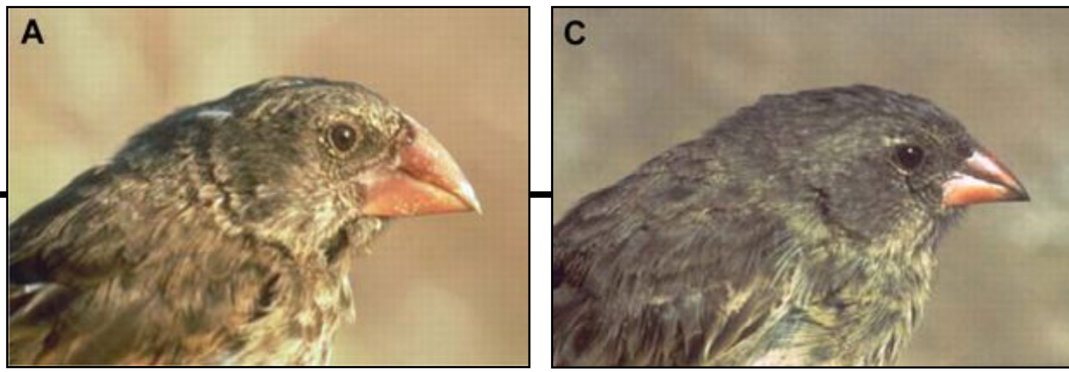
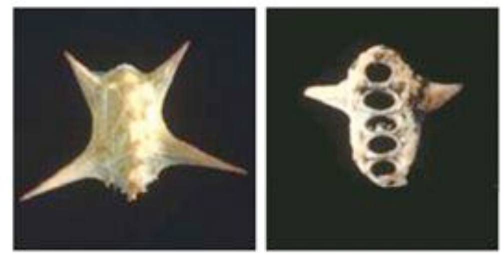
Natural selection...

a difference, on average, in the survival or fecundity of individuals with certain phenotypes compared to individuals with alternative phenotypes



Geospiza fortis



Four tenets of natural selection…

(1) Individuals within populations are variable
(2) Variation is heritable
(3) Organisms differ in their ability to survive and reproduce
(4) Survival & reproduction are non-random

Divergent Induced Responses to an Invasive Predator in Marine Mussel Populations

SCIENCE VOL 313 11 AUGUST 2006

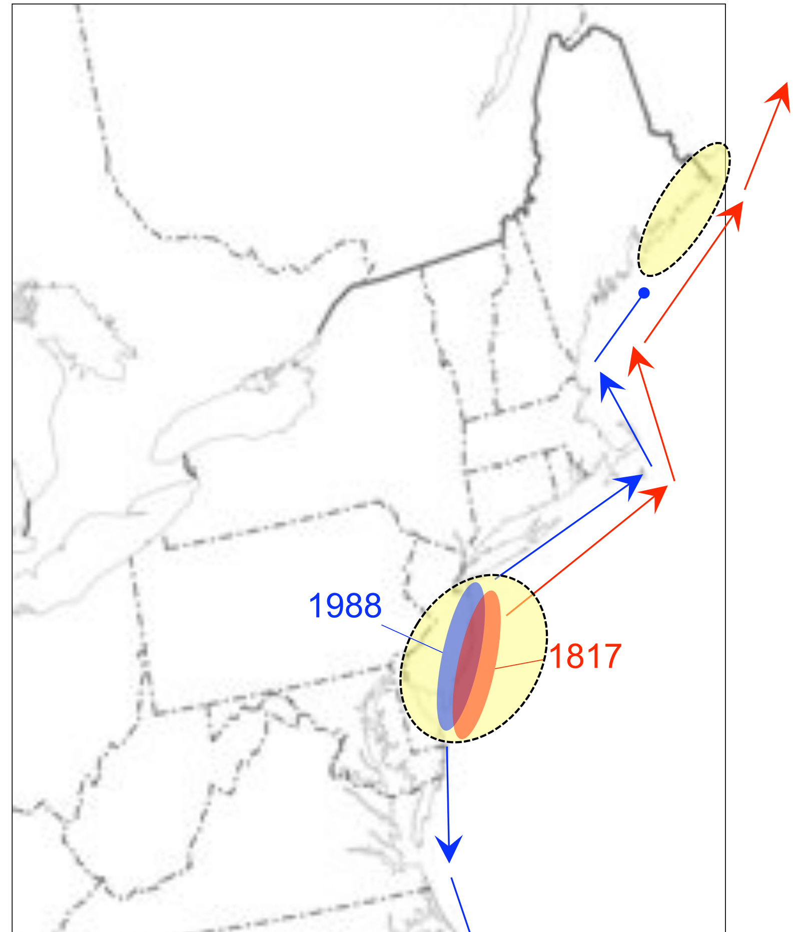
Aaren S. Freeman* and James E. Byers

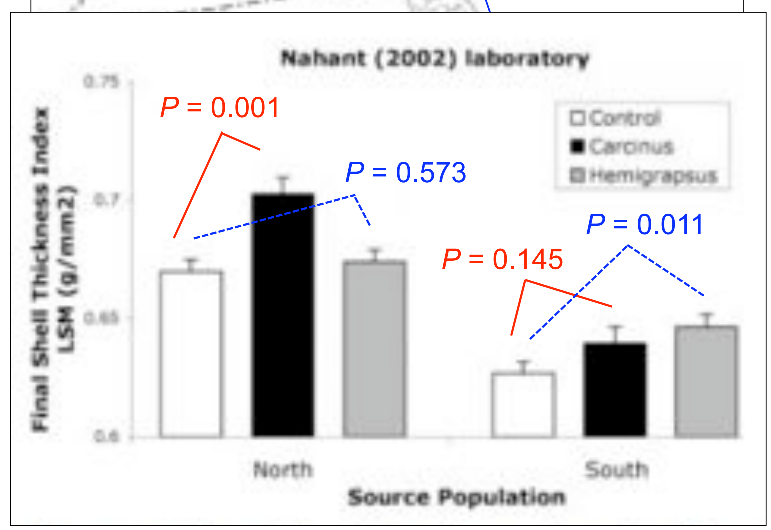
Mytilus edulis, Blue mussel

Respond to presence of predators by thickening shells
– defense response is inducible –

Hemigrapsus sanguineus
Asian shore crab

Carcinus maenas
European green crab





Rapid Temporal Reversal in Predator-Driven Natural Selection

SCIENCE VOL 314 17 NOVEMBER 2006

Jonathan B. Losos,[1*†] Thomas W. Schoener,[2] R. Brian Langerhans,[1*] David A. Spiller[2]

Anolis sagrei typically terrestrial
(longer legs ~ faster escape from predators)

Invasion by Leiocephalus carinatus causes
Anolis sagrei to be arboreal

…predicted that leg length would DECREASE in arboreal populations of Anolis sagrei lizards following invasion by Leiocephalus carinatus

Rapid Temporal Reversal in Predator-Driven Natural Selection

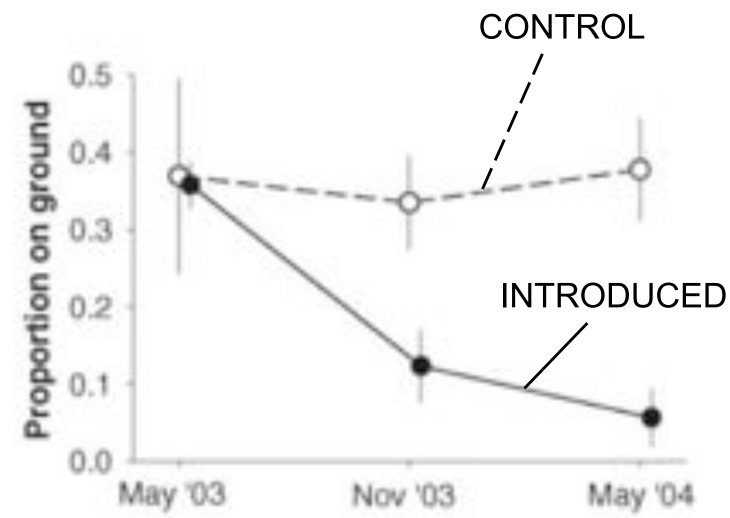
SCIENCE VOL 314 17 NOVEMBER 2006

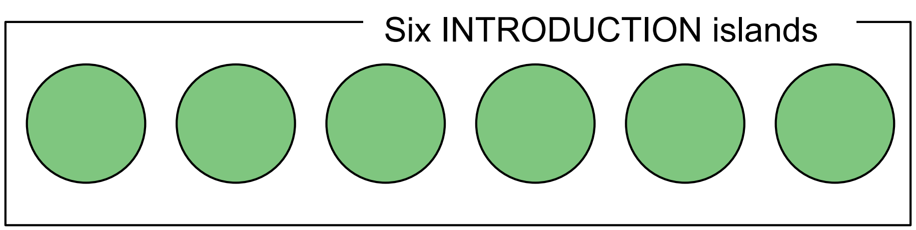
Jonathan B. Losos,[1*†] Thomas W. Schoener,[2] R. Brian Langerhans,[1*] David A. Spiller[2]

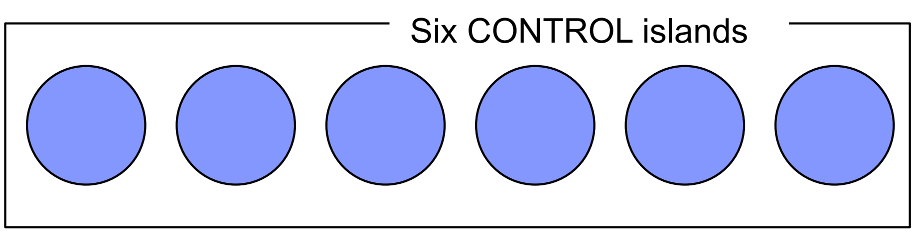
All Anolis sagrei individuals tagged / measured

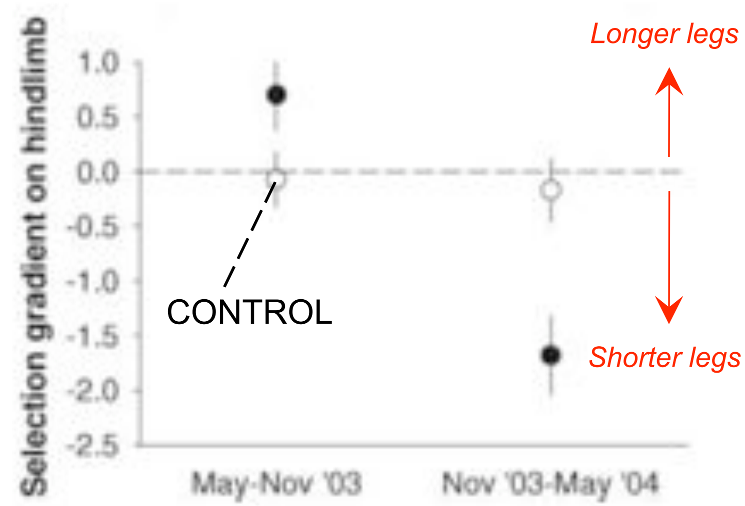
Leiocephalus carinatus were introduced on 6 islands

Censused after 6 (and 12) months to record survival





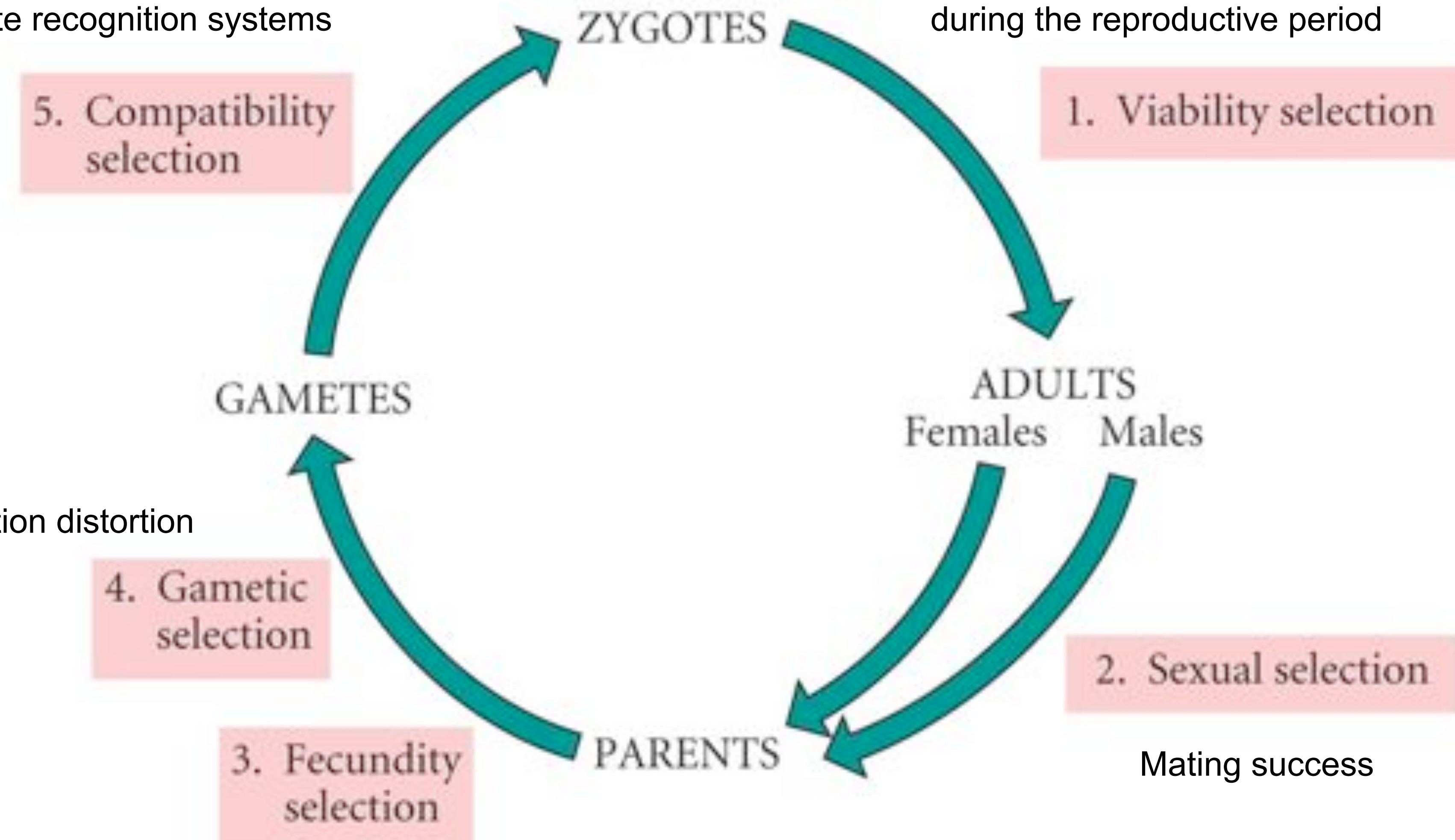




Components of natural selection

Gamete recognition systems

Probability of survival before and during the reproductive period



Segregation distortion

Mating success

Average number viable offspring

Natural selection is an average difference in the survival or fecundity of individuals with certain phenotypes

---

Demonstrating adaptation

What is a trait for? Do individuals that possess the trait contribute more offspring to future generations? How does a trait develop? Who has it?

Adaptation

Any heritable **trait** (structure, physiological ability, behavior) that makes an organism better able to survive & reproduce

The **evolutionary process** leading to the persistence of such a trait in populations

Natural selection is the differential contribution of offspring to the next generation by certain genotypes

---

Demonstrating adaptation

What is a trait for? Do individuals that possess the trait contribute more offspring to future generations? How does a trait develop? Who has it?

