Real populations are *structured* in space and *finite* in size

These realities give rise to two evolutionary "forces":

1. Migration (the *movement* of alleles between partially isolated subpopulations),

2. Drift (the random *sampling* of alleles in reproduction and in non-selective mortality).

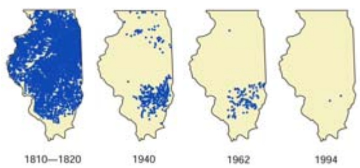
Migration tends to make subpopulations more *similar* to each other genetically.

Drift tends to make them more *different*.

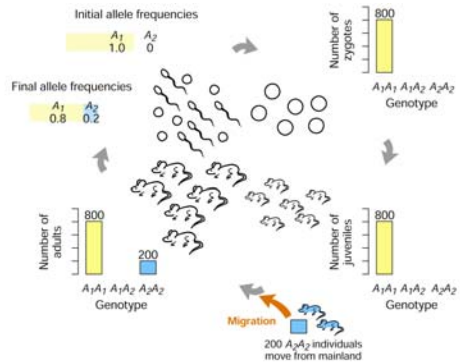
Biol 3410, 9 February 2009

The greater prairie chicken, *Tympuchus cupido pinnatus*

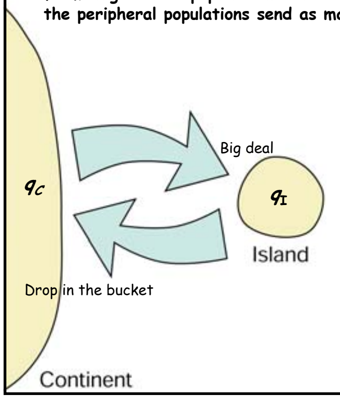
… and its habitat in the state of Illinois



Migration changes allele frequencies *if* the immigrants are *different*



Small peripheral subpopulations are affected more by immigration from large "core" populations than the other way around, even if the peripheral populations send as many migrants as they receive



The model is easy

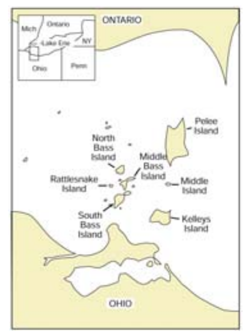
Ignoring the island's effect on the continent (which is tiny), the *migration*-selection balance model for the island (q_I) is *exactly* like that for the *mutation*-selection balance:

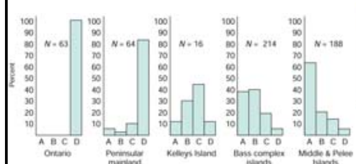
We have a term for the allele-frequency change caused by *migration* (Δq_{mig}) and a term for the allele-frequency change caused by *selection* (Δq_{sel}).

At equilibrium, they must balance each other exactly:

$$\Delta q_{mig} + \Delta q_{sel} = \Delta q_I = 0$$

Banded water snakes are conspicuous on rocky limestone islands





D fully banded
C,B partially banded
A unbanded

Interaction of migration and selection: a model for the water snakes

Let A_1 be the dominant allele for the banded pattern, with A_2 recessive for unbanded.

Let q be the frequency of A_2 on the islands, and assume $q = 0$ on the mainland.

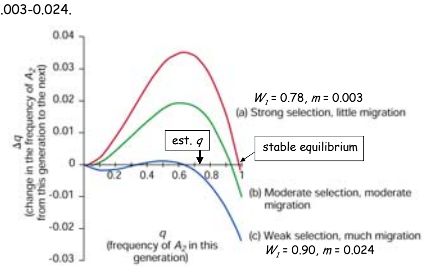
Then $\Delta q_{mig} = m(0 - q)$, where m (the migration rate) is the *proportion of immigrants*.

Δq_{sel} is our usual model for selection on a recessive allele, except that now the recessive homozygotes are *fitter* than the dominant homozygotes and heterozygotes.

Richard King and colleagues estimated W_1 (the fitness of banded snakes) as 0.78-0.90.

They estimated m as 0.003-0.024.

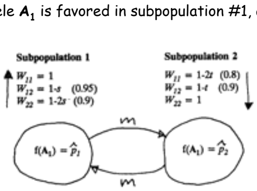
The curves show $\Delta q = \Delta q_{mig} + \Delta q_{sel}$ as a function of q, for three different choices of W_1 and m.

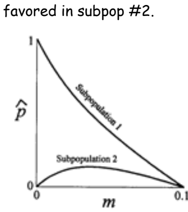


A symmetrical migration model for two subpopulations of equal size

Each subpopulation receives m (proportion) migrants from the other.

Allele A_1 is favored in subpopulation #1, and A_2 is favored in subpop #2.

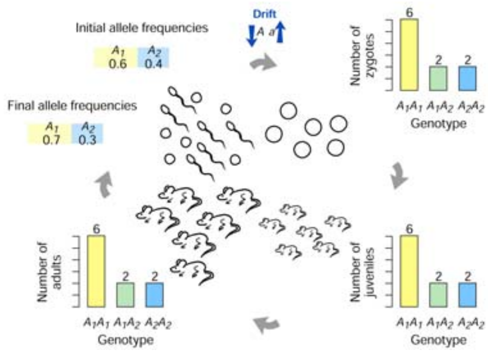




As the migration rate increases, the subpopulations become more similar in allele frequency, and above $m = 0.1$ they both become fixed for A_2.

