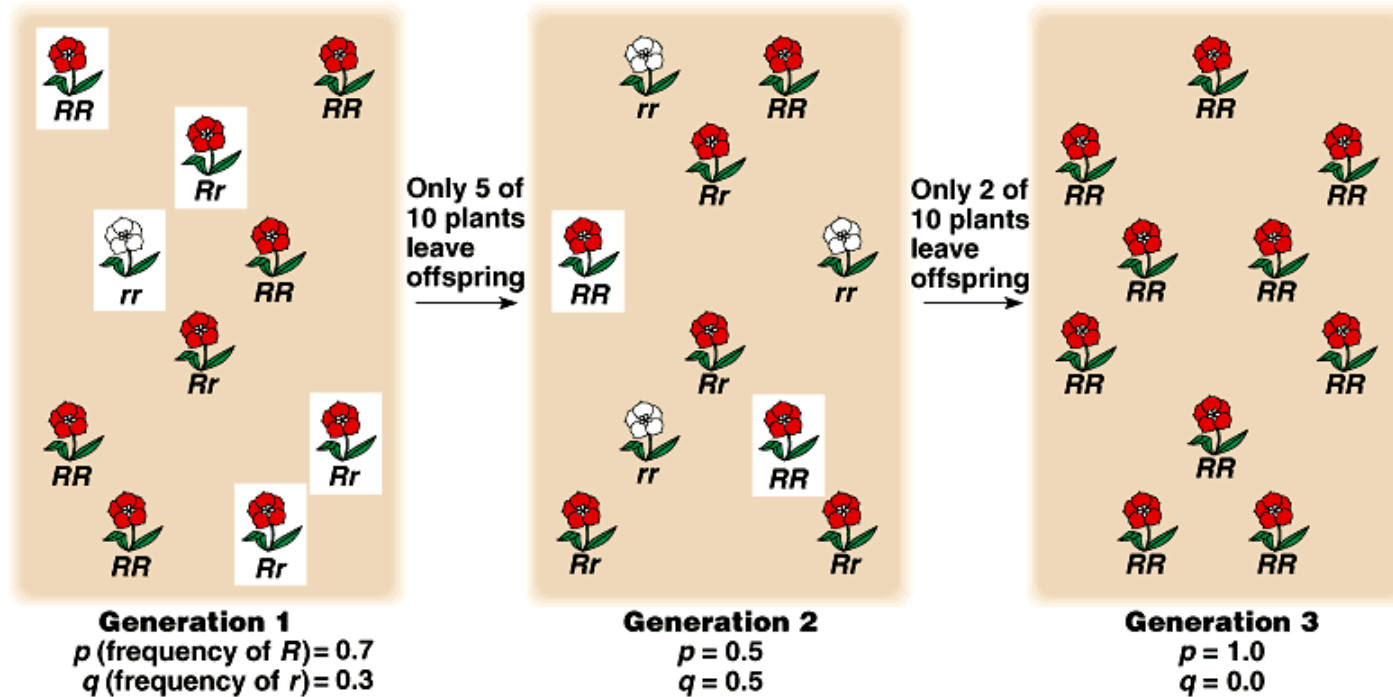


Gene Flow, Genetic Drift Natural Selection

Lecture 9

Spring 2013

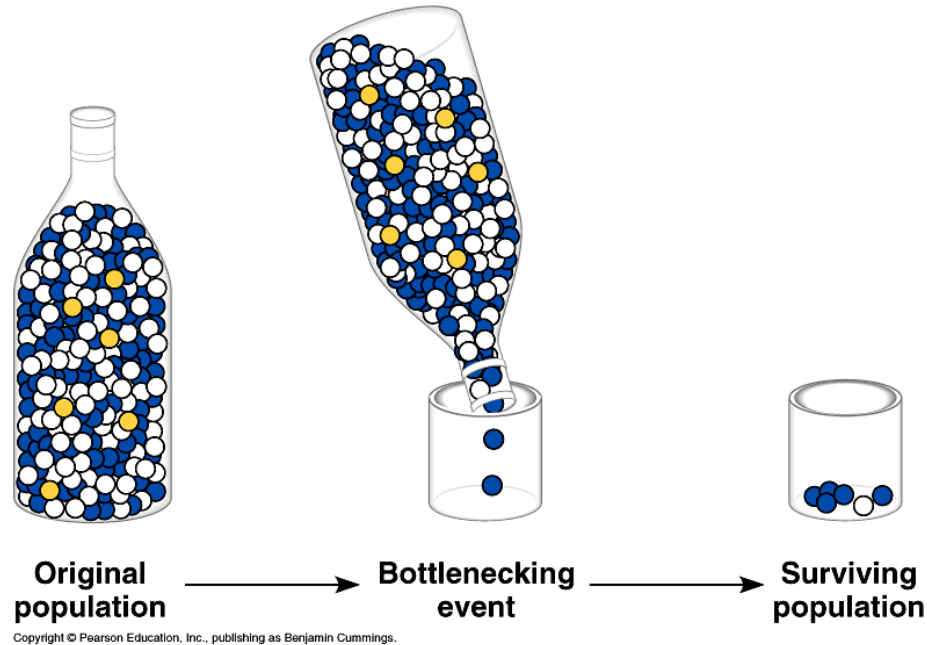
Genetic drift



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Examples of genetic drift in nature?

Bottleneck effect: an analogy ~ genetic drift → founder effect



Ex. 's Bottleneck effects on founding population size in nature?