Adaptation

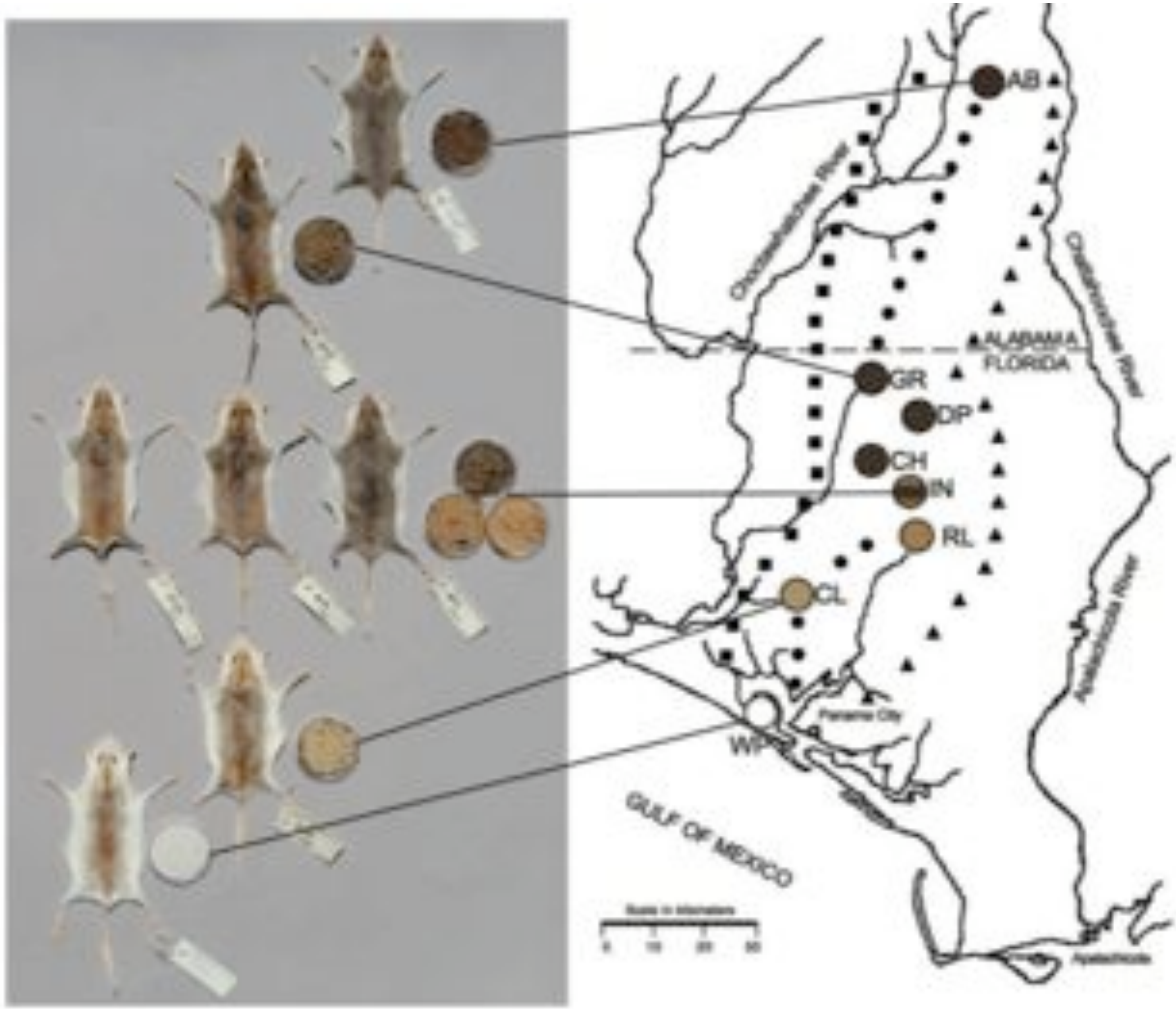
Any heritable **trait** (structure, physiological ability, behavior) that makes an organism better able to survive & reproduce

The **evolutionary process** leading to the persistence of such a trait in populations

NATURAL SELECTION ALONG AN ENVIRONMENTAL GRADIENT: A CLASSIC CLINE IN MOUSE PIGMENTATION

Lynne M. Mullen[1,2] and Hopi E. Hoekstra[1,3]

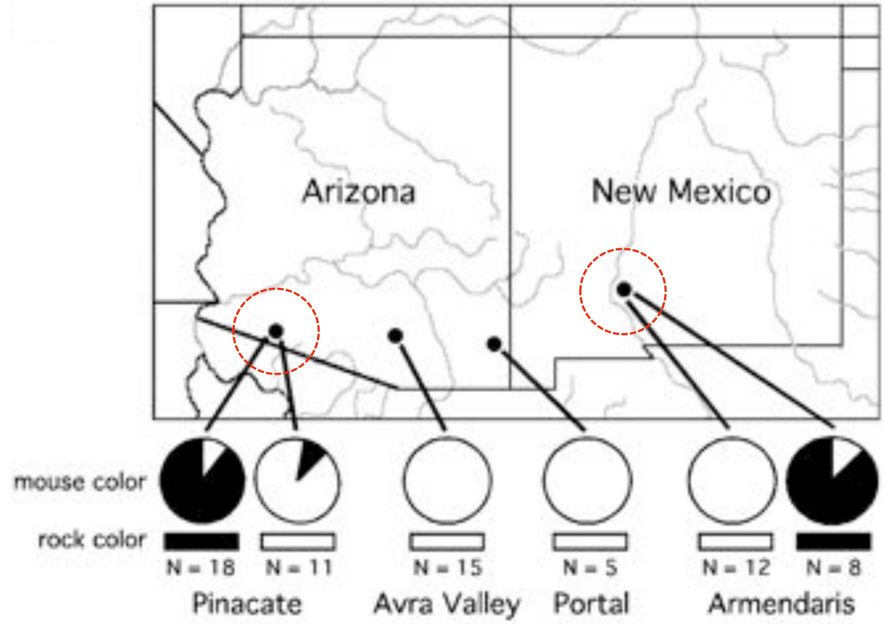
Evolution 62-7: 1555–1570



The genetic basis of adaptive melanism in pocket mice

Michael W. Nachman*, Hopi E. Hoekstra, and Susan L. D'Agostino

5268–5273 | PNAS | April 29, 2003 | vol. 100 | no. 9



(Upper) Collecting localities, substrate color, and mouse color. Sample sizes at each site are given.

Pie charts are the proportion of light and dark mice at each site. Rectangles indicate substrate color.

(Lower) Light and dark C. intermedius from the Pinacate locality on light and dark rocks.

The genetic basis of adaptive melanism in pocket mice

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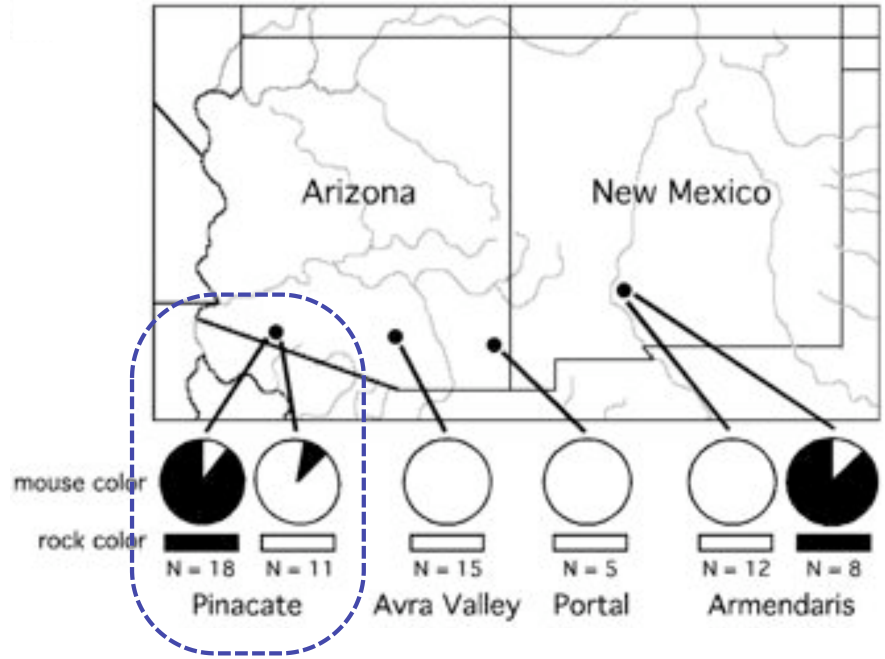


	Mouse phenotype	
Genotype	Light	Dark
DD	0	11
Dd	0	6
dd	12	0

Coat color variation **well studied** in mammals

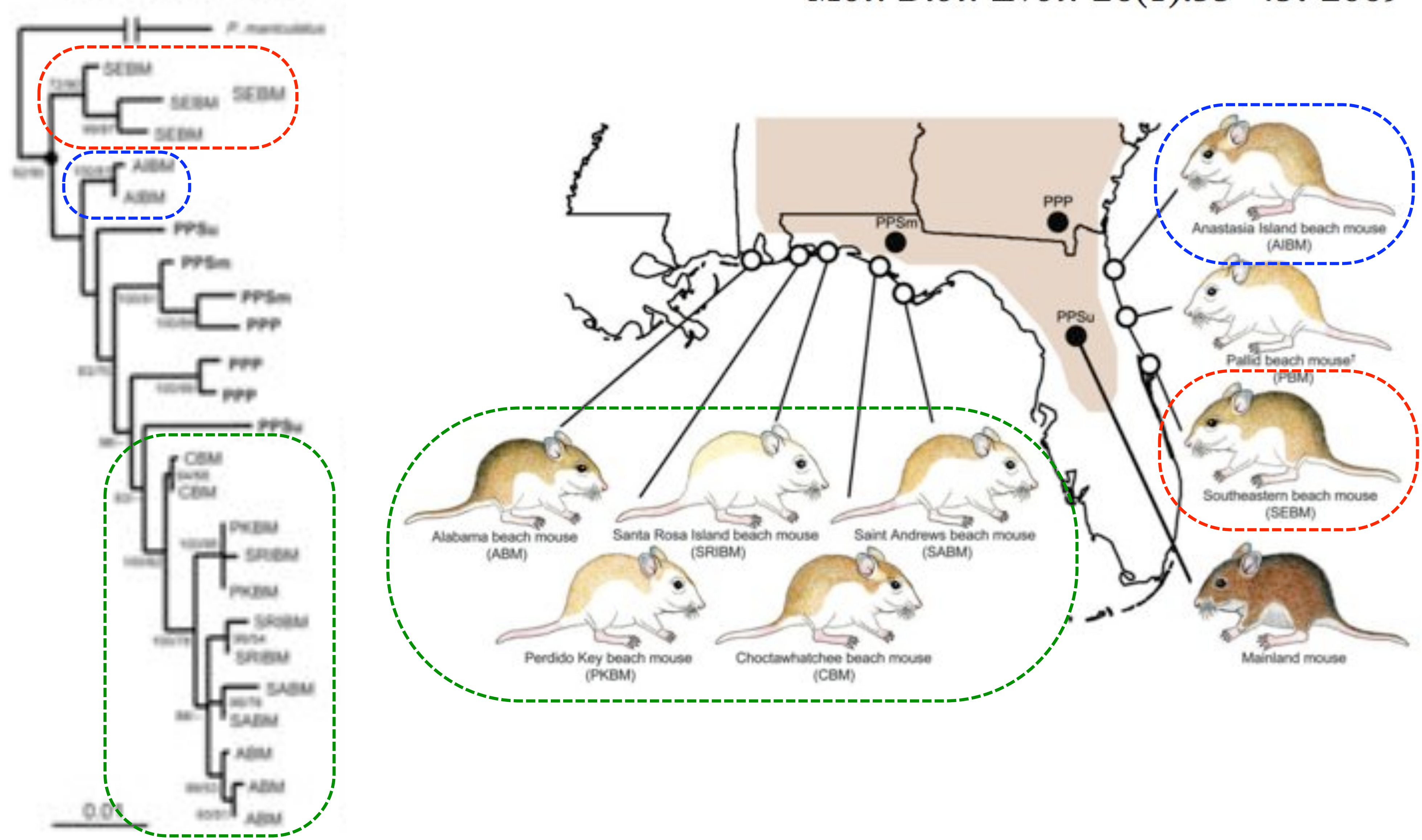
Association studies using markers in candidate pigmentation genes (Agouti & Mc1r)

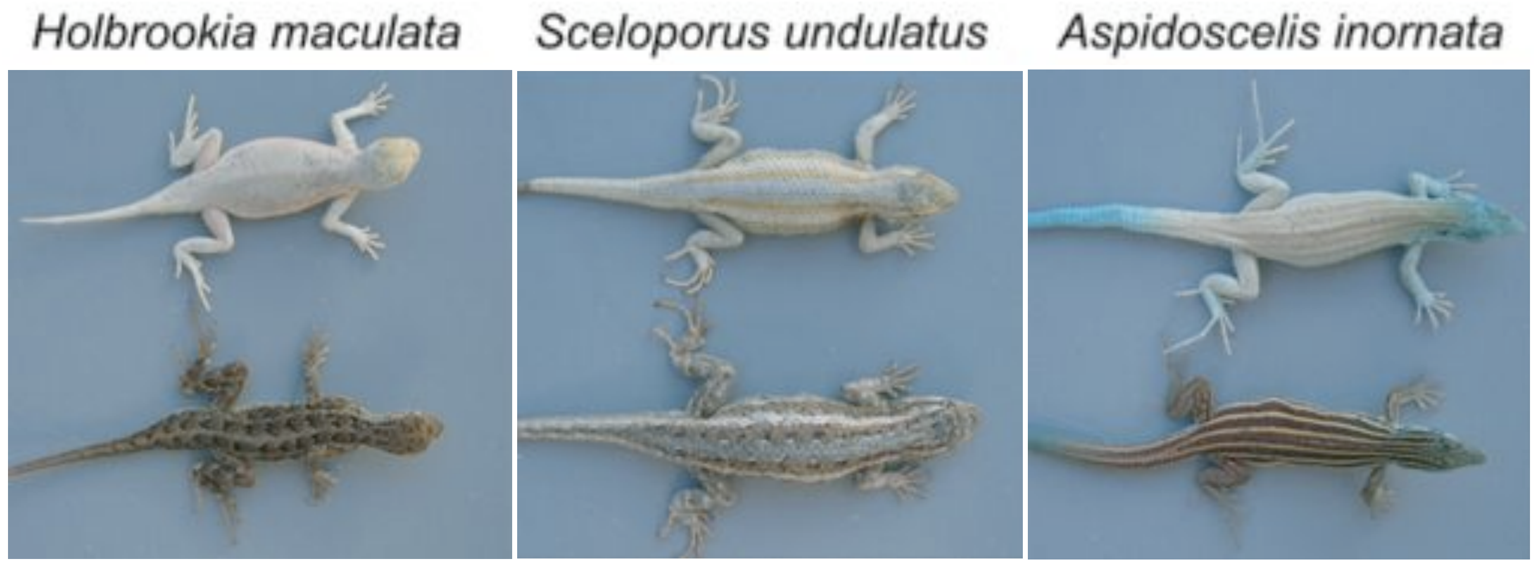
Genotype-phenotype association between **Mcr1 alleles & coat color** in animals from Pinacate.

