Evolutionary Time

Proportion Genotype of Type A

Environment changes to favor A

1

Suppose a mixture of genotypes in a population, of which one is 'Type A.'

What happens to the frequency of Type A when Environment changes to favor it?

Documented examples of such change:
- Industrial melanism in Biston betularia pepper moths
- Pesticide resistance in insects
- Antibiotic resistance in pathogens

What We Would Like to See

Maybe the next best thing?

Examine different populations in which one might expect selection to differ.

See if behavior is, in fact, locally adapted.

Three criteria for local adaptation:

1. Geographic variation in a trait
2. Variation at least partly genetically-based
3. Genetic variation in the trait consistent with geographic variation in some environmental factor affecting fitness

Case Study #1: Local Adaptation in Feeding Preference in the Spider, Agelenopsis aperta

Site

Habitat

Proportion Attacked

Attack Latency (sec)

Arizona

Riparian

0.25

55.0 (0.3)

New Mexico

Grassland

0.90

2.6 (0.3)

CRITERION 1 MET!

Reichert and Hedrick found that spiders in Arizona populations attack less vigorously than spider populations in New Mexico.

Agelenopsis aperta builds funnel webs, opening out onto silken platform.

The spider sits at funnel entrance, running out when insects fall onto platform.
Criterion 2 (differences genetically-based) can be tested with 'common garden' experiment.

Spiders originating from each population and reared in a 'common garden' environment maintain differences in behavior even in F2 generation.

<table>
<thead>
<tr>
<th>Site</th>
<th>Habitat</th>
<th>F2 Attack Latency (sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizona</td>
<td>Riparian</td>
<td>70.0 (15.2)</td>
</tr>
<tr>
<td>New Mexico</td>
<td>Grassland</td>
<td>14.1 (6.6)</td>
</tr>
</tbody>
</table>

CRITERION 2 MET!

Is there an agent of selection?

Possibility #1. Predation Risk

Experiment: Put bird-exclusion cages over some webs, but not others. Record spider disappearance in both treatments at both sites.

Disappearance due to birds is equal to:

\[\% \text{ spiders remaining in bird-exclusion treatment} - \% \text{ spiders remaining in control treatment}\]

<table>
<thead>
<tr>
<th>Site</th>
<th>Habitat</th>
<th>% Disappearance Due to Birds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizona</td>
<td>Riparian</td>
<td>33; 21</td>
</tr>
<tr>
<td>New Mexico</td>
<td>Grassland</td>
<td>4; 6; 3</td>
</tr>
</tbody>
</table>

Spiders in riparian habitat are more vulnerable to predators than spiders in grassland habitat, hence more cautious.

CRITERION 3 MET!

Mean Amt. Of Prey per Day (mg)

<table>
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<tr>
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<th>Habitat</th>
<th>Mean Amt. Of Prey per Day (mg)</th>
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<tbody>
<tr>
<td>Arizona</td>
<td>Riparian</td>
<td>80</td>
</tr>
<tr>
<td>New Mexico</td>
<td>Grassland</td>
<td>29</td>
</tr>
</tbody>
</table>

BUT. Possibility #2. Spiders in riparian habitat have more food available than spiders in grassland habitat, hence could afford to be more cautious.

In either case, CRITERION 3 MET!
Summarizing Case for Local Adaptation in *Agelenopsis aperta* populations:

1. Geographic differences in behavior.
   riparian spiders are more 'hesitant' than grassland spiders in attacking prey.

2. Differences are at least partly genetically-based.
   differences remain after rearing in 'common garden'.

3. Differences in behavior associated with differences in factor affecting reproductive success.
   predation and food abundance both higher in riparian habitat than grassland habitat.

Funnel web spider video - Starts at 2:46
http://www.youtube.com/watch?v=utKkMUJI9qM

Case Study #2: Local Adaptation in Feeding Preference in Garter Snakes

Garter snakes tend towards aquatic lifestyle, often feeding on aquatic prey.

*Thamnophis elegans* populations vary:

• some populations take aquatic prey.
• other populations are terrestrial and specialize on the land slug *Ariolimax*.

Ariolimax slugs occur on land, but mainly along the coast of California.

Snakes collected from coastal populations show strong preference for slugs; snakes collected from inland populations show little response to slugs.

Snakes smell with their tongue, inserting tongue into Jacobson's organ in roof of mouth.

Rate of tongue flicking is good measure of food preference.
This geographic difference is due to differences in **TASTE**. Coastal snakes tongue-flick more at slugs than do inland snakes.

Naïve, newborn snakes raised in common garden show same population differences.

AND...

Hybrid offspring show slug preferences intermediate between two parental stocks.

**CRITERION 2 MET!**

In this case, case for Criterion 3 (an agent of selection that accounts for the population differences)... ...seems obvious. Coastal snakes eat slugs because slugs are there!

**BUT... why do the inland snakes refuse slugs??**

Possibly because inland snakes also refuse leeches!