Role of inbreeding and drift in Prairie Chickens

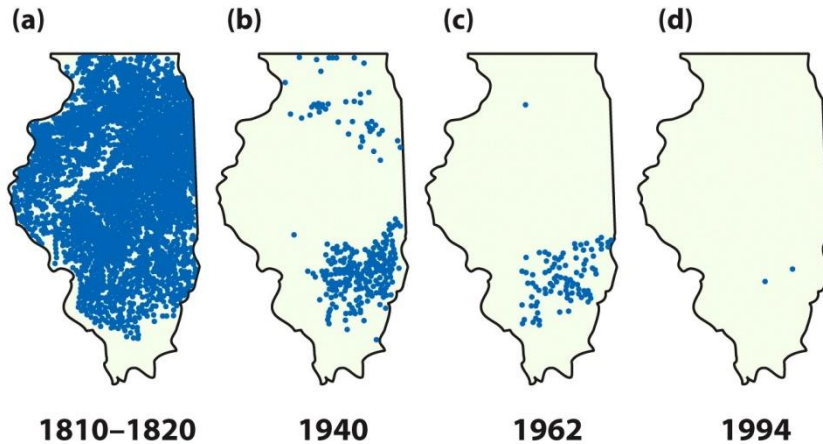
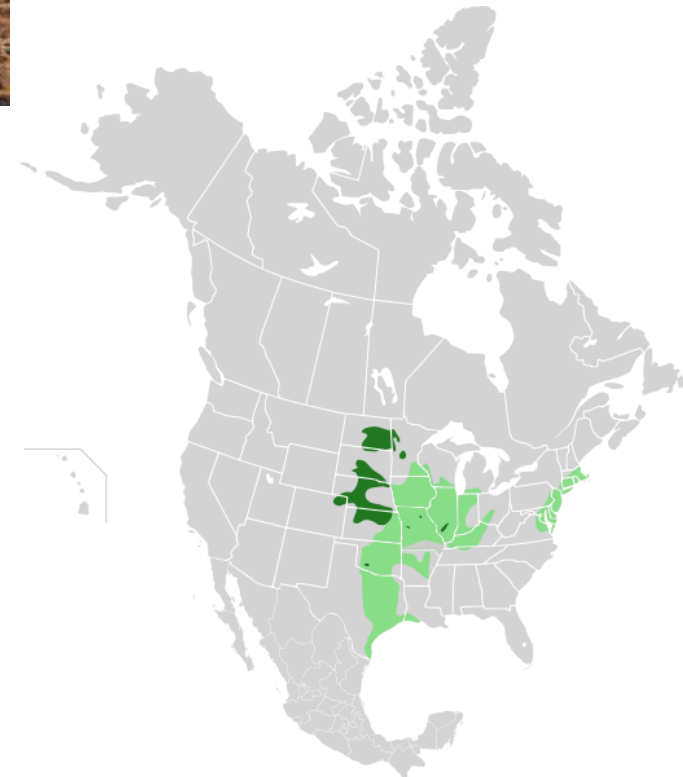


Figure 7-2 Evolutionary Analysis, 4/e
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Illinois population decline



2009 update – dark green current
and light green pre-settlement

Prairie Chicken populations

Table 7.6 Number of alleles per locus found in each of the current populations of Illinois, Kansas, Minnesota, and Nebraska and estimated for the Illinois prebottleneck population

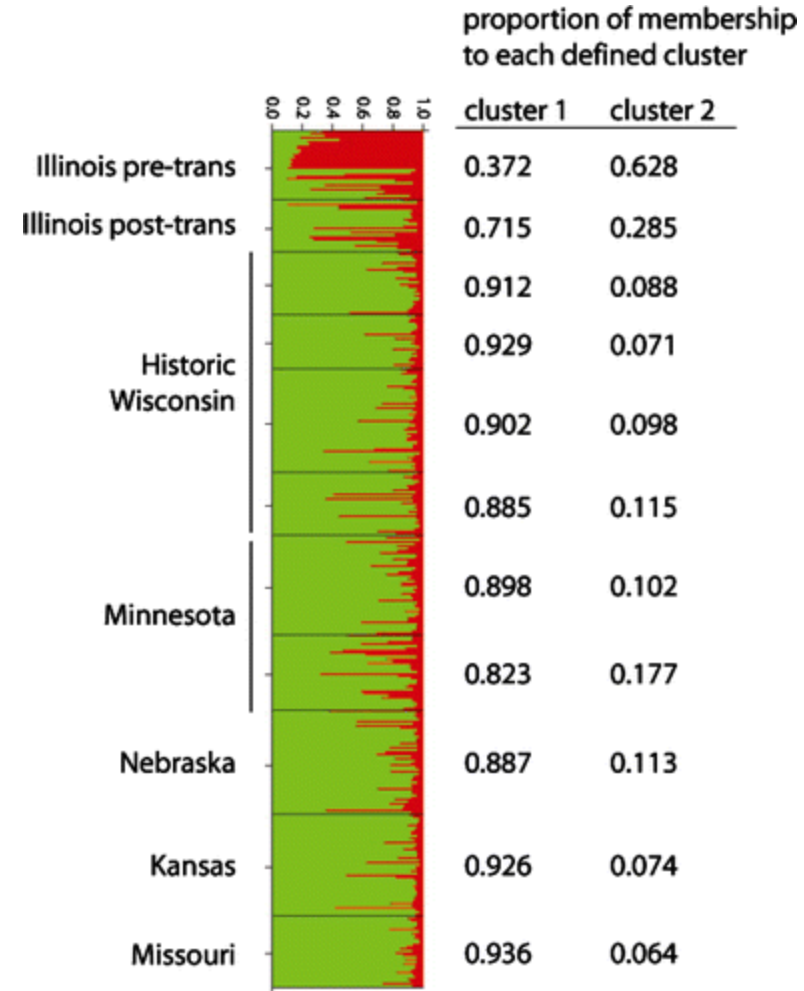
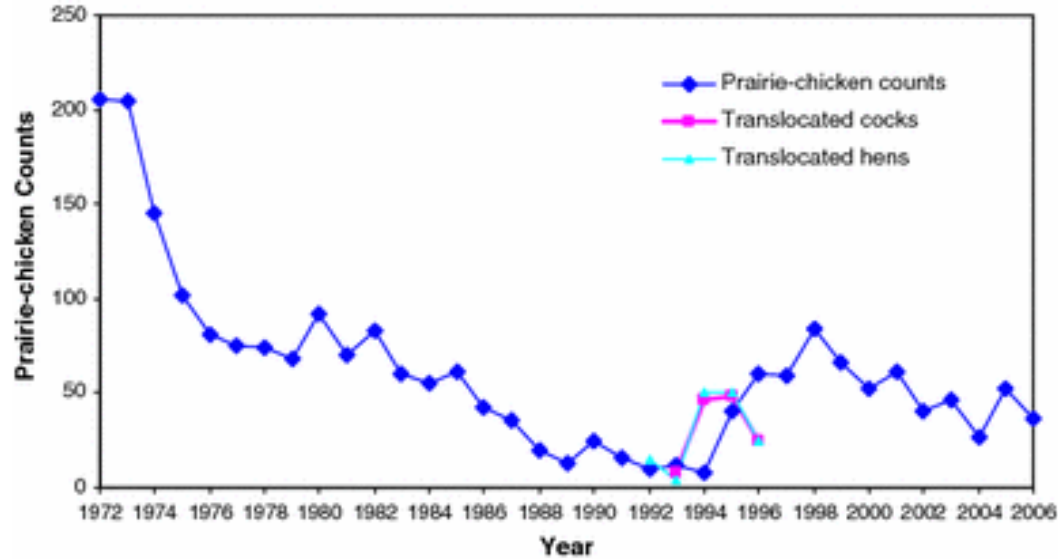
Locus	Illinois	Kansas	Minnesota	Nebraska	Illinois prebottleneck*
ADL42	3	4	4	4	3
ADL23	4	5	4	5	5
ADL44	4	7	8	8	4
ADL146	3	5	4	4	4
ADL162	2	5	4	4	6
ADL230	6	9	8	10	9
Mean	3.67	5.83	5.33	5.83	5.12
SE	0.56	0.75	0.84	1.05	0.87
Sample size	32	37	38	20	15

Note:

- SE indicates standard error of mean number of alleles per locus. The Illinois population in column 1 shows significantly less allelic diversity than the rest of the populations ($P < 0.05$).
- Number of alleles in the Illinois prebottleneck population include both extant alleles that are shared with the other populations and alleles detected in the museum collection.