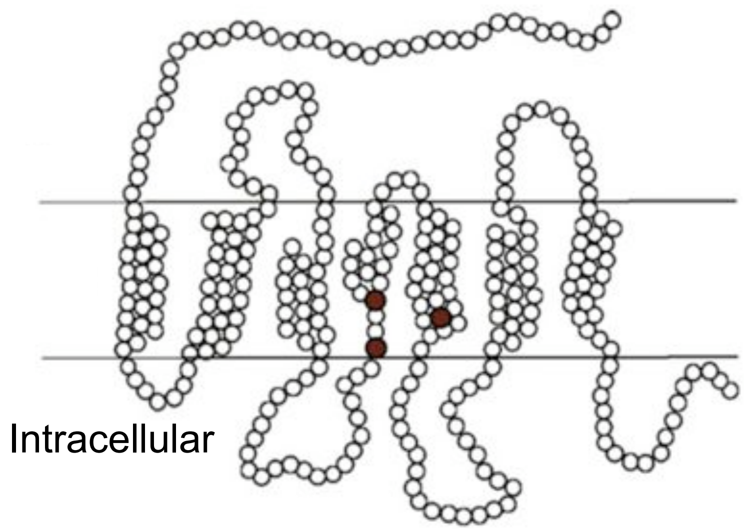
The Genetic Basis of Phenotypic Convergence in Beach Mice: Similar Pigment Patterns but Different Genes

Cynthia C. Steiner, Holger Römpler,†‡[1] Linda M. Boettger,* Torsten Schöneberg,† and Hopi E. Hoekstra‡*

Mol. Biol. Evol. 26(1):35–45. 2009







Derived amino acid replacements (1 in each species) are statistically associated with blanched coloration

(Rosenblum et al. Evolution 2004)

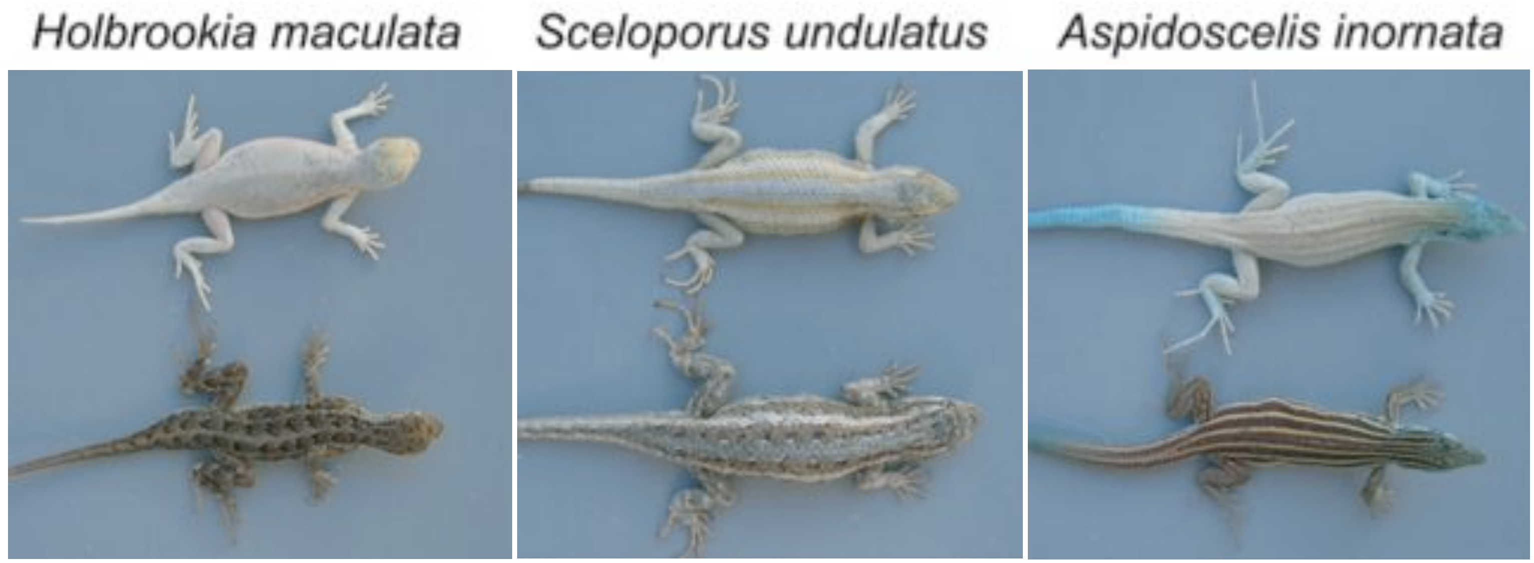
Biochemical studies indicate a different molecular mechanisms for the derived mutations

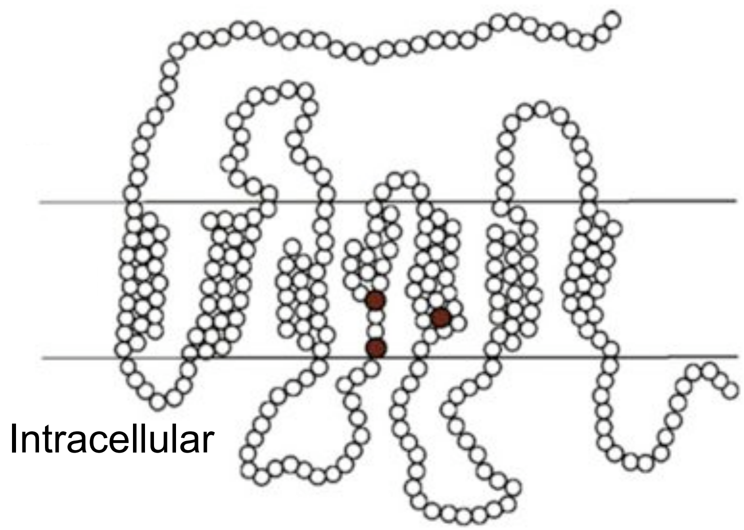
(Rosenblum et al. PNAS 2010)

- Integration of receptor into membrane
- Receptor signaling

His^{208}Tyr substitution for *Sceloporus undulatus*
Thr^{170}Ile substitution for *Aspidoscelis inornata*
Val^{168}Ile substitution for *Holbrookia maculata*

Implications for convergence…





Derived amino acid replacements (1 in each species) are statistically associated with blanched coloration

(Rosenblum et al. Evolution 2004)

Species and habitat	Number of wild-type alleles	Number of derived alleles
Sceloporus undulatus		
Dark soil	58	0
White sands	30	26
Aspidoscelis inornata		
Dark soil	41	3
White sands	8	48
Holbrookia maculata		
Dark soil	52	0
White sands	0	36

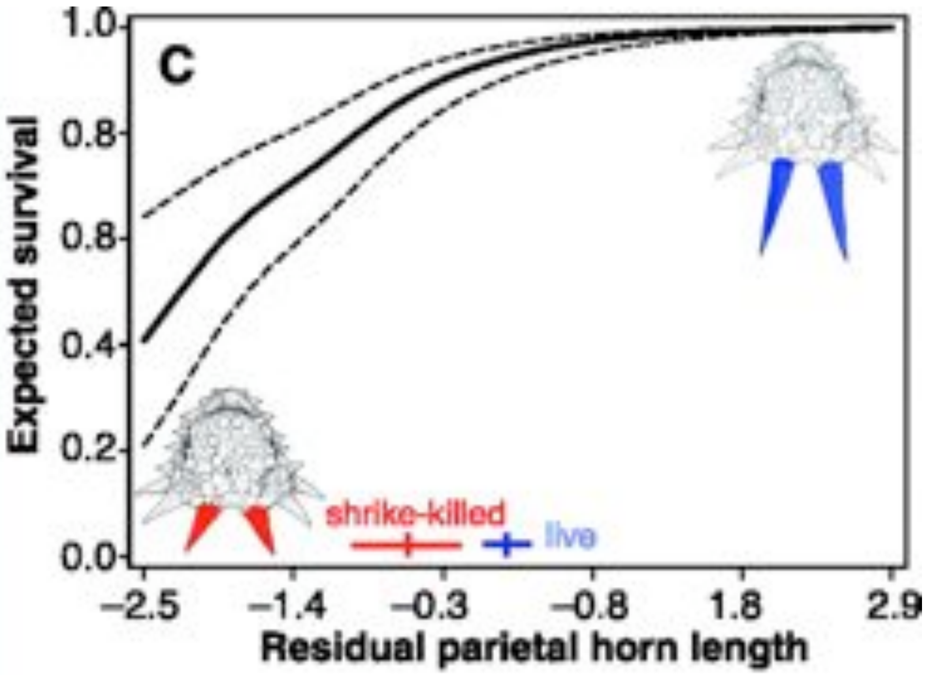
Derived alleles: the $His^{208}Tyr$ substitution for *Sceloporus undulatus*; the $Thr^{170}Ile$ substitution for *Aspidoscelis inornata*; the $Val^{168}Ile$ substitution for *Holbrookia maculata*

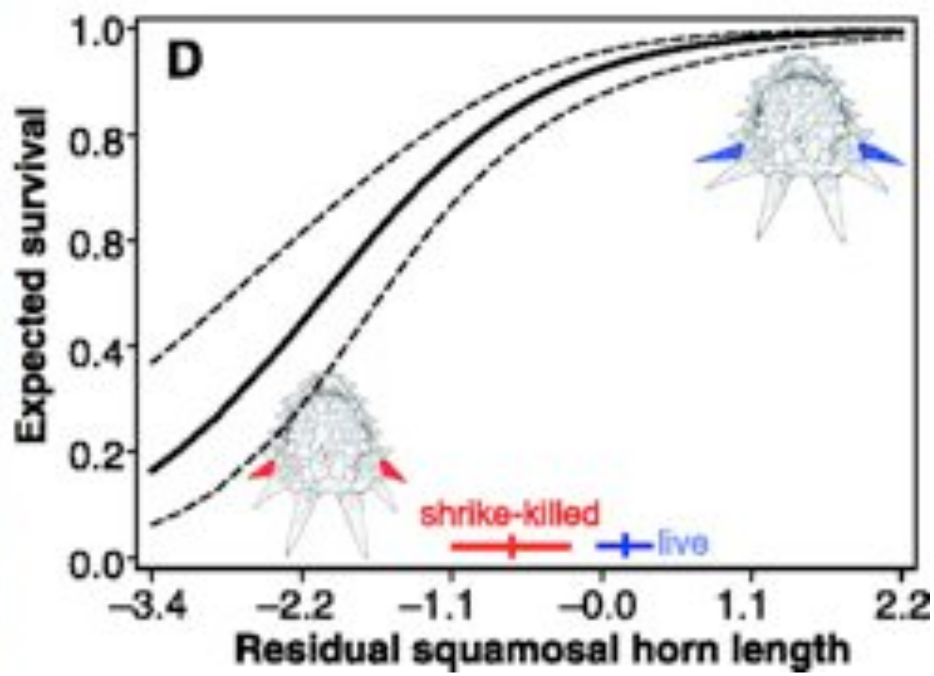
Fisher's Exact Test (FET) was highly significant for each species.

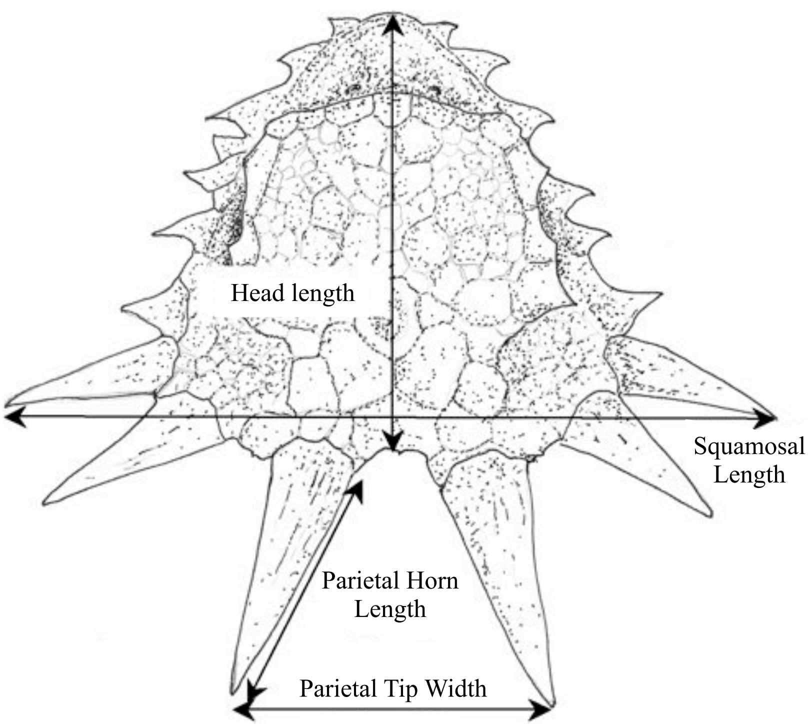
How the Horned Lizard Got Its Horns

Kevin V. Young,[1] Edmund D. Brodie Jr.,[1] Edmund D. Brodie III[2]*

www.sciencemag.org SCIENCE VOL 304 2 APRIL 2004


C
Expected survival
1.0
0.8
0.8
0.4
0.2
0.0
shrike-killed
live
-2.5
-1.4
-0.3
-0.8
1.8
2.9
Residual parietal horn length


D
Expected survival
1.0
0.8
0.8
0.4
0.2
0.0
shrike-killed
live
-3.4
-2.2
-1.1
-0.0
1.1
2.2
Residual squamosal horn length


Head length
Squamosal
Length
Parietal Horn
Length
Parietal Tip Width

Phylogenetic relationships of horned lizards (*Phrynosoma*) based on nuclear and mitochondrial data: Evidence for a misleading mitochondrial gene tree