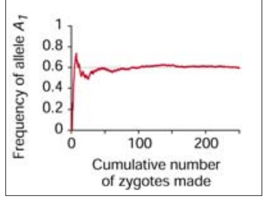
In a spatially variable world, migration can reduce local adaptation!

Drift: an inevitable consequence of sampling

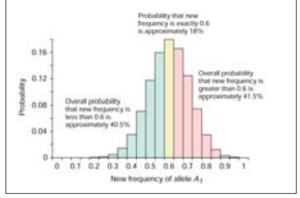


Sampling A_1 and A_2 gametes from a population with 60% A_1

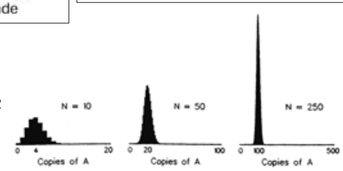
A typical sample: far from p = 0.6 at first, but closer and closer (on average) as more gametes are sampled.



Distribution of final outcomes for many such samples, when N = 10 zygotes (20 gametes).



Distributions of outcomes for populations of three different sizes, when p = 0.2 (20% **A**, 80% **a**).

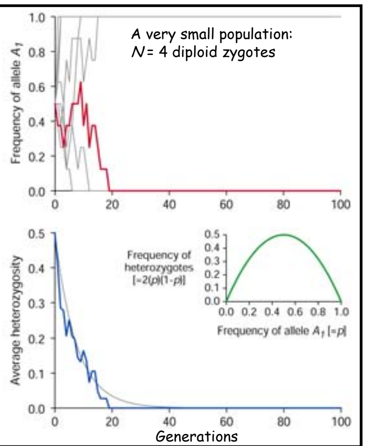


Drift happens because populations remember nothing!

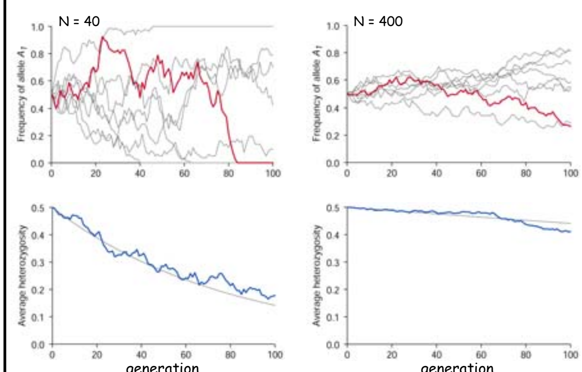
Each generation begins from where the previous generation ended.

Drift is *equally* likely to *increase* or *decrease* the allele frequency, going from the current generation to the next.

Thus random allele-frequency changes build on each other and eventually lead to fixation of one allele.



Rates of random allele-frequency change (and loss of heterozygosity) are inversely proportional to population size

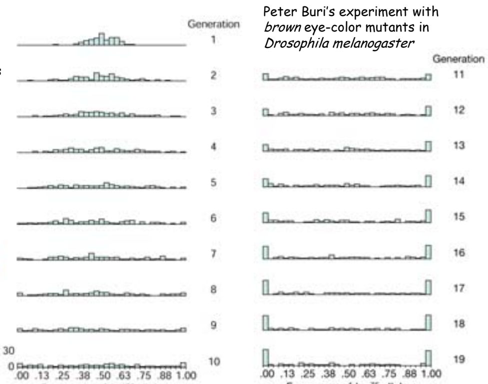


An allele's chance of fixation is equal to its present frequency

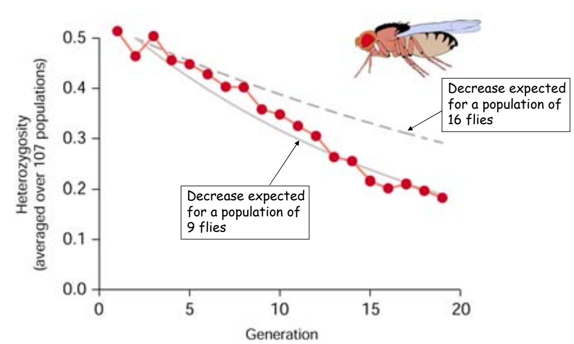
107 vials were set up with 8 male and 8 female heterozygotes (bw/bw^{75})

Eight males and 8 females were then selected randomly in each line, for each of the next 19 generations.