Source: From Bouzat et al. (1998).

Prairie Chicken populations 2009 update



Habitat fragmentation occurs in 2 ways:

- 1) Reduction in overall available habitat
- 2) Generation of isolated patches

Challenges faced by organisms in separate patches:

❖ Decrease in popln size, gene flow & increase risk of genetic drift effects

The effects of fragmentation on **gene flow** depend on:

- number of popln fragments
- distribution of fragment popln sizes
- distance between fragments
- spatial pattern of populations
- dispersal ability of species

The effects of fragmentation on gene flow depend on:

- migration rates among fragments
- immigrants ability to establish and breed
- matrix among fragments & impact on dispersal
- time since fragmentation
- extinction & recolonization rates across fragments

Measuring popln fragmentation: F statistics:

- Wright (1969) derived F statistics
- = The degree of differentiation among fragments can be described by partitioning the overall **inbreeding** (inheritance by common descent) into components within and among populations (F statistics)
- Inbreeding (I) of individual relative to whole popln (T) = F_{IT}
- Inbreeding of individual relative to their deme or fragment (S) = F_{IS}
- Inbreeding due to differentiation among demes or fragments relative to total popln = F_{ST}

Measuring popln fragmentation: F statistics:

- Wright (1969)
- F_{IT} , F_{IS} , and F_{ST} are referred to as F statistics
- F_{IS} is the inbreeding coefficient avg. relative to all individuals from their population fragment
- F_{ST} is the effect of popln subdivision on inbreeding
- F_{IT} is inbreeding coefficient relative to all indiv. across all subpoplns
- Thus, when $F_{ST} = 0$, then sub-poplns have similar allele freq.
- Thus. when $F_{ST} = 1$, then sub-poplns have different allele freq.

Calculating : F statistics:

- Following Wright (1969):
- $F = 1 - [H_o/H_e]$ relates heterozygosity and inbreeding

H_o = observed heterozygosity

H_e = exp. heterozygosity (or gene diversity)

$1-F$ = obs. heterozygote freq in popln / exp. heterozygote freq

$$1-F = H_o/H_e$$

$$F_{st} = 1 - H_o/H_e = H_e - H_o/H_e$$

***Expected heterozygosity calculated by assuming Mendelian inheritance & Hardy Weinberg Equilibrium

Calculating : F statistics:

$$F_{st} = H_e - H_o / H_e$$
$$= (0.5 - 0.3) / 0.5 = 0.4$$

Popln		p allele freq Obs	Ho (2pq)
	1	1.0	0
	2	0.9	0.18
	3	0.8	0.32
	4	0.7	0.42
	5	0.6	0.48
	6	0.5	0.50
	7	0.4	0.48
	8	0.3	0.42
	9	0.2	0.32
	10	0.1	0.18
	11	0	0
He = 0.5			0.3

***Expected heterozygosity calculated assuming Mendelian inheritance & Hardy Weinberg Equilibrium

- F_{ST} increases across generations in fragmented populations, rate inversely dependent on popln size
- Thus decrease in popln size, increase of F_{ST}
- $F_{ST} \sim 0.15$ suggest significant differentiation among popln fragments If F_{st} is LARGE suggests that selection is operating!
- A single migrant per generation is considered sufficient to prevent complete differentiation of idealized populations, irrespective of their size (Wright 1969)
- A migrant has a larger effect on a smaller than larger popln

Why?

Gene flow and Gene establishment (Fenster 1991 a, b)