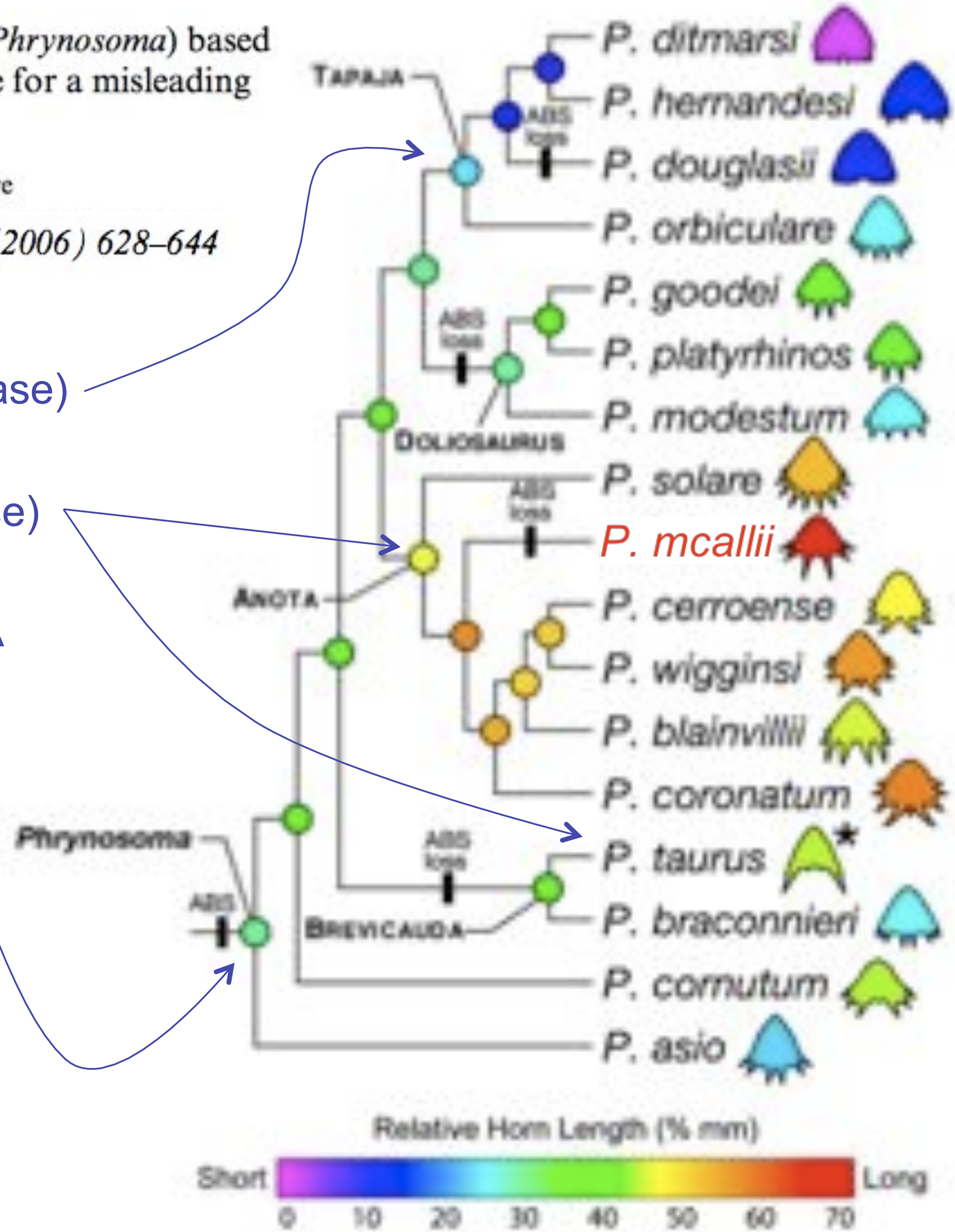
Adam D. Leaché *, Jimmy A. McGuire

Molecular Phylogenetics and Evolution 39 (2006) 628–644

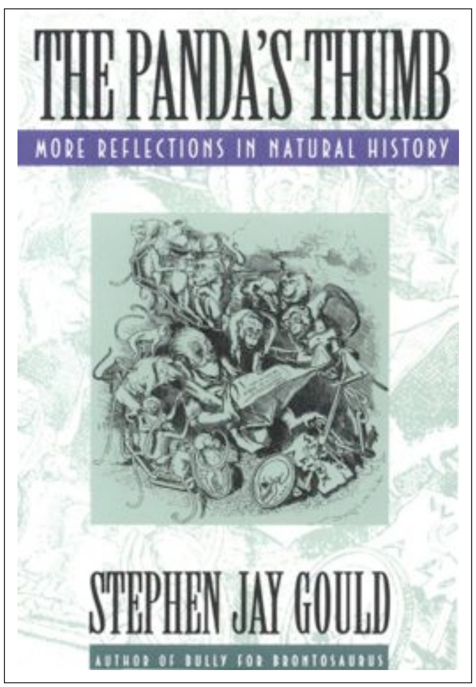
Evolution of shorter horns (decrease)

Evolution of longer horns (increase)

Medium-sized horns in the MRCA



A **pre-adaptation** is an existing feature that serves a NOVEL function



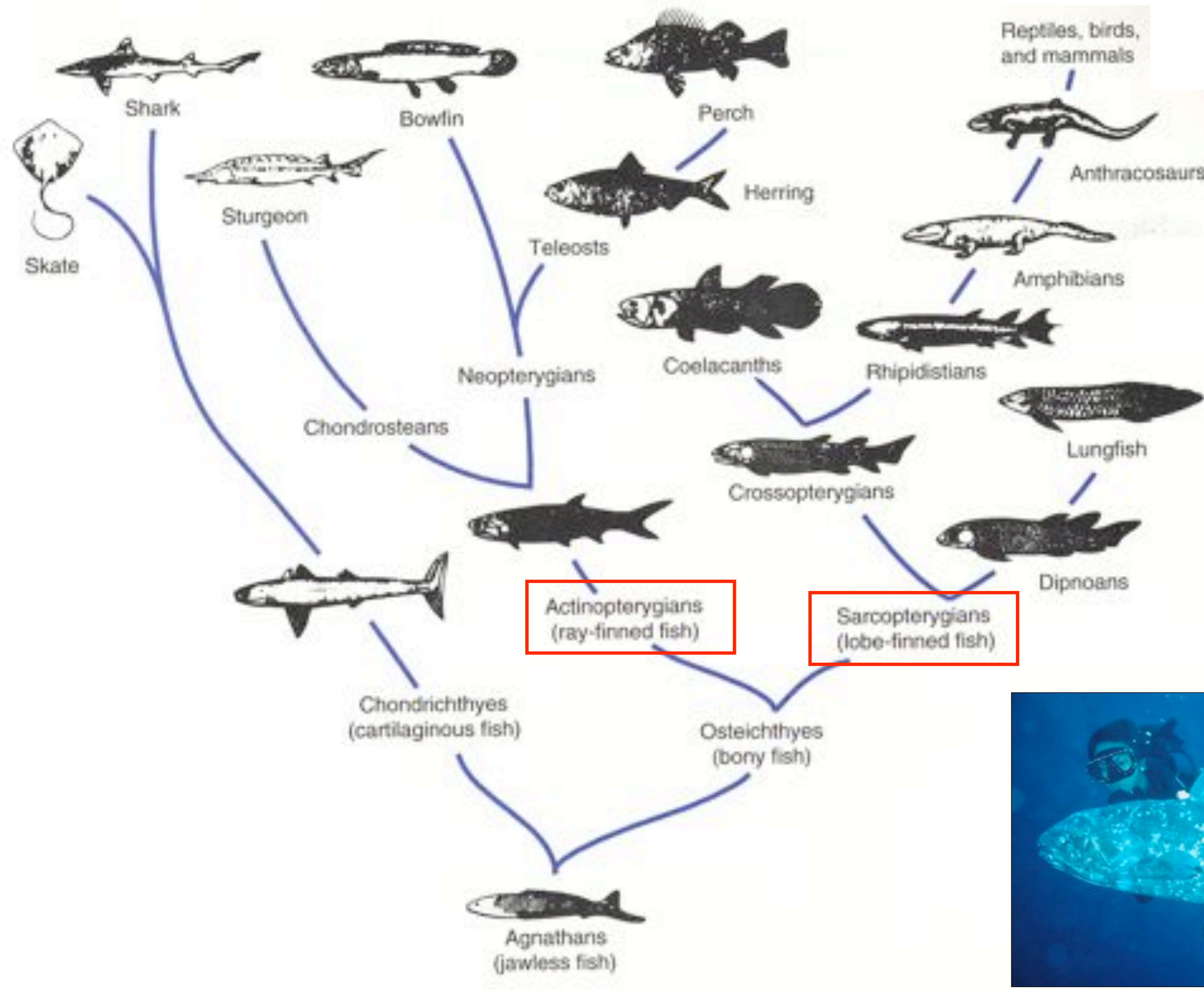


Figure 13.4 There are two main groups of bony fish: the Actinopterygians (which include nearly all modern fish) and the Sarcopterygians (from which humans, and all other tetrapods) evolved. Cartilaginous fish are a related group. Modified from Strickberger (1990). Reprinted by permission of the publisher.

The **fitness** of a genotype is the average lifetime contribution of individuals of that genotype to future generations

(1) probability of survival to reproductive age
(2) average number of offspring produced

Probability and average refer to **groups of organisms**, thus fitness is usually defined for a set of individuals (e.g., members of a particular genotype)

Absolute fitness

Lifetime total fitness (= total number of offspring)

Relative fitness

Degree to which individuals with a particular genotype fare compared to other genotypes in the population

GENETIC ESTIMATES OF ANNUAL AND LIFETIME REPRODUCTIVE SUCCESS IN MALE RED-WINGED BLACKBIRDS

PATRICK J. WEATHERHEAD AND PETER T. BOAG

Ecology, 78(3), 1997, pp. 884-896

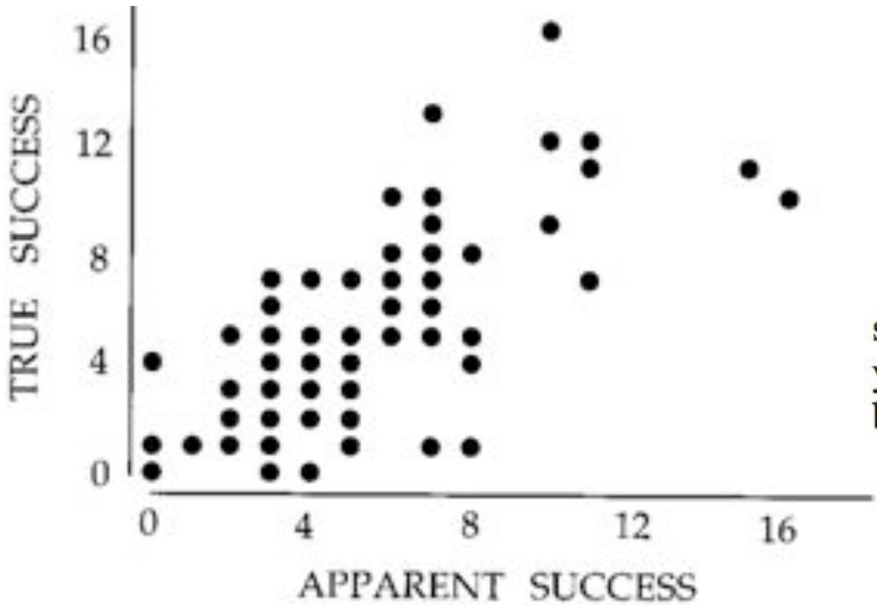


FIG. 1. True annual reproductive success (no. fledglings sired) relative to apparent annual reproductive success (no. young fledged from territory) for male Red-winged Blackbirds for all six years.

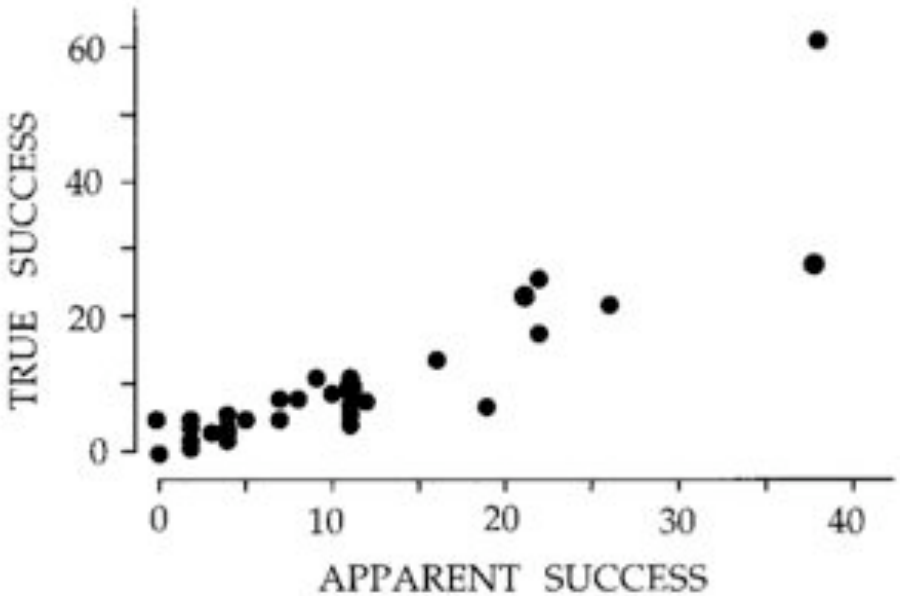
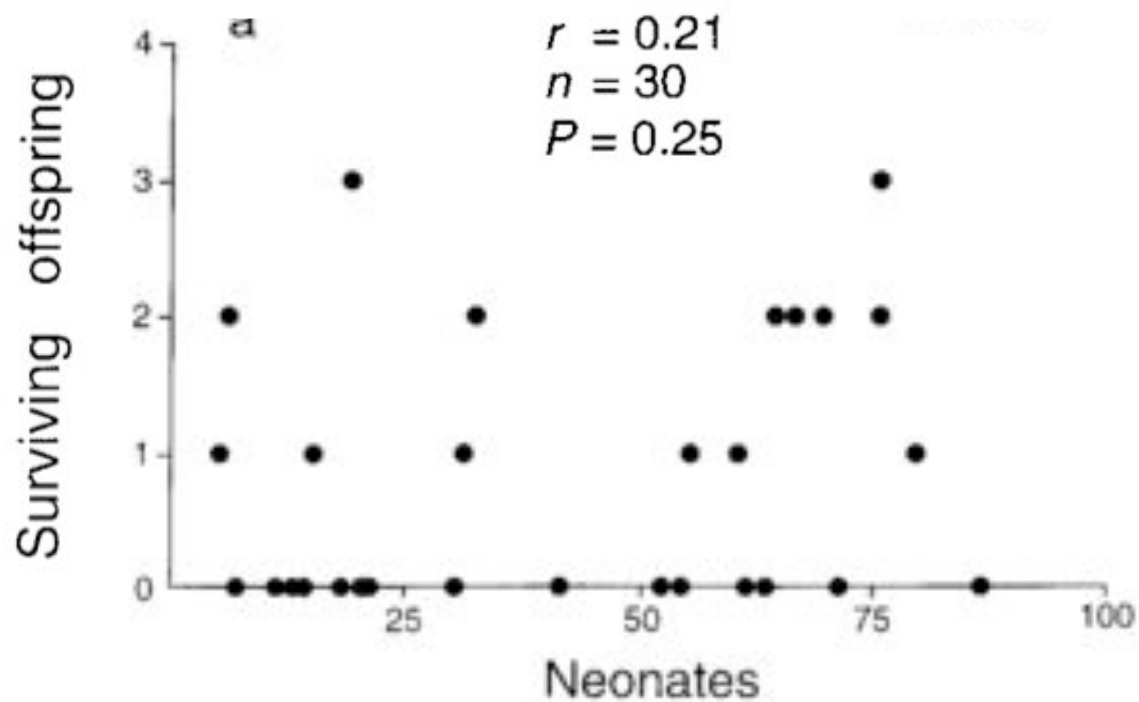


FIG. 5. True lifetime reproductive success (no. fledglings sired) relative to apparent lifetime reproductive success (no. young fledged from territory) for males.

OM Fincke and H Hadrys (2001) Evolution 55:762



See also F&H, box 6.3

Generalized notation...

Absolute $\overline{w}$	Relative $\overline{w}$				
$AA = 10$	$10/10 = 1.0$	1	1	$1-s$	1
$Aa = 8$	$8/10 = 0.8$	1	$1-s$	1	$1-hs$
$aa = 8$	$8/10 = 0.8$	$1-s$	$1-s$	1	$1-s$

Modeling natural selection...