Leeches live in ponds where snakes are found and, if ingested, could kill snake.

Slugs are nutritionally poorer than fish.

Coastal populations have higher net assimilation efficiency for slugs

Both populations assimilate fish equally...

**Net assimilation efficiency**

fraction of assimilated energy from food remaining after digestive costs are subtracted

**TRADEOFF! CRITERION 3 MET!**

Case Study #3: Local Co-Adaptation of Toxicity and Resistance in Newts and Garter Snakes

Rough-skinned newt *Taricha granulosa* is defended by tetrodotoxin (TTX) in tissues.

**DEADLY!**
Tetrodotoxin (TTX)
- neurotoxin, affects nerves & muscles
- blocks pores of Na+ channel proteins
- toxin found also in fugu (pufferfish)

Sympatric populations of the common garter snake *Thamnophis sirtalis* have evolved resistance to TTX.

Resistance positively correlated with TTX tolerance of Na+ channel in skeletal muscle.
**Partially-overlapping changes in amino acid composition of channel protein account for change in resistance.**

**Coevolution!**

- Hotter the spot, the greater the snake’s resistance to newt
- AND the greater the level of TTX in newt tissues.
- Two hotspots are independently evolved.

**Reciprocal coevolution:**

- Local adaptation by the snake,
- Is followed by local counter-adaptation in the newt,
- Then more local adaptation by the snake,
- and so on...

**Three criteria for local adaptation:**

1. Geographic variation in a trait
2. Variation at least partly genetically-based
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**Killer Whales**

- Do we see local adaption in killer whales?
- Killer whale pods are matriarchal (mothers, daughters, and sons form groups).
- Killer whales are found throughout marine waters, from poles to tropics.
- We will discuss differences among killer whales found in the Northern Pacific.
Transients also ‘quieter’ than residents. Video!

Different types are genetically distinct, according to mtDNA analysis.

"resident/transient mtDNA differences greater than human-chimp differences"

But are behavioral differences genetically based?

NOT KNOWN. CRITERION 2 NOT YET MET.

Agents of selection of various differences not yet worked out in detail.

Example. Cause of vocalization differences between residents and transients not understood.

CRITERION 3 NOT YET MET.

* New information: These types may soon be re-classified as subspecies or even separate species!

Gombe and Mahale Chimps Show Many Differences

CRITERION 1 MET!

<table>
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<th>Tool Use</th>
<th>Greeting</th>
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<tr>
<td>Gombe</td>
<td>Eat palm nuts</td>
<td>Probe for termites only</td>
<td>Arms raised, grasping branches</td>
</tr>
<tr>
<td>Mahale</td>
<td>Eat no palm nuts</td>
<td>Probe for tree-ants only</td>
<td>Handshakes</td>
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</table>
What about Criterion 2? Are differences genetically-based?

very difficult to do common garden experiment or hybrid crosses. Not yet done.

Differences very possibly due to cultural processes, involving imitation and even teaching.

**CRITERION 2 NOT MET!**

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Why do populations differ? Unclear.

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**Ditto for CRITERION 3!**

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**Summarizing search for local adaption in chimpanzee behavior:**

1. Are there geographic differences in chimp behavior? **YES**
2. Are differences in chimpanzee behavior genetically-based? **Probably Not**
3. Are differences due to differences in some factor affecting reproductive success? **Not Known**

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**Behavior as Agent of Selection:**

Local Adaptation for Coat Color in the Rock Pocket Mouse, *Chaetodipus intermedius*

Research by UA's Michael Nachman and colleagues

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Dark and light forms found at each of 4 sites

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Typical habitat for rock pocket mouse, showing light and dark surface types

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Photo from Hoekstra & Nachman, *Molecular Ecology* 2003
At each site, mice are found on matching background.

In Pinacates, dark morph genotypes have 4 amino acid changes in the Mc1-r receptor, a protein known to affect hair color in mammals.

In the 3 New Mexico populations, dark morph individuals do not differ from light morph individuals at Mc1-r locus.

Therefore, different gene(s) involved in those populations!

‘neutral gene’ shows different pattern

Morph frequencies along a longitudinal transect

Summarizing color coat story:
- Spatial variation in mouse coat color corresponds to spatial variation in soil color.
- Dominant mutation at one gene accounts for dark phenotype in Pinacates but not in other populations.
- ‘neutral gene’ shows different spatial pattern.

What is agent of selection?
Agent of selection on coat color is presumed to be visually-guided predation by raptors. Here, behavior is the driving force for morphological adaptation.

Local Adaptation at White Sands

The white gypsum sand spans 275 square miles and is 'younger' than the surrounding dark soils.

Three species of brown lizards in scrub; all species have mainly white forms in the dunes.

Loss-of-function mutations may be more common than others, giving natural selection the 'opportunity' to change the phenotype given an agent of selection.
Two possible issues encountered when using the Local Adaptation approach:

1. There might be geographic variation but it might not reflect local adaption.
2. We might not find local adaptation when