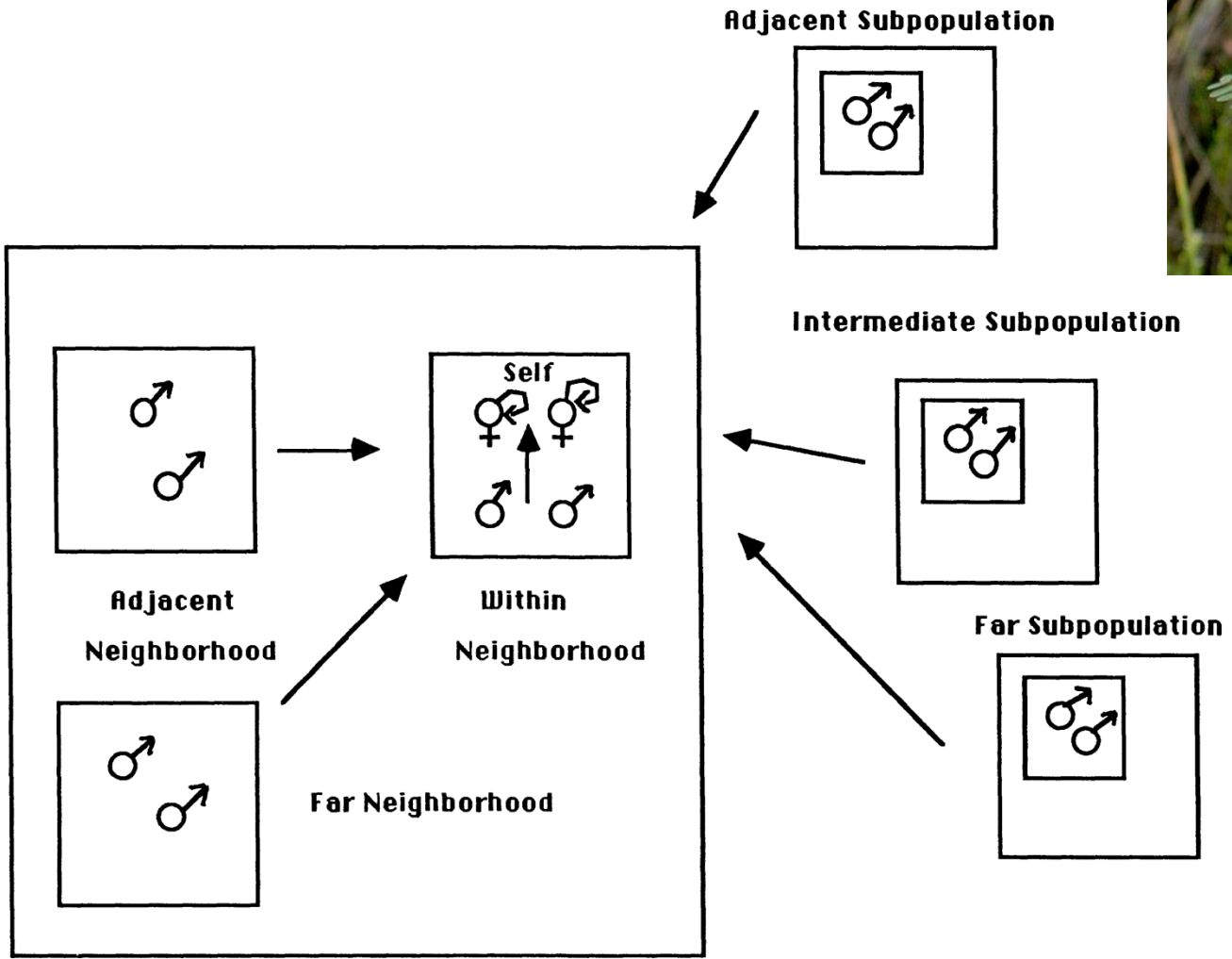
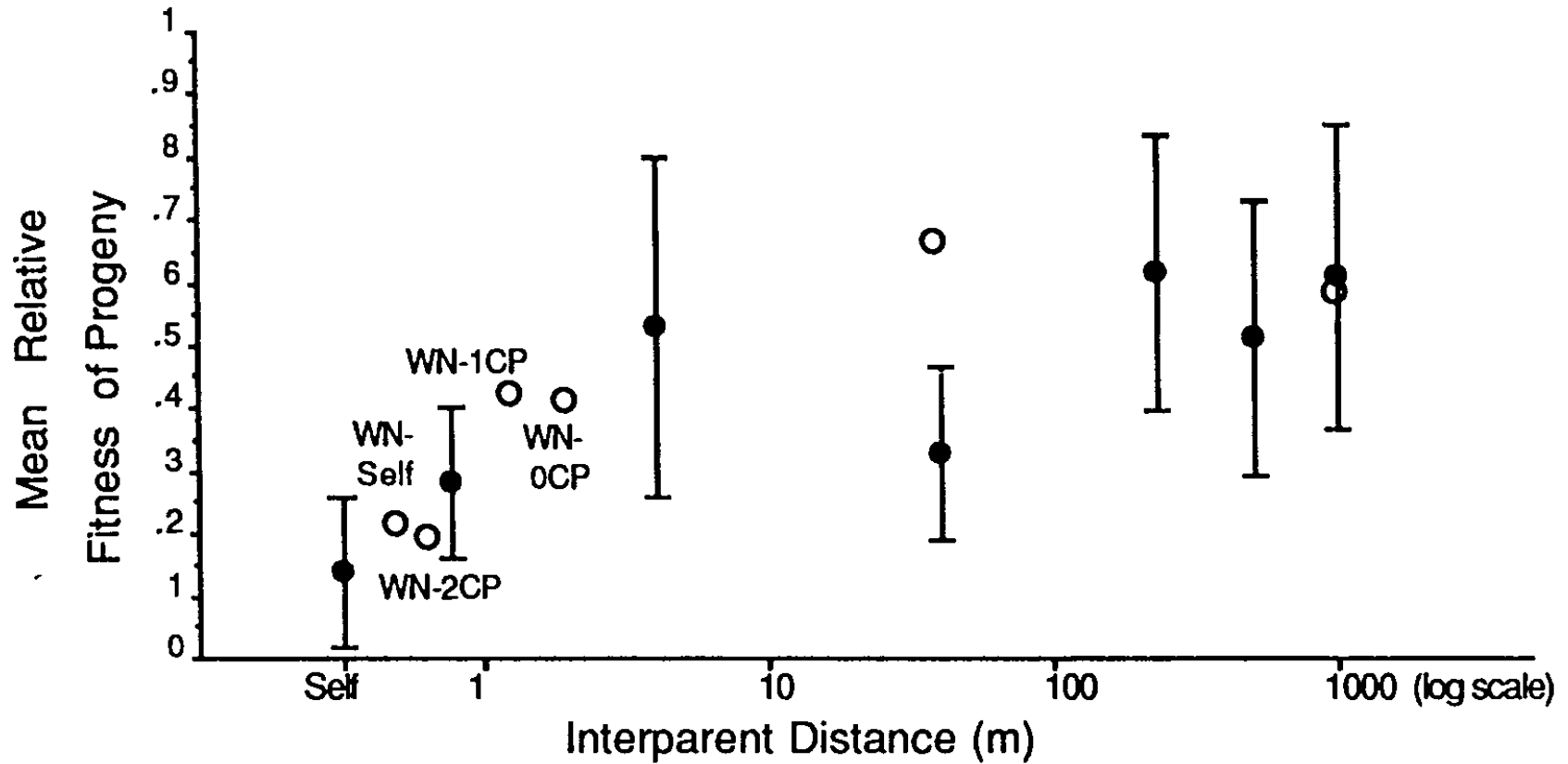
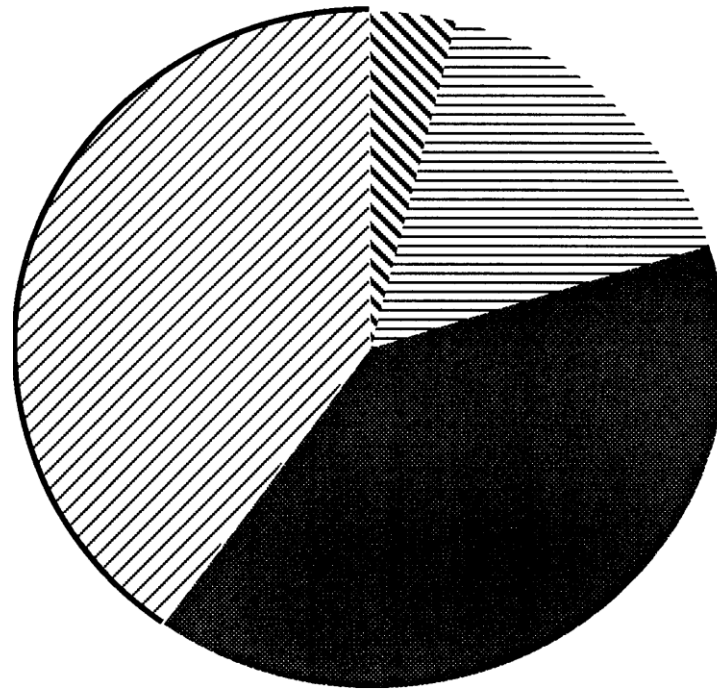


FIG. 1. Spatial distribution of plants used in the greenhouse crossing experiment.

Gene establishment (Fenster 1991, Evolution)





- ▨ - Seed Dispersal
- ▤ - Pollinator Flight Distance
- - Pollen Carry-Over
- ▧ - Gene Establishment

FIG. 4. The relative contribution of gene dispersal and gene establishment to gene flow.

Gene establishment based on inter-parent distance: selfing to outcrossing (at variable distances)

(Fenster 1991, Evolution)

TABLE 1. **Allozyme** polymorphism within subpopulations and populations of a *Chamaecrista fasciculata* metapopulation from Gooselake Prairie, IL.

A = number of alleles per locus; **Ho** = observed heterozygosity; **He** = gene diversity; **FI** = inbreeding coefficient. (Statistics are given as multilocus estimates averaged over replicates, and standard errors are within parentheses).