Allele frequencies among gametes

Genotype frequencies among zygotes

Genotype frequencies among surviving adults

$$\overline{w}_{pop} = p^2\overline{w}_{AA} + 2pq\overline{w}_{Aa} + q^2\overline{w}_{aa}$$

$$AA = \frac{p^2\overline{w}_{AA}}{\overline{w}_{pop}}$$

$$Aa = \frac{2pq\overline{w}_{Aa}}{\overline{w}_{pop}}$$

$$aa = \frac{q^2\overline{w}_{aa}}{\overline{w}_{pop}}$$

Allele frequencies among mating adults

Genotype frequencies among offspring

Patterns of natural selection

Strength of selection (selection coefficients)

Allele frequencies

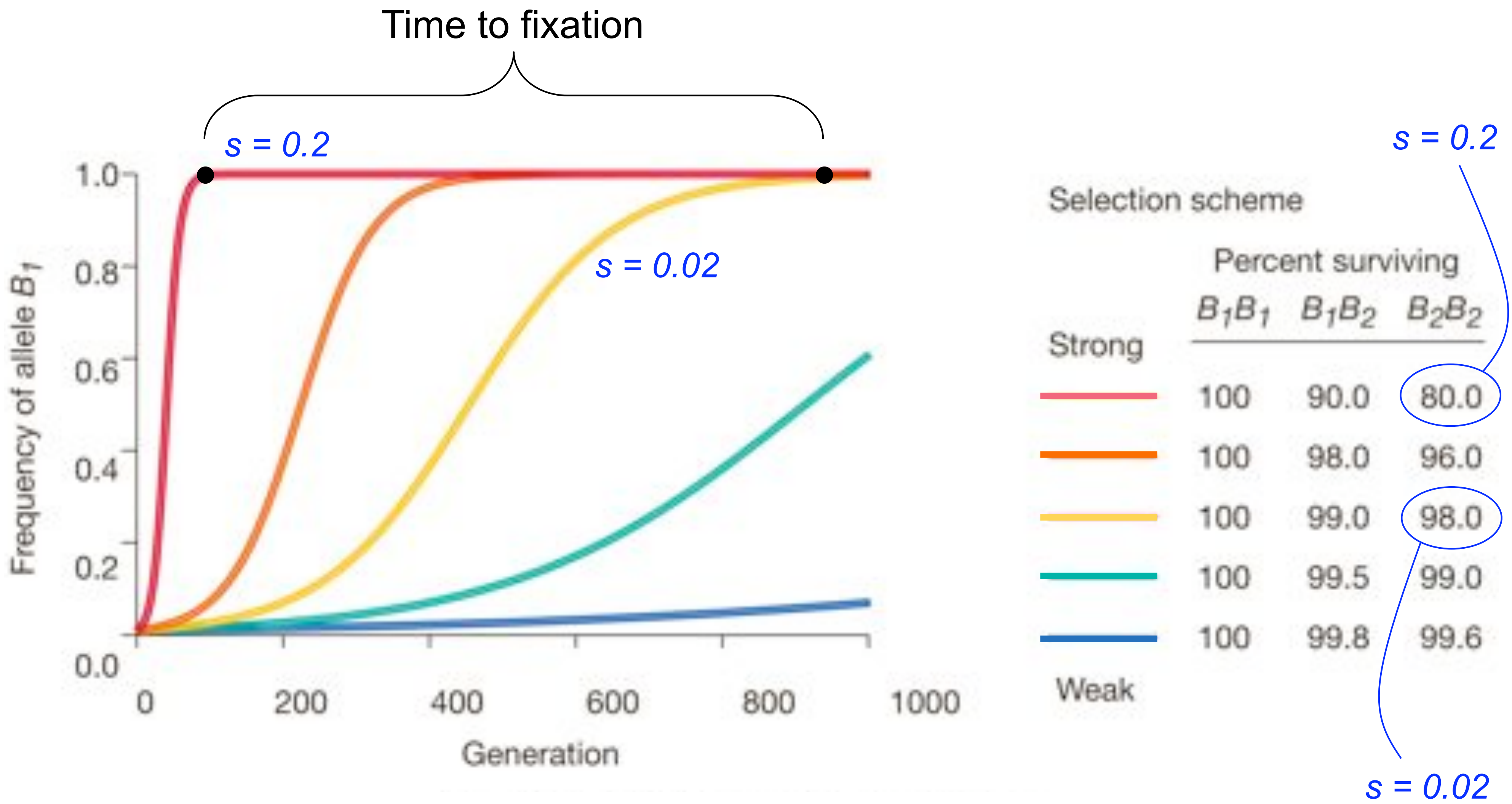
Dominance relationships

Heterozygotes & Homozygotes

Frequency dependence (positive & negative)

Interactions with other evolutionary forces (coming up…)

Strength of selection – selection coefficients



Emerging Infectious Diseases • Vol. 10, No. 3, March 2004

Antibiotic Selection Pressure and Resistance in *Streptococcus pneumoniae* and *Streptococcus pyogenes*

Werner C. Albrich,* Dominique L. Monnet,† and Stephan Harbarth‡

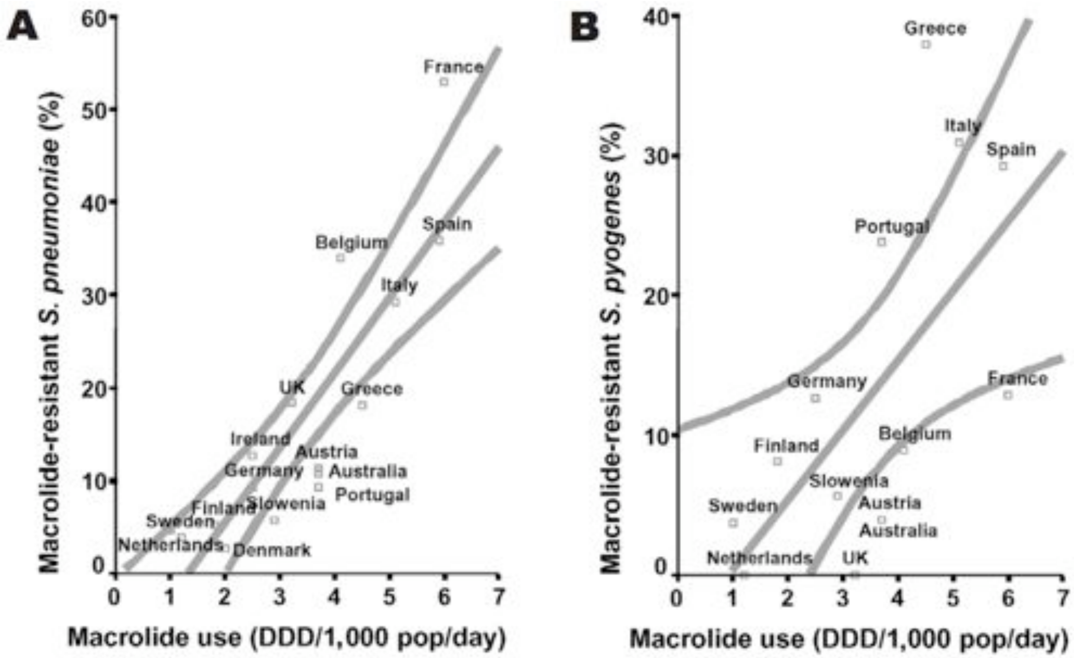


Figure 2. A. Relationship between macrolide use in the outpatient setting (horizontal axis) and prevalence of macrolide-resistant *Streptococcus pneumoniae* (vertical axis) in 16 industrialized countries. A regression line was fitted with 95% confidence bands ($r = 0.88$; $p < 0.001$). B. Relationship between macrolide use in the outpatient setting (horizontal axis) and prevalence of macrolide-resistant *S. pyogenes* (vertical axis) in 14 industrialized countries. A regression line was fitted with 95% confidence bands ($r = 0.71$; $p = 0.004$).

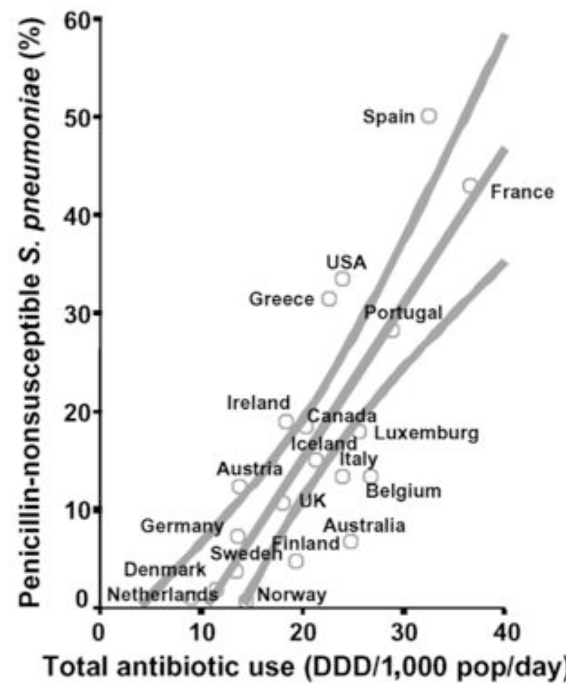
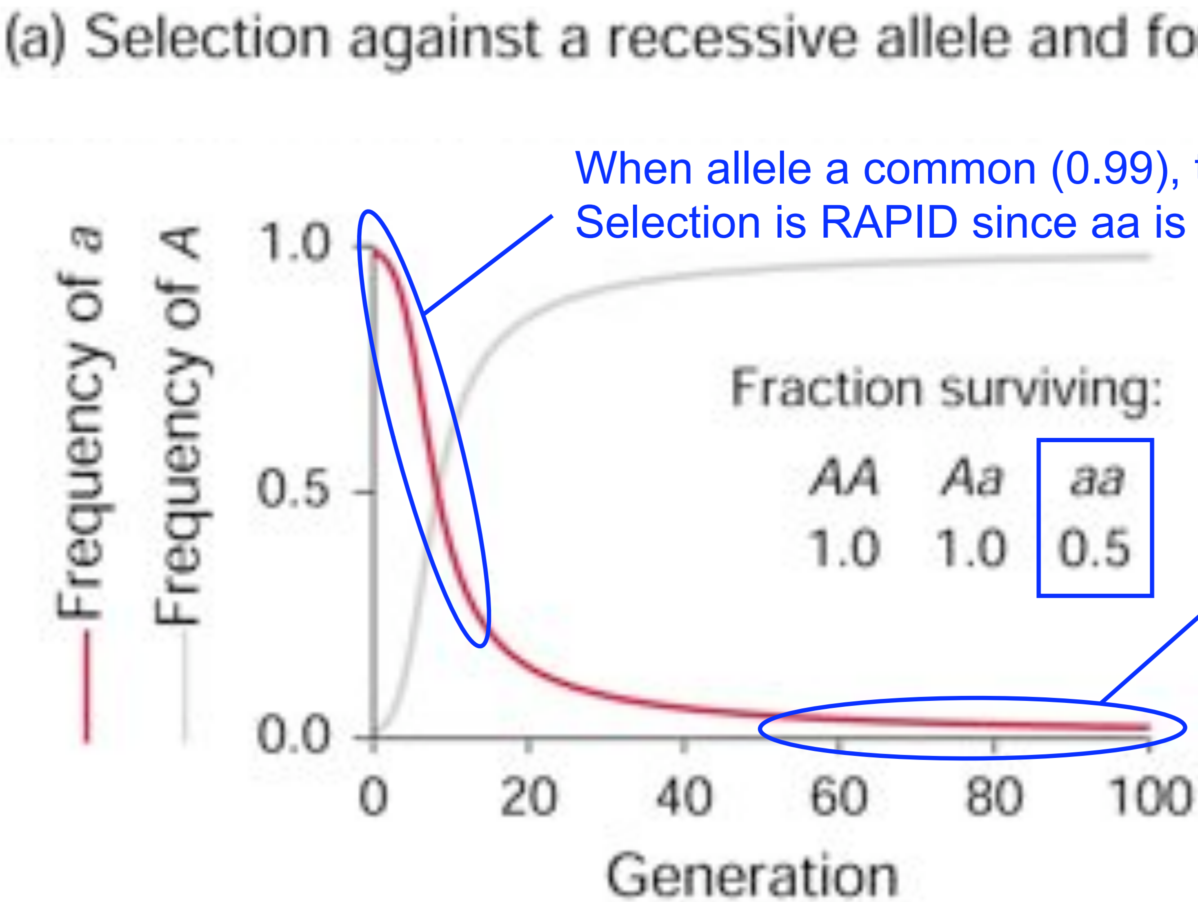


Figure 1. Total antibiotic use in the outpatient setting (vertical axis) versus prevalence of penicillin-nonsusceptible *Streptococcus pneumoniae* (horizontal axis) in 20 industrialized countries. A regression line was fitted with 95% confidence bands ($r = 0.75$; p < 0.001).

Dominance relationships interact with allele frequencies



When allele a common (0.99), there are many aa genotypes
Selection is RAPID since aa is exposed to selection

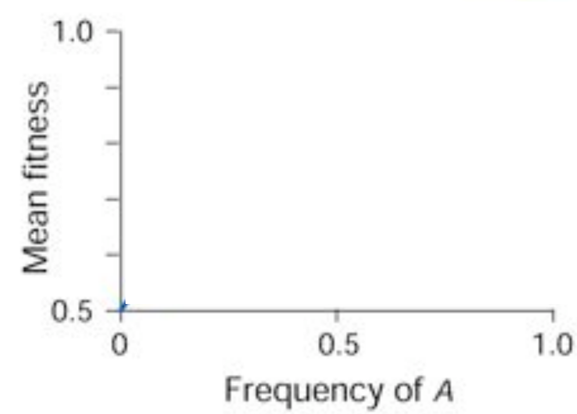
As allele a becomes rare, selection against it slows down

Selection cannot "see" a in Aa heterozygotes

Difficult to lose allele a entirely

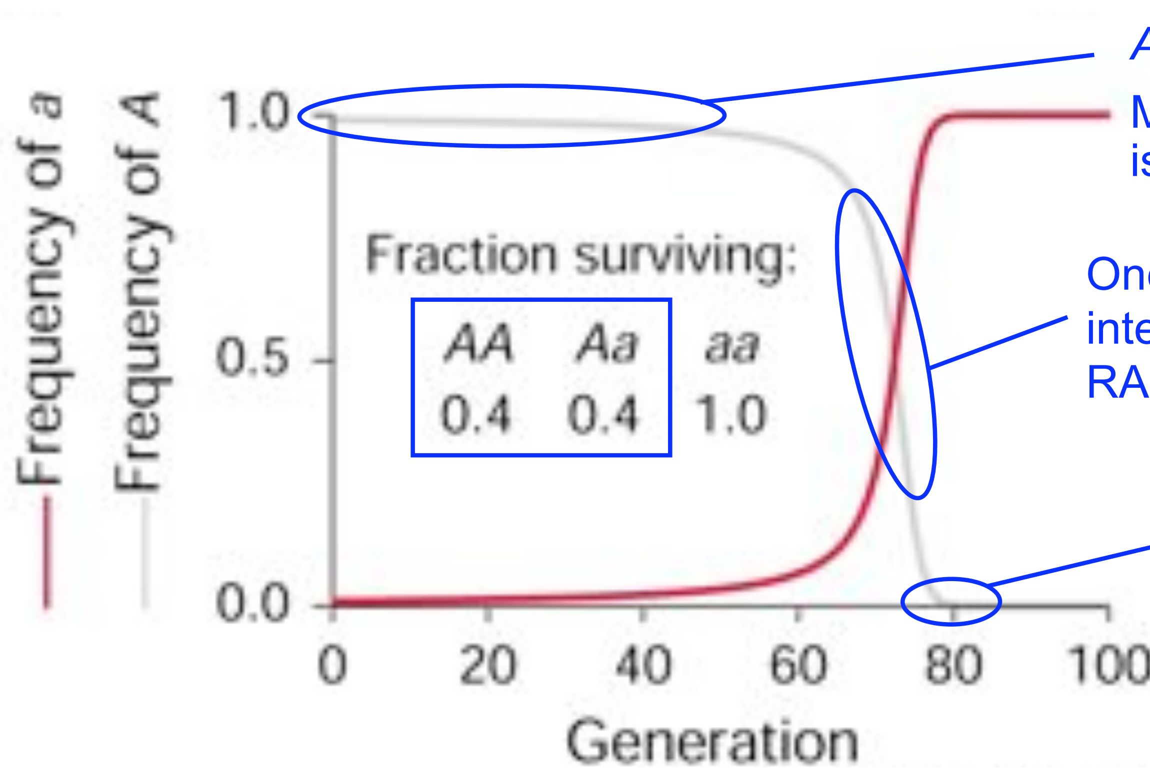
An **adaptive landscape** graphs the mean fitness of a population as a function of allele frequency

– where is a population is heading –



Dominance relationships interact with allele frequencies

(b) Selection for a recessive allele and against a dominant allele



A allele is very common (0.99)

Most individuals are *AA*, so the *A* allele is maintained initially

Once the frequency of *A* declines and is intermediate in frequency, selection is RAPID against the dominant *A* allele

Allele A is eventually lost (& allele a fixed) in the population

An **adaptive landscape** graphs the mean fitness of a population as a function of allele frequency

– where is a population is heading –

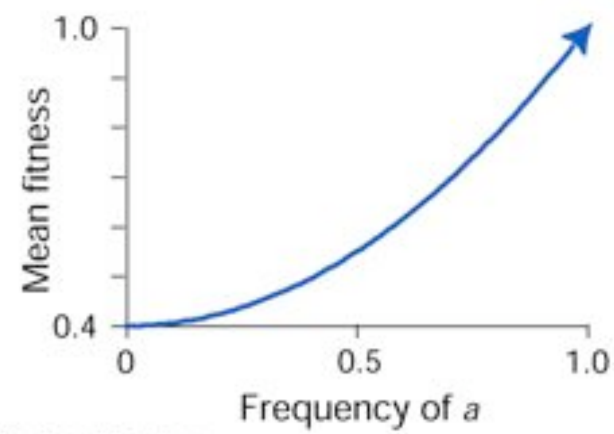


Fig. 3. Dominance relationships of *Mc1r* alleles. Dorsal coloration (mean and standard deviation for area under the spectral curve) for *Mc1r* genotypes showing the derived allele is dominant in *S. undulatus* and recessive in *A. inornata*. *n*, number of alleles sampled; "light" and "dark" refer to statistically distinguishable groups.