Peter Buri's experiment with *brown* eye-color mutants in *Drosophila melanogaster*

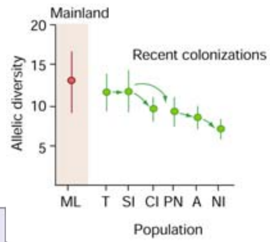


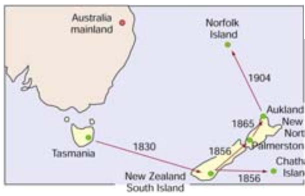
Allele frequencies diverged randomly, but the average (overall) heterozygosity decreased each generation



The "founder effect" is short episodes of strong drift (small *N*)

The silvereye, *Zosterops lateralis*





ML Australian mainland
T Tasmania
SI South Island
CI Chatham Island
PN Palmerston North
A Auckland
NI Norfolk Island

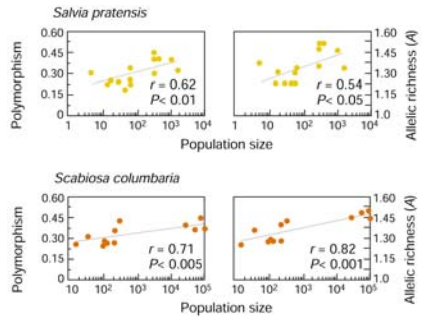
Small populations lose variation faster than large ones, so we expect them to have less variation at equilibrium under the combined effects of all four "forces" (mutation, selection, migration, drift)

Enzyme polymorphisms in flowering plants

Each point is a subpopulation.

"Polymorphism" is the proportion of polymorphic loci.

"Allelic richness" is the average number of alleles per locus.

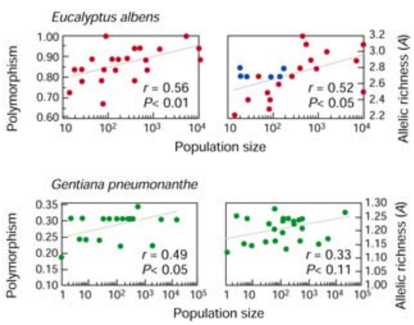


More enzyme polymorphism data for flowering plant subpopulations of different sizes

Eucalyptus is a tree. The blue points are small populations less than 250 meters from each other.

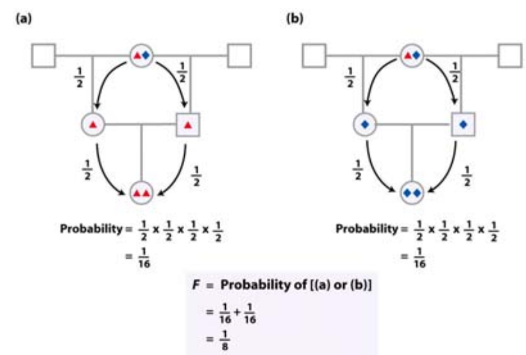
Note that both measures of polymorphism are absolutely much higher for *Eucalyptus* than for the other three species, which are flowering herbs.

Question: What might explain this difference?

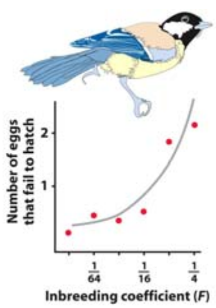


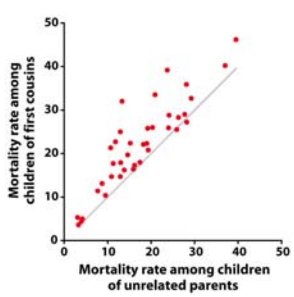
Inbreeding can be viewed as extremely strong genetic drift.

A child of half-siblings is homozygous at 1/8 of its genetic loci for alleles inherited "identical by descent" from its double-grandparent.



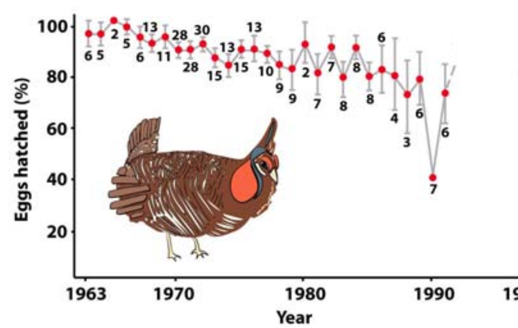
This increases the offspring's homozygosity, including its homozygosity for rare deleterious recessive alleles.





Genetic drift can be viewed as *weak inbreeding*: it also increases homozygosity, including homozygosity for rare deleterious recessives.

Prairie chickens in Illinois showed declining fitness …
… until individuals "migrated" in from populations in other states.



The Illinois populations are less variable genetically at unselected loci than populations in other states (but they weren't 100 years ago*).

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 signficantly 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).

Summary

Migration makes subpopulations more *similar* to each other by mixing their gene pools.

It is a "strong" evolutionary force (*i.e.,* a "fast" process).

It can *increase* genetic diversity *locally*, by bringing new alleles into a population (including ones that are not locally favored by selection).

It may also *decrease* genetic diversity *globally*, by causing the fixation of alleles that are favored in certain subpopulations.

Drift makes subpopulations (and species) more *different* by causing random fixations of neutral or effectively neutral alleles.

It is "strong" and "fast" in smaller populations, but "weak" and "slow" in larger populations.

On average, it always *decreases* genetic diversity. (As some alleles are fixed, others are lost.)

In small populations (where drift is "strong"), fitter alleles will sometimes be among those lost, and deleterious recessives may be among those fixed.