Level of analysis	A	Ho	He	FI
Within subpopulations	2.52 (0.27)	0.261 (0.052)	0.279 (0.041)	0.090 (0.015)
Within populations	2.67 (0.25)	0.256 (0.032)	0.282 (0.029)	0.098 (0.016)
Metapopulation	3.67	0.257	0.291	0.121

- ❖ Pollinator observations & seed dispersal estimates agree w/allozymes
- ❖ Average neighborhood area corresponded to a 3 m radius
- ❖ Minimal role of seed bank in this system

Gene Flow and Dispersal Ability

Gene flow can be estimated from the degree of genetic differentiation among populations (F_{st}).

Gene flow among fragmented populations is related to dispersal ability

Degree of genetic differentiation among populations (F_{ST}) is expected to be greater:

- in species with lower vs. higher dispersal rates
- in subdivided vs. continuous habitat
- in distant vs. closer fragments
- in smaller vs. larger population fragments
- in species with longer vs. shorter divergence times
- In species with shorter vs. longer generation time
- with adaptive differences vs. those without adaptive differences

(F_{ST}) in a range of taxa:

Species	N species	F_{st}	reference
Mammals	57	0.24	1
Birds	23	0.05	2
	22	0.26	1
	33	0.32	1
	79	0.14	1
Selfing plants		0.51	3
Mixed mating	Animal poll.	0.22	3
	Wind poll.	0.10	3
Outcrossing	Animal poll.	0.20	3
	Wind poll.	0.10	3

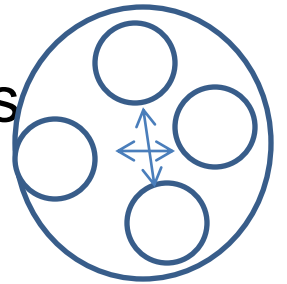
References: 1. Ward et al. (1992); 2. Evans (1987); 3. Hamrick & Godt (1989).

Movement of Migrants:

We are already familiar with:

- Mainland-island
- Source- sink
- Inverse- mainland-island
- Hot spots, cold spots

Island Model (Wright 1931) – gene flow among subpops
pops of equal size and migration can occur among demes



Stepping – stone Model (Kimura 1955) common in nature - gene
flow only occurs between adjacent subpops



Neighborhood Model (Wright 1943) – isolation by distance
most common in nature in many systems



Movement of Migrants:

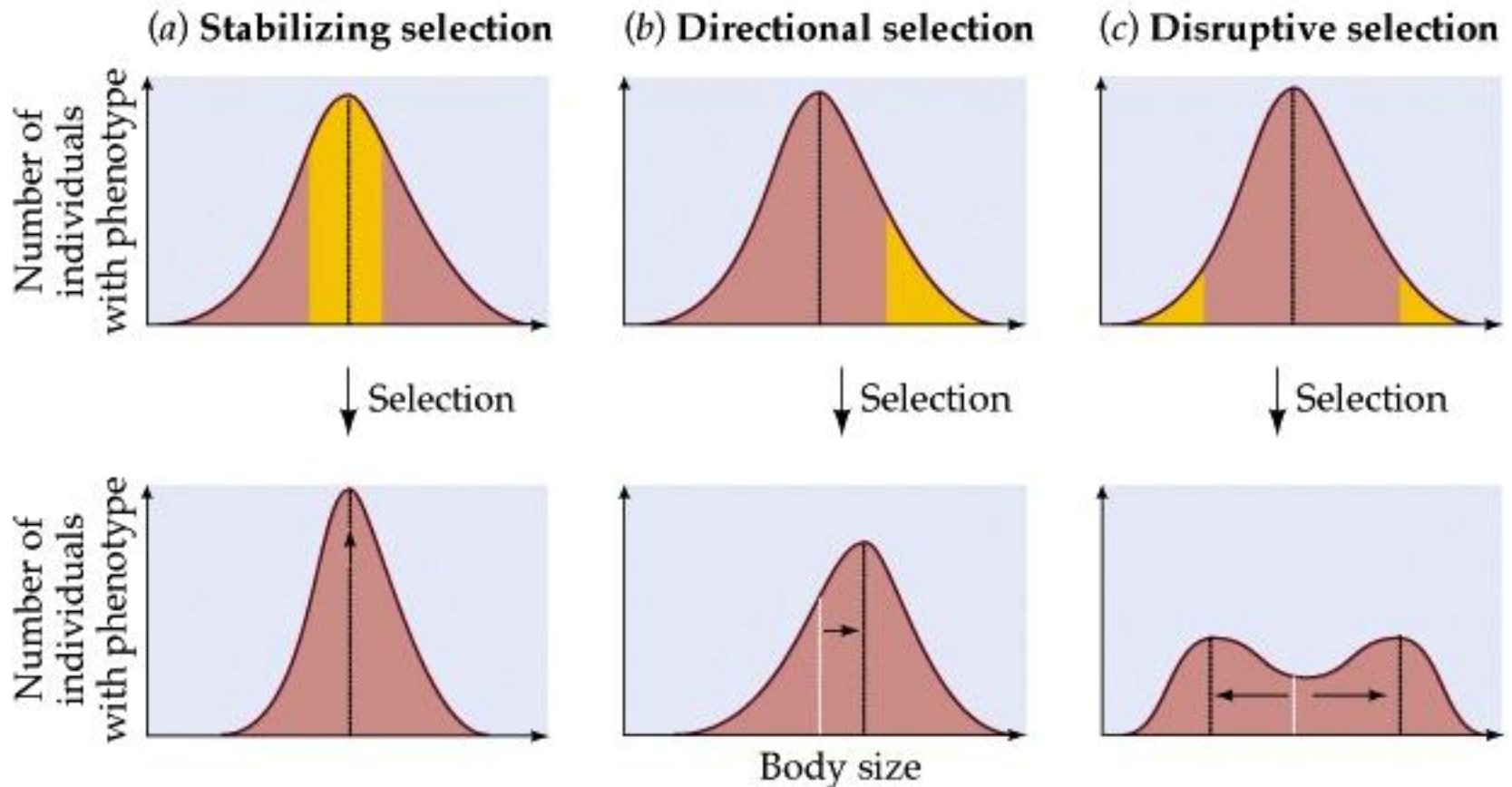
Propagule Pool Model – all gene flow (emigration) from single source, thus expect larger F_{st} in newly established poplns

- Ex.,

Migrant Pool Model – gene flow from multiple sources (~subpops or demes), thus do not expect large F_{st} , if anything smaller F_{st} in newly established poplns

- Ex.,

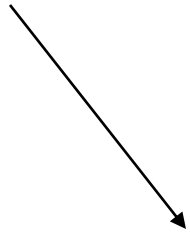
Types of Natural Selection



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Demonstration of Environmental Covariance

Other sources

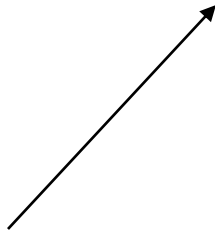


Phenotype

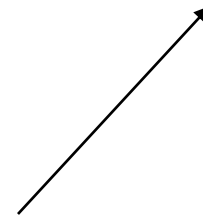
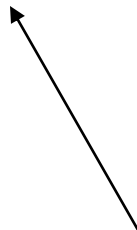