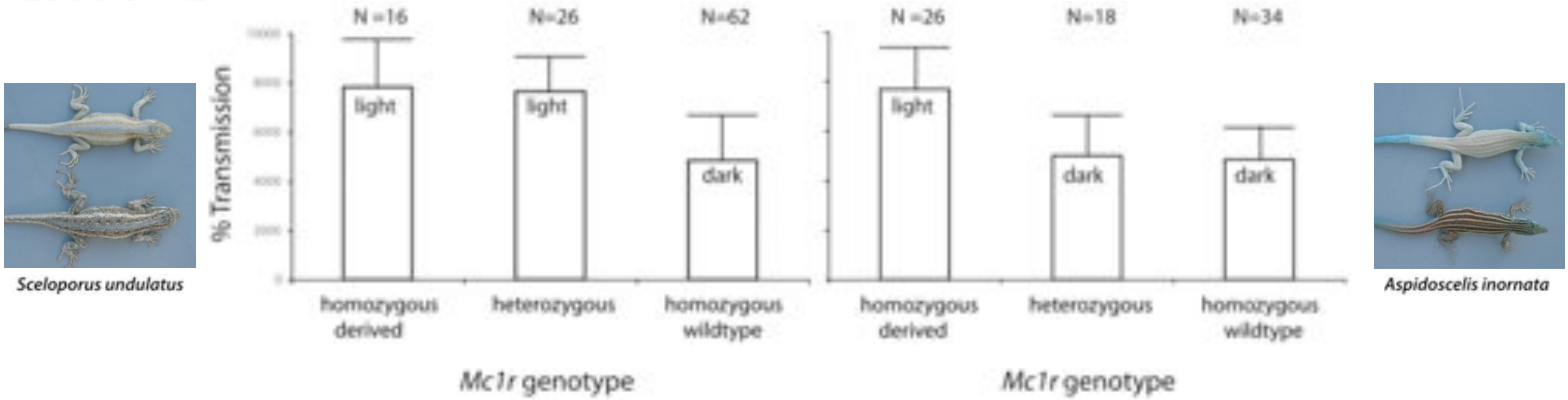
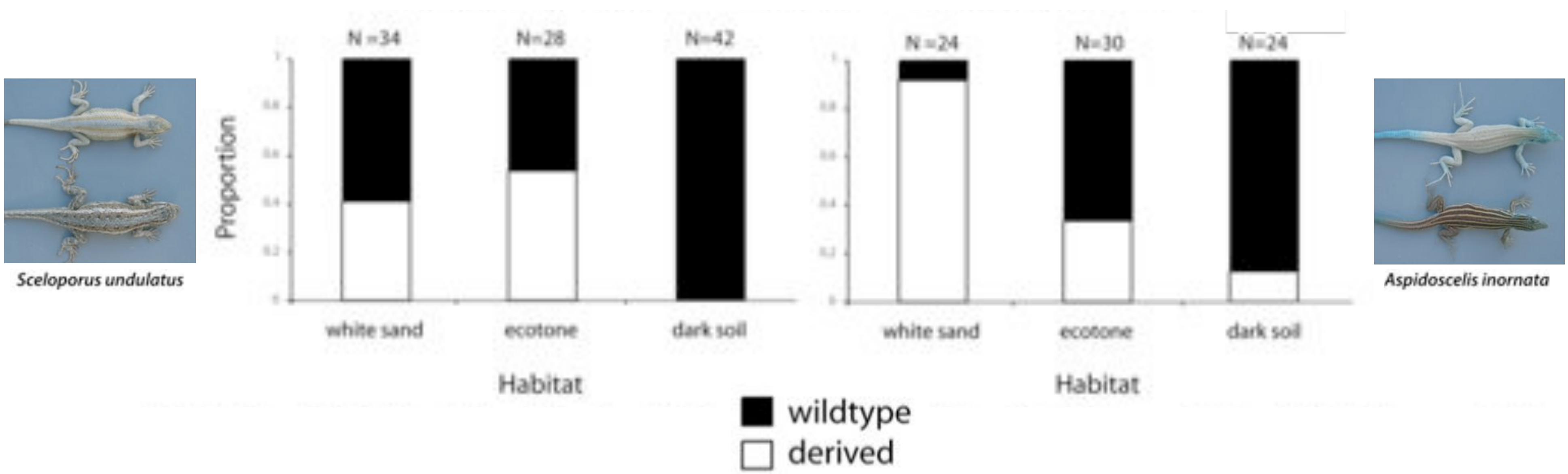


Fig. 4. Spatial distribution of *Mc1r* alleles in the wild for *S. undulatus* (derived *Mc1r* allele dominant) and *A. inornata* (derived *Mc1r* allele recessive). Proportion of wild-type (black) and derived (white) alleles across dark soil, ecotone, and white sand habitat. *n*, number of alleles sampled.



Selection for heterozygotes

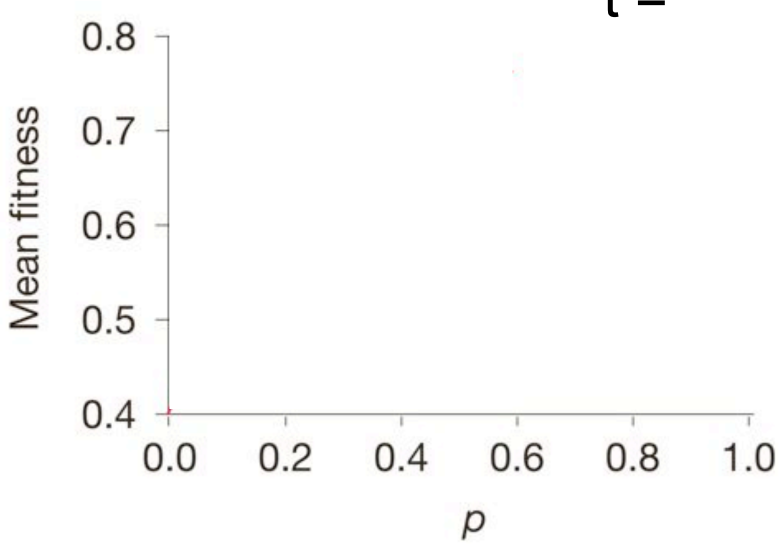
Heterozygote advantage • Overdominance

	$\bar{w}$	
AA	0.6	1-*s*
Aa	1.0	1
aa	0.4	1-*t*

s =
t =

BB	0.8	1-*s*
Bb	1.0	1
bb	0.8	1-*t*

s = t = 0.2



Equilibrium frequency of p given by…

$$\hat{p} = \frac{t}{s+t}$$

Selection against heterozygotes

Heterozygote inferiority • Underdominance

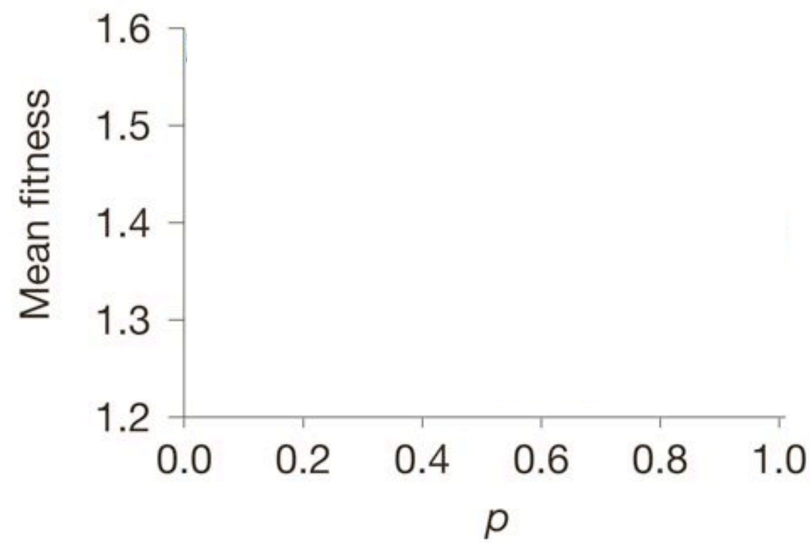
	$\bar{w}$		
AA	1.4	1-*s*	*0.875*
Aa	1.0	1	*0.625*
aa	1.6	1-*t*	*1.0*

s = -0.4
t = -0.6

Scale fitness values
(vary b/w 0 – 1)

$s = 0.875 - 0.625 = 0.25$

$t = 1.0 - 0.625 = 0.375$

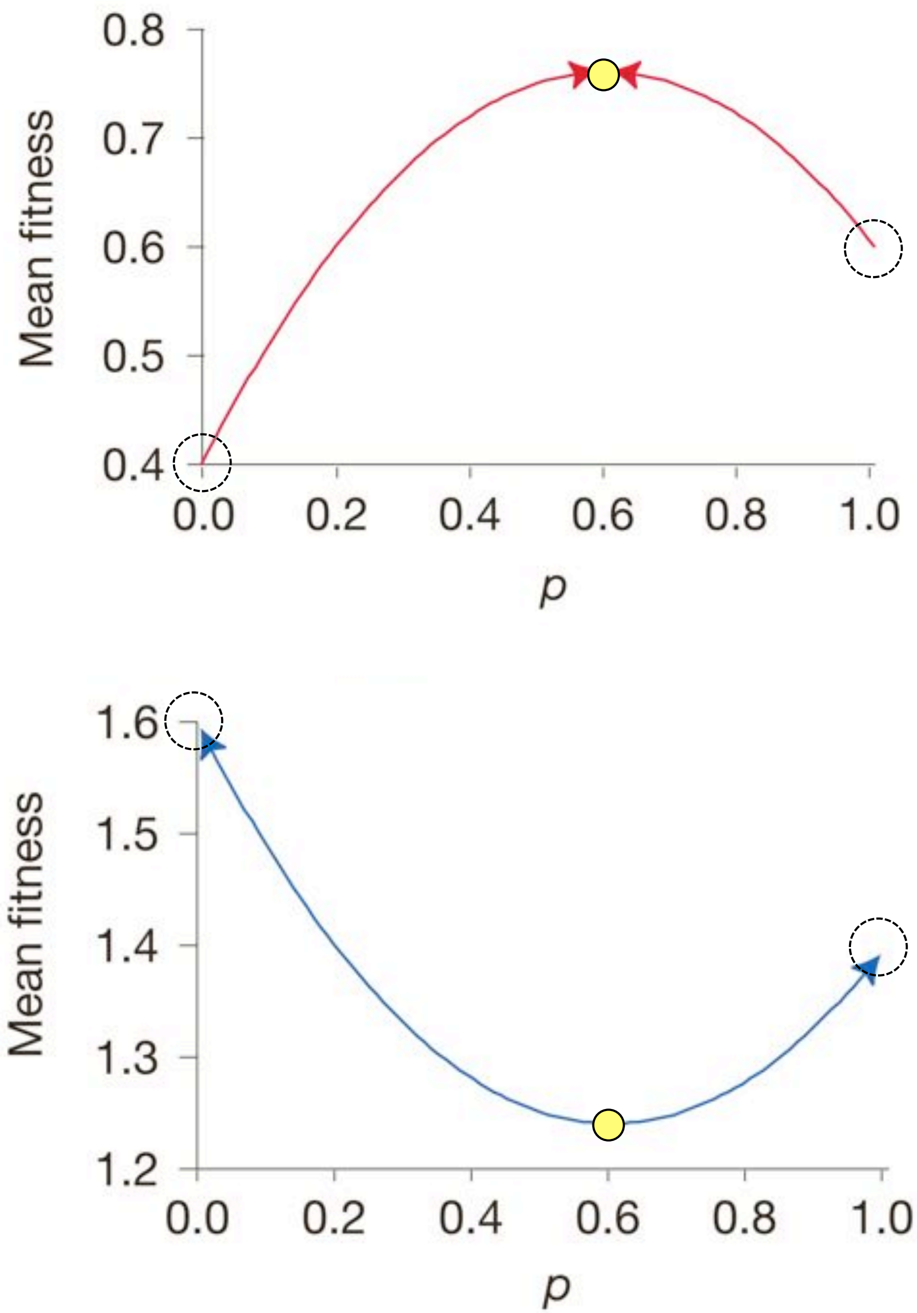


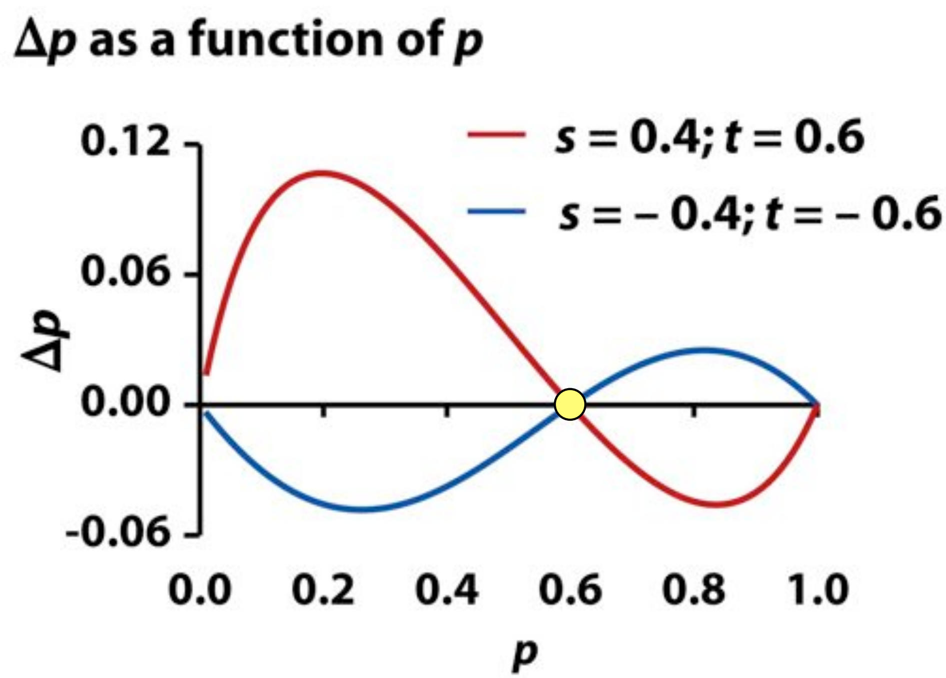
BB	1.0	
Bb	0.4	*Equilibrium?*
bb	0.8	

Equilibrium frequency of p given by…

$$\hat{p} = \frac{t}{s+t}$$

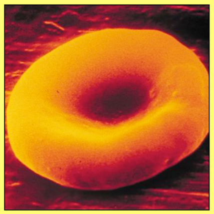
Equilibrium



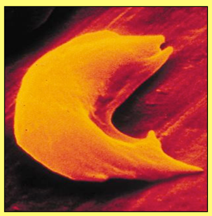


Selection for heterozygotes

Sickle cell anemia



Normal RBC (**A**)



Sickled RBC (**S**)

Malaria (*Plasmodium falciparum*)

Vector-borne infectious disease caused by protozoan parasite

Complex life cycle: reproduces inside human RBCs

Critical public health concern

Normal	**A/A**	Susceptible to malaria
Slightly afflicted by SCA	**A/S**	Slightly protected from malaria
Afflicted by SCA	**S/S**	Protected from malaria

Ward Watt, *Colias* butterflies



Phosphoglucose isomerase (PGI) plays a key role in allocating carbohydrates among biochemical pathways

Butterflies are ectothermic & fly only when body temperature is high

Selection should favor PGI variants with high catalytic efficiency (i.e., those that enable butterflies to metabolize glucose efficiently & allow them to fly quickly)

Allozymes differ in their functional properties & are correlated with the prevalence of genotypes in different environments

Do the allozyme alleles affect the fitness of Colias butterflies?