FITNESS

Genotype



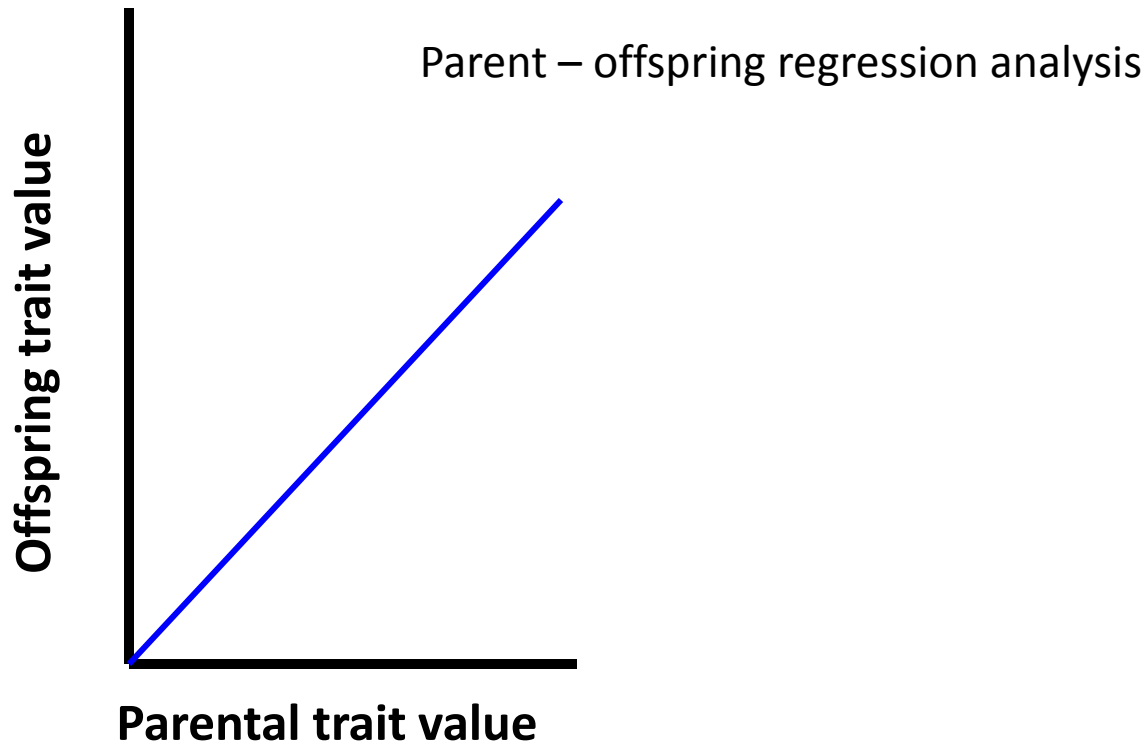
Environmental Covariance



Phenotypic Selection readily quantified in the field:

- Measure traits, collect fitness data, perform analysis
- Caveats:
 - Whether all traits under natural selection are actually measured ~ target of selection
 - This measure includes environmental nuisance variables
- Directional selection measurements are robust to sample sizes but large sample sizes are needed to estimate stabilizing and correlational selection.

Genetic basis of trait = heritability

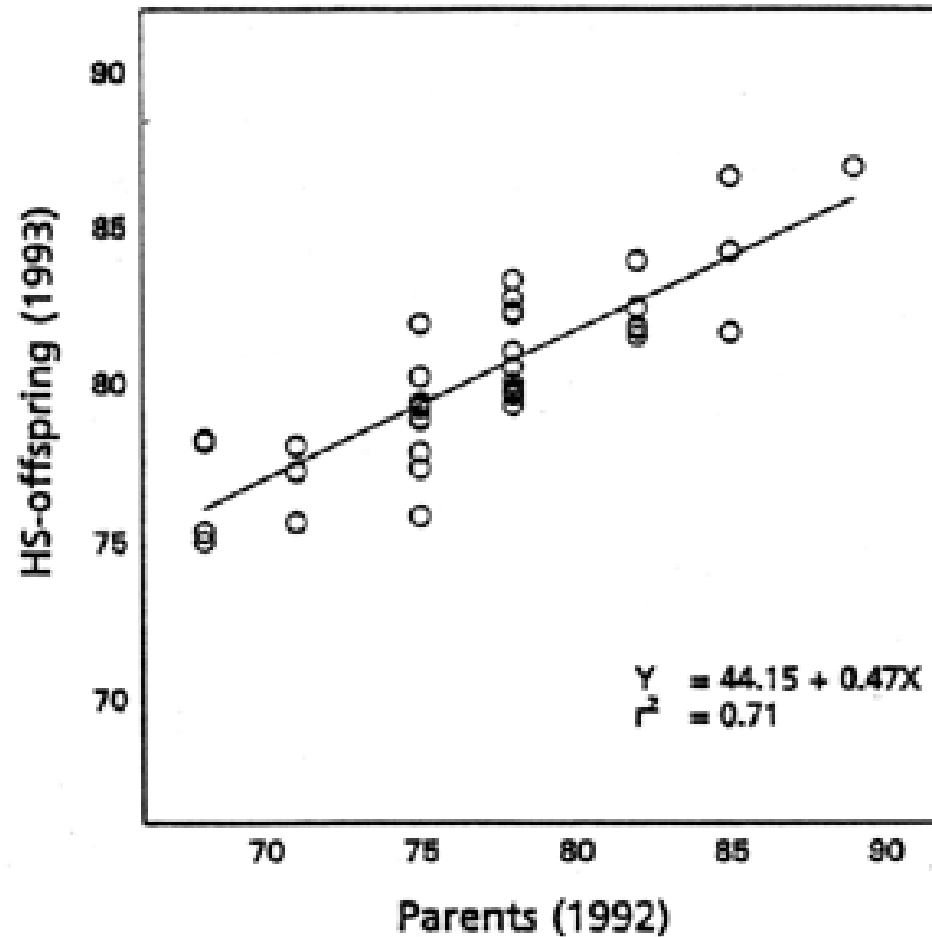


- $\text{Var}(P) = \text{Var}(G) + \text{Var}(E) + 2 \text{Cov}(G,E)$
- If assume $2 \text{Cov}(G,E) = 0$, then:

Broad sense heritability: $V_G/V_P = H^2$

Narrow sense heritability: $V_A/V_P = h^2$

Parent – offspring regression, flower initiation



Linear Selection Lande and Arnold 1983 U. Chicago School

Univariate approach w/ simple regression $w = m(\text{trait } x) + b$
(m =slope, b = intercept)

Linear = Change in trait mean before and after selection ($Z^* - Z$)

Relative fitness = fitness of each indiv./ avg. fitness of popln

Standardize phenotypes in popln = $(z_i - z_{\text{avg}}) / v_z$



Selection can be:

- **Linear ~ directional selection ~ β (beta)**
 - Change in the trait mean before and after selection
($Z^* - Z$)

* = after selection
 - $\text{Cov}(W, Z) = \text{Cov}(\text{fitness}, \text{trait})$
 - univariate approach with simple regression

Selection Coefficient or differential = S

Non-standardized:

$S = \text{mean of trait(after)} - \text{mean of trait (before)}$

$S = z(\text{mean})^* - z(\text{mean})$

* = after selection

Intensity of selection = i

Standardized selection differential: with Z transformation such
mean = 0 and variance = 1

Then can calculate intensity of selection = i

$$i = \frac{\text{mean (after)} - \text{mean (before)}}{\sigma \text{ (before)}} = \text{Intensity of Selection}$$

$$i = \frac{S}{\sigma_{\text{before}}}$$

Interpretation of regression approach:

$$w = mx + b$$

w = fitness

m = slope

x = trait

b = y intercept

i = intensity of selection = + 0.10

- ❖ If you are one standard deviation above the mean then your w (fitness) is increased by 10%

Linear Selection Approaches:

Univariate Approach:

Selection differential, S = Total estimate of phenotypic selection including BOTH direct and indirect selection

Multivariate Approach:

Selection gradient, β , = estimates directional selection ALONE while holding all other factors constant. \sim partial regression analysis

Single multiple regression approach:

Direct Selection Standard Equation:

$$w = \alpha + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \dots + \beta_n x_n$$

α = intercept

x = traits

$\beta_1 x_1 =$ partial regression slope between each “ x ” and w while removing the effects of correlations among other traits or variables (\sim is held constant)

$$i = \beta \ x \ \sigma$$

$$i = S / \sigma \quad \text{such that} \quad \beta = S / \sigma^2$$

Total and Direct selection gradients and intensities on floral traits of *S. virginica*

Trait	TOTAL = direct + indirect		DIRECT	
	S	i	β	i
# flowers with Female function	1.26***	2.32	1.1***	1.98
Avg. flowers/day	0.66*	0.23	-0.02	0
Display Ht.	1.97***	0.49	0.79**	0.20
Petal length	2.20***	0.28	0.65	0.08
Petal width	1.77***	0.25	-0.11	-0.02
Date of 1 st Fl	-1.34	-0.28	0.22	0.05
Avg. flower date	0.26	0.04	-0.30	-0.05
Corolla tube length	0.43	0.03	-0.79	-0.05
Nectar-stigma distance	2.73**	0.24	0.32	0.03



Selection can be:

- **Non-linear ~ Quadratic ~ γ (gamma)**
 - $\gamma \Rightarrow$ **stabilizing selection**, $+\gamma \Rightarrow$ **disruptive selection**
 - (Decrease in variance) (Increase in variance)
 - \sim Convex \sim Concave
 - Change in the trait variance before & after selection
 - $\text{Cov}(W, Z^2)$
 - Quadratic regression

Selection can be:

Quadratic ~ stabilizing selection ~ γ (gamma)

= Change in the trait variance before & after selection, $\text{Cov}(W, Z^2)$

Quadratic regression:

$$w = \alpha + \beta_z + \gamma/2 (Z^2)$$

α = y intercept

β = slope of fitness function (~ to S with std. data)

γ = measure rate of change of slope with increasing Z

= estimated amt of curvature in fitness function ~ nonlinear

= or variance of selection gradient or stabilizing/disruptive Sel.



- $\gamma \Rightarrow$ **stabilizing selection** $+\gamma \Rightarrow$ **disruptive selection**

(Decrease in variance)

(Increase in variance)

~Convex

~Concave

Selection can be:

- **Directional selection** $\sim \beta$ (beta)
- **Stabilizing/disruptive or diversifying selection** $\sim \gamma$ (gamma)

Z denotes first standardization of data then conduct regression analysis for 2 traits:

$$w = \alpha + \beta_i z_i + \beta_j z_j + \frac{1}{2} \gamma_{ii} z_i^2 + \frac{1}{2} \gamma_{jj} z_j^2 + \gamma_{ij} z_i z_j + \epsilon$$

Correlational Selection

$$w = \alpha + \gamma_{ij} z_i z_j + \epsilon$$

- ❖ Correlational selection occurs across generations and is caused by genetic correlations.

Correlational Selection

- Selection favors combinations of traits over single traits alone.
- Traits become functionally integrated with each other.
- Promotes genetic integration or coupling too.

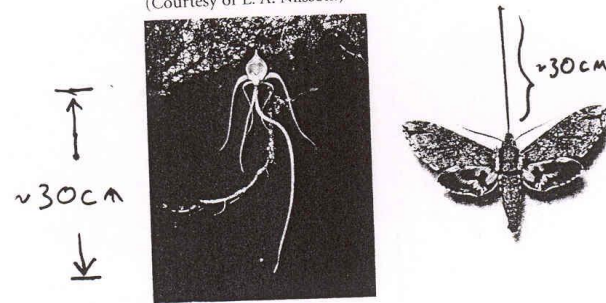
If considering only two traits:

- Directional selection – trait means shift before & after selection
- Stabilizing/diversifying or disruptive selection – variance of traits shift before and after selection as well as the correlation between two traits (~correlational)
- ❖ Thus need to consider 3 forms of selection utilizing multiple regression techniques.

Flowers are adaptations



FIGURE 18.15 The Madagascan orchid *Angraecum sesquipedale* bears nectar in an exceedingly long spur (left), and is pollinated by the long-tongued hawkmoth *Xanthopan morgani praedicta* (right). (Courtesy of L. A. Nilsson.)



An Orchid from Madagascar and the Moth Pollinator

(from A. Nilsson)



MULTIYEAR STUDY OF MULTIVARIATE
LINEAR AND NONLINEAR PHENOTYPIC
SELECTION ON FLORAL TRAITS OF
HUMMINGBIRD-POLLINATED
SILENE VIRGINICA

Richard J. Reynolds,^{1,2,3,4} Michele R. Dudash,^{1,2} and Charles B. Fenster^{1,2}

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Phenotypic Selection in the Field

(Reynolds et al., *Evolution* 2010)

8 year study (1992-95, 2002-06)

Female Reproductive Success

(Total Fruit & Seed)

Attraction

Petal Size (Length x Width)

Display Height

Display Size (# Flowers)