Colias meadii (high elevation sp.)

alleles 2, 3 common

2/2 & *2/3* relatively high activity @ low temps., but lose activity @ high temps.

Tested enzyme activity of genotypes @ various temperatures (10–50°)

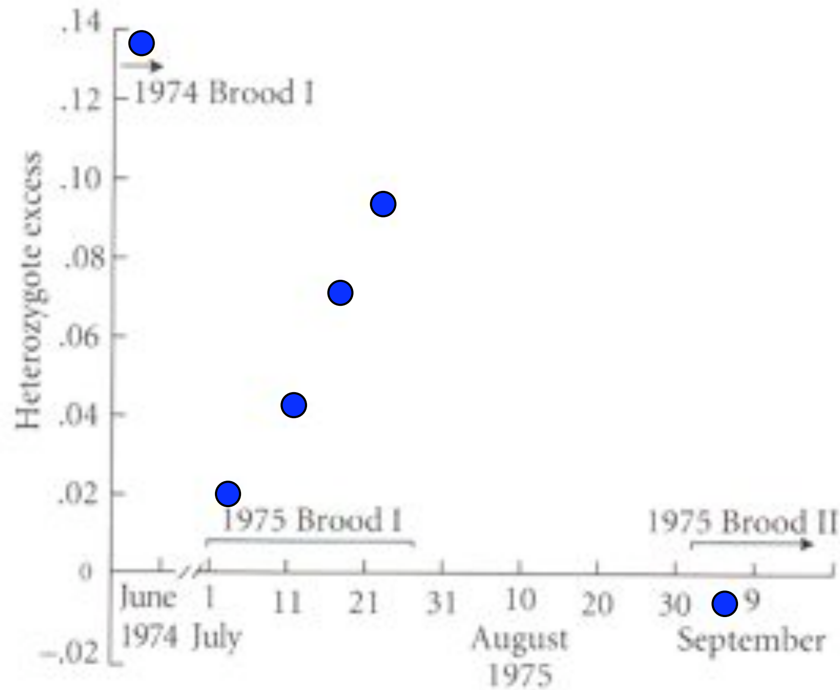
heterozygous genotypes (esp. *3/4*) had high efficiencies

alleles 3, 4 common

Colias philodice, C. eurytheme (lower elevations)

Allozymes differ in their functional properties & are correlated with the prevalence of genotypes in different environments

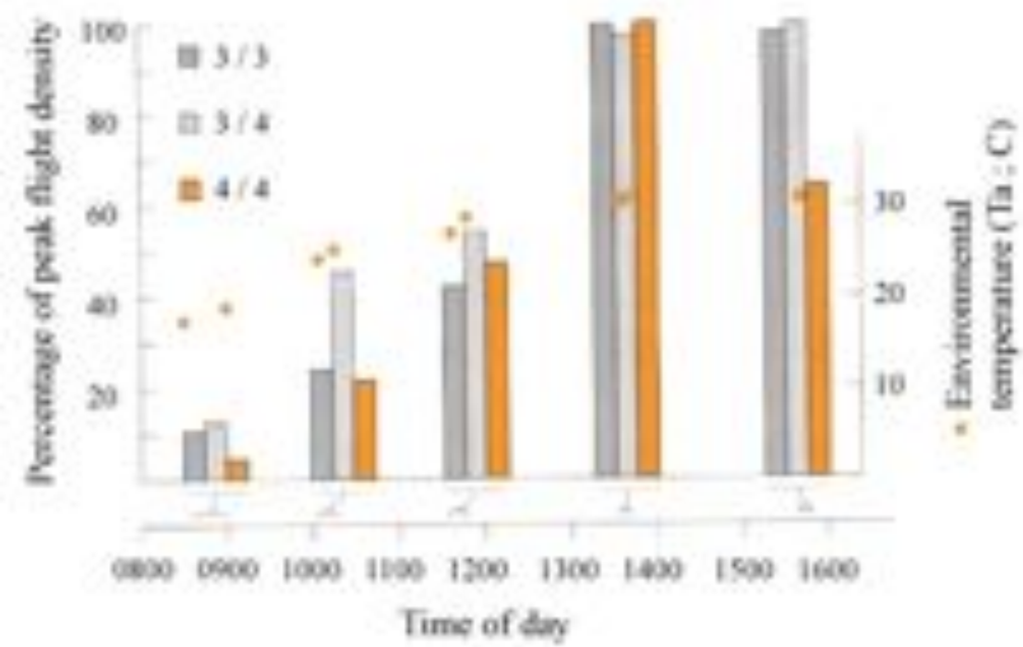
Do the allozyme alleles affect the fitness of Colias butterflies?



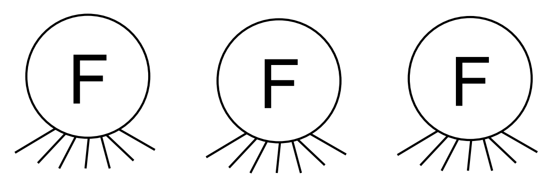
Given biochemistry, 3/4 genotypes should…

(1) fly more frequently

(2) fly a greater span of the day



Captured flying females, let them have babies & genotyped all offspring



etc…

3/4 males made up 44% of population, but accounted for 69% of all matings

Frequency dependent selection

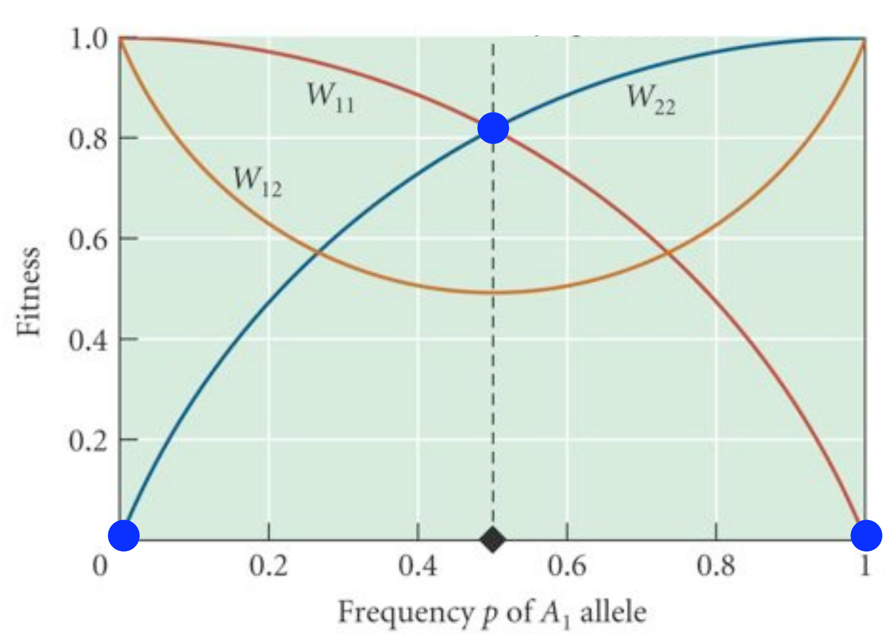
When the fitness values (of genotypes) varies depending on the FREQUENCY of the genotype in a population

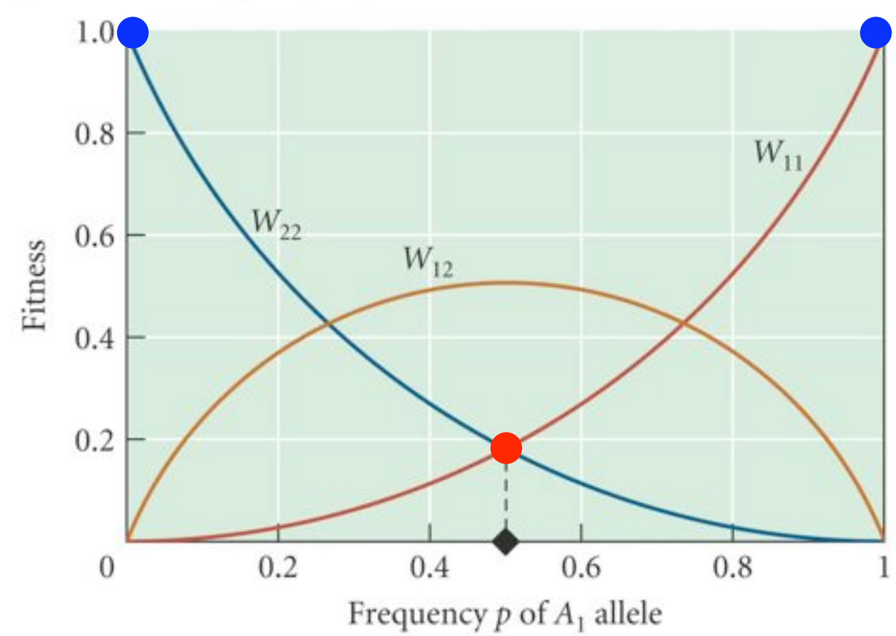
- **Positive frequency dependence**

  the MORE COMMON a genotype in a population, the GREATER its fitness

- **Negative frequency dependence**

  the RARER a genotype in a population, the GREATER its fitness





Positive frequency dependence

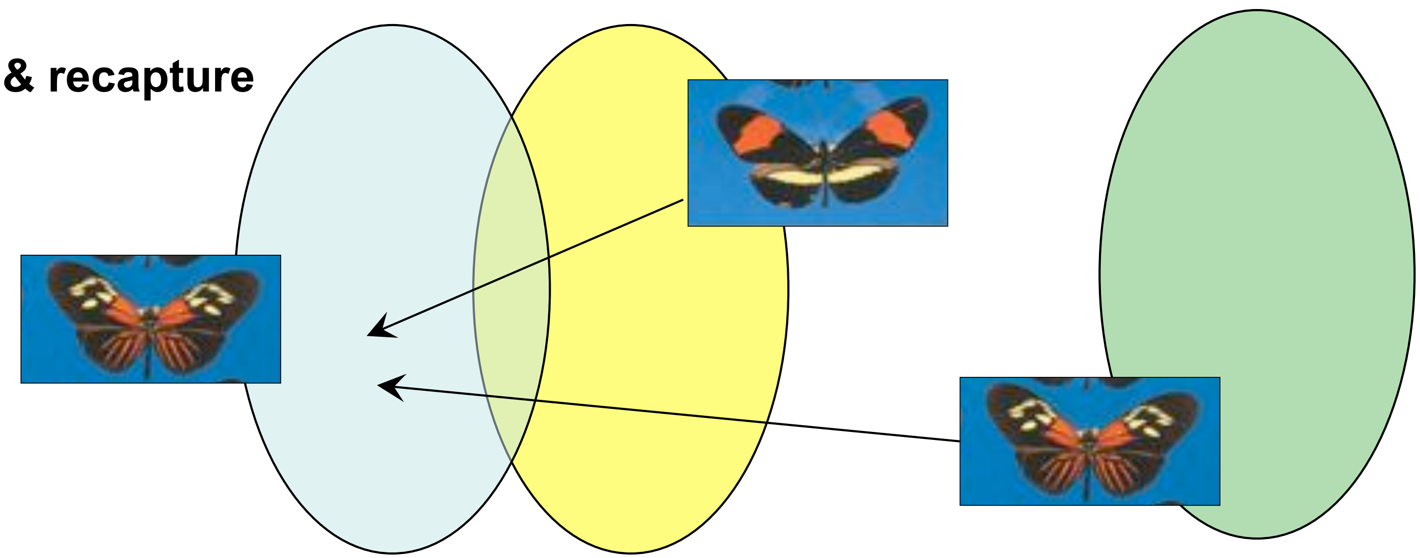
Heliconius erato

Unpalatable species with many distinctive geographic varieties, each variety is monomorphic

Adjacent varieties breed in zones only a few kilometers wide

Mallet & Barton (1989) suggested that gene flow between races is countered by positive frequency dependence

Mark & recapture



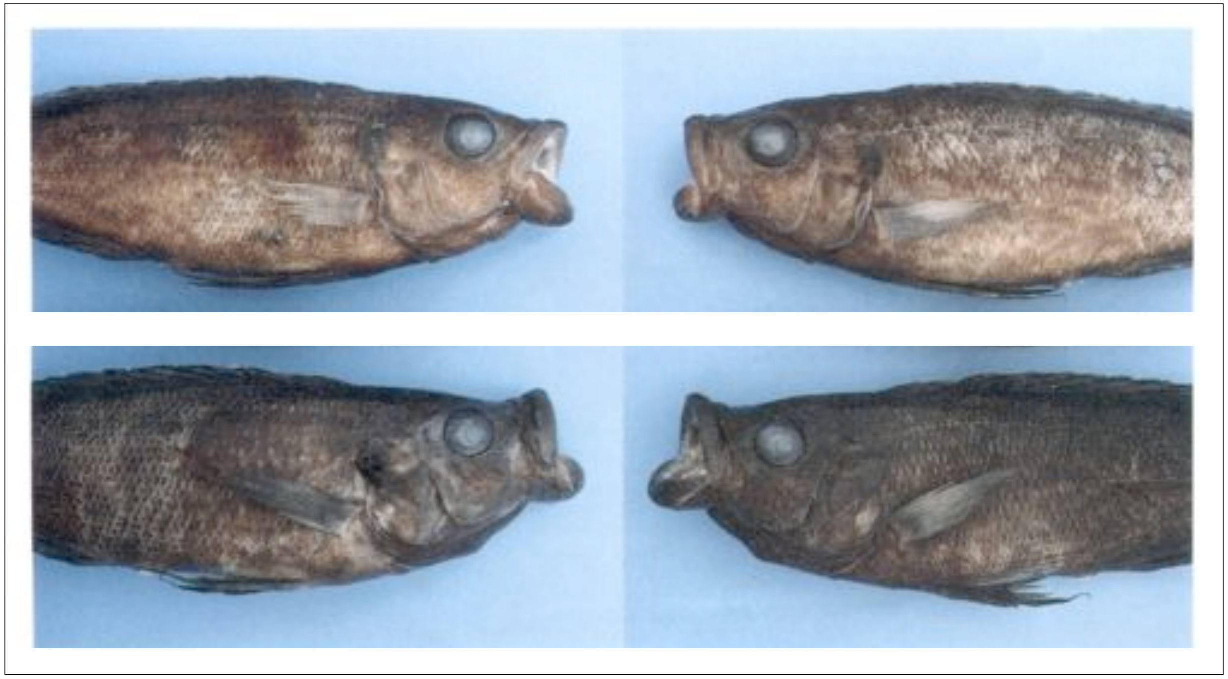
Predators learn to avoid butterflies of the most COMMON pattern, but attack (eat?) butterflies of UNCOMMON patterns they do not recognize

Negative frequency dependence

Frequency-Dependent Natural Selection in the Handedness of Scale-Eating Cichlid Fish

Michio Hori

SCIENCE • VOL. 260 • 9 APRIL 1993



Right-handed (dextral) feed on LEFT flank of prey

Left-handed (sinistral) feed on RIGHT flank of prey

Four tenets of natural selection…

(1) Individuals within populations are variable

(2) Variation is heritable

(3) Organisms differ in their ability to survive and reproduce

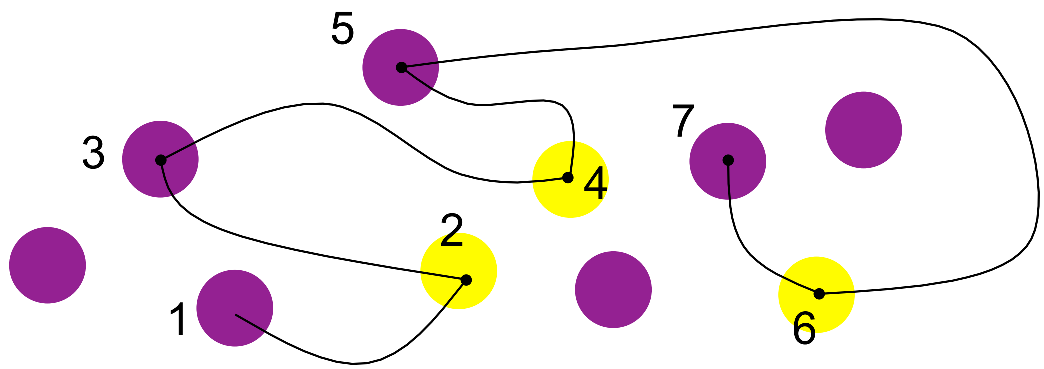
(4) Survival & reproduction are non-random

Dactylorhiza sambucina

Pollinated by bumblebees, but flowers are ***rewardless***

Orchids make pollinia (making pollen unavailable) & there is no nectar

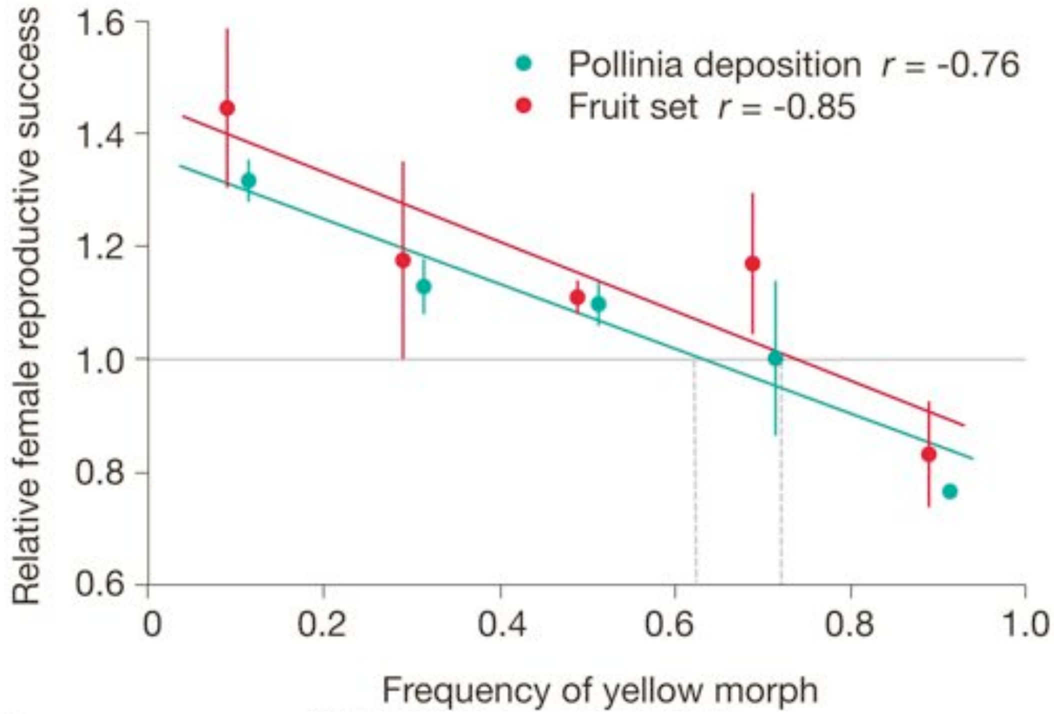
– pollination by deceit –

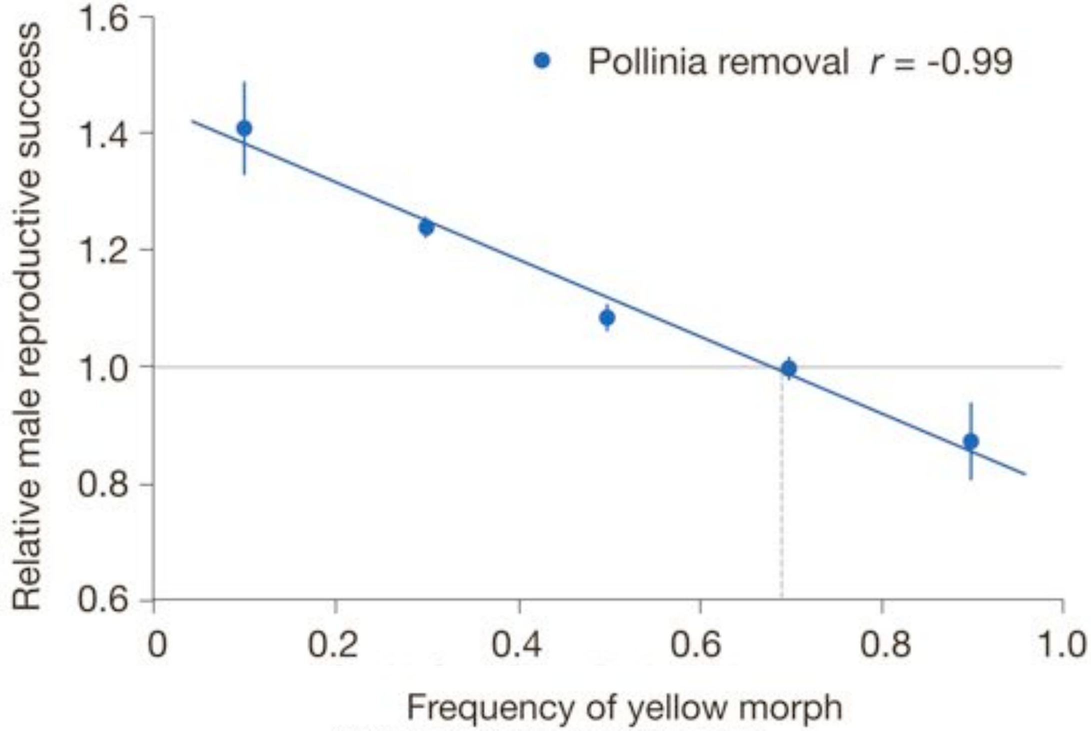


What does such movement mean for the number of times each type (color) is visited?

On average, which morph will receive more visits?

How will such visitation affect fitness?


Pollinia deposition r = -0.76
Fruit set r = -0.85
Relative female reproductive success
1.6
1.4
1.2
1.0
0.8
0.6
0
0.2
0.4
0.6
0.8
1.0
Frequency of yellow morph


Pollinia removal r = -0.99
Relative male reproductive success
1.6
1.4
1.2
1.0
0.8
0.6
0
0.2
0.4
0.6
0.8
1.0
Frequency of yellow morph

Multiple niches & polymorphism

Contrasting selection can maintain genetic diversity

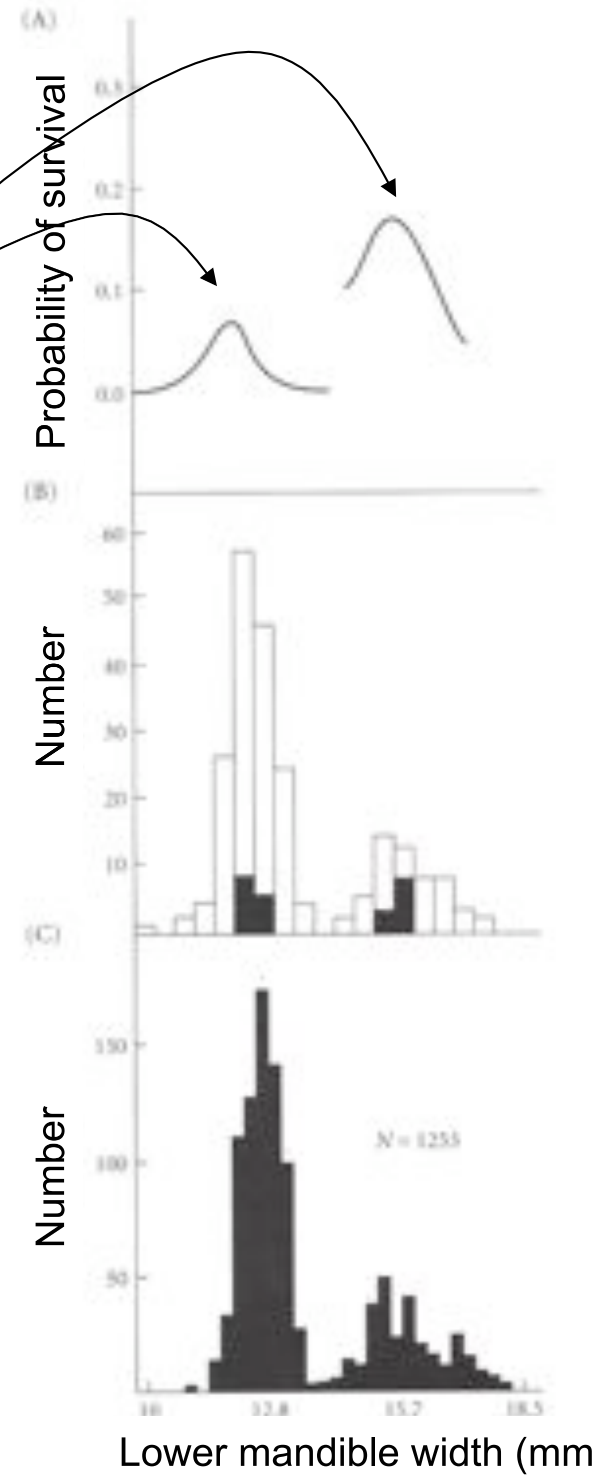
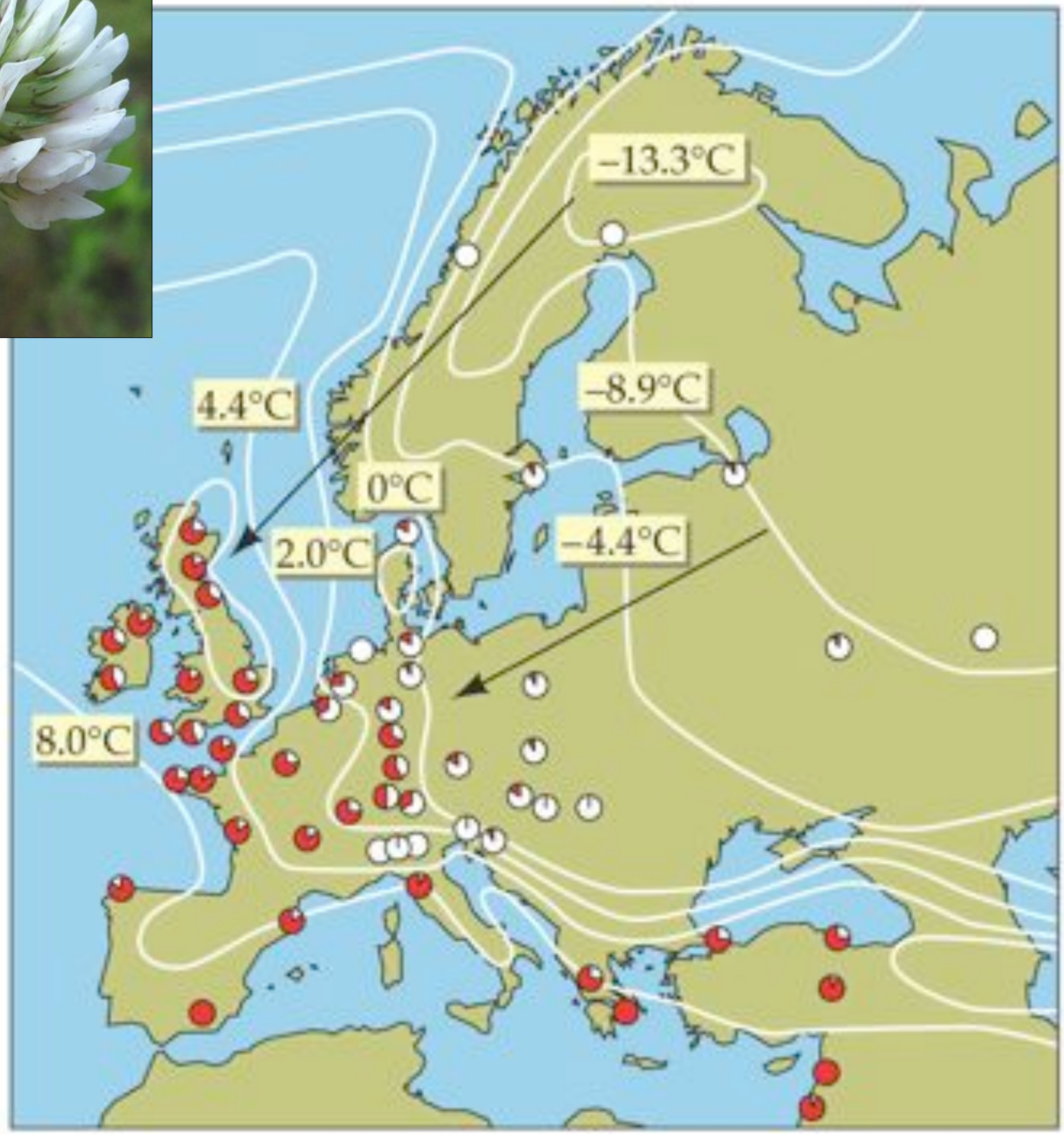


FIGURE 13.24 Multiple-niche polymorphism in the black-bellied seedcracker. (A) Probability of survival to adulthood of juvenile birds in relation to their lower mandible width, a measure of bill size. These curves are based on the data in (B), which shows the number of banded juveniles that survived (solid bars) and that did not survive (open bars). The distribution of lower mandible width among adults (C) is bimodal. The peak centered at 12.8 mm corresponds to recessive homozygotes, the other peak to heterozygotes and dominant homozygotes. (After Smith 1993.)



White indicates proportion of plants not producing cyanide

Red indicates proportion of plants producing cyanide