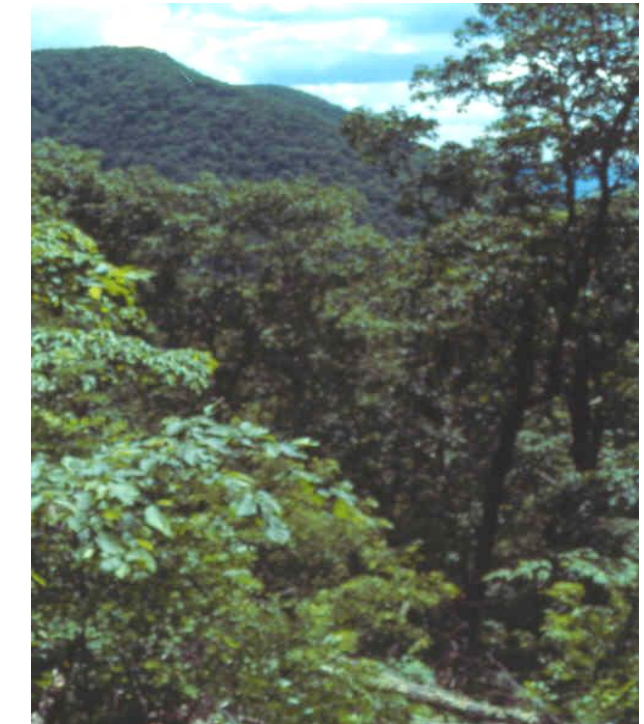


Mechanics of Pollen Deposition

Corolla Tube Length

Stigma Exsertion

Corolla Tube Diameter



Covariates

Flower Number

Various Vegetative Traits

150-300 individuals/year

Mtn. Lake Biol. Station

How to document patterns of natural selection

Quantify Phenotypic Selection:

- Directional Selection (Linear)
- Stabilizing Selection (non-linear)
- Correlational selection – traits selected simultaneously

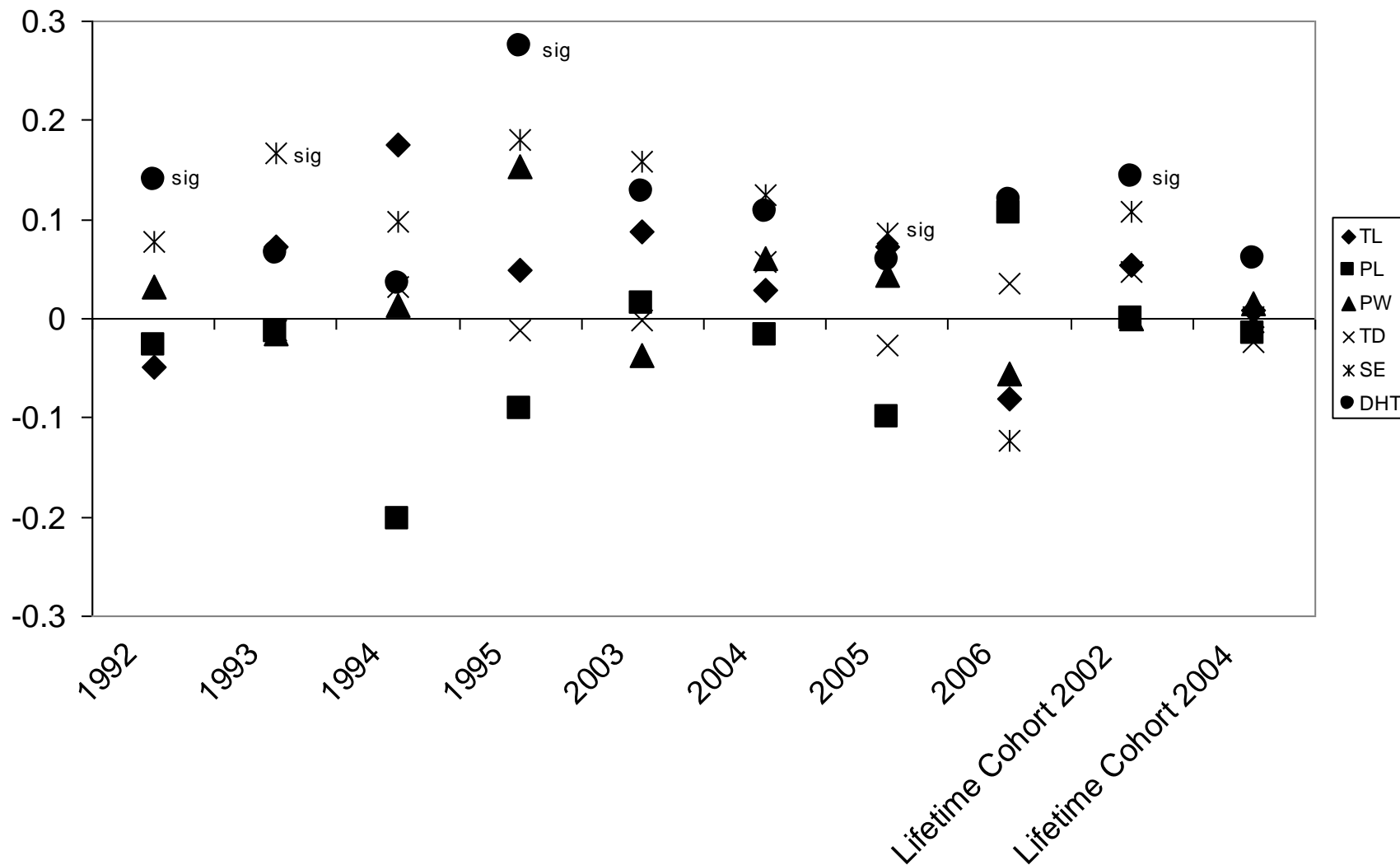


Figure 1a. Variation among years in **directional selection** gradients through (A) **fruit production**. Trait codes: TL = Corolla tube length, PL = Petal length, PW = Petal width, TD = Corolla Tube diameter, SE = Stigma exertion, DHT = Display height. Sig = Significant at the FDR adjusted type 1 error rate of $Q = 0.05$.

How to document patterns of natural selection:


Quantify Phenotypic Selection:

- Directional Selection (Linear)
- Stabilizing Selection (non-linear)
- Correlational selection – traits selected simultaneously

Female Reproductive Success

Petal Size Display Height Display Size CorollaTubeLength StigmaExertion CorollaTubeDiameter

CorollaTubeDiameter StigmaExertion CorollaTubeLength DisplaySize DisplayHeight Petal Size

Var PS	Cov(PS, DH)	Cov(PS, DS)	Cov(PS, CTL)	Cov(PS, SE)	Cov(PS, CTD)
	VarDH	Cov(DH, DS)	Cov(DH, CTL)	Cov(DH, SE)	Cov(DH, CTD) Positive**
		VarDS	Cov(DS, CTL)	Cov(DS, SE)	Cov(DS, CTD)
			VarCTL	Cov(CTL, SE) Negative**	Cov(CTL, CTD)
				VarSE	Cov(SE, CTD)
					VarCTD

Reynolds et al. *Evolution* 2010

Conclusion:

Correlational selection on part of the Gamma Matrix

Highlights

- Gene Flow – unifying or diversifying force, F_{st}
- Genetic Drift – random changes in allele frequencies within a population, effects >er for small than large populations
- Natural Selection – individual variation in survival and reproduction within a population
- Types of Natural Selection: Directional, Stabilizing, and Correlational
- Evolution – changes in allele frequencies owing to natural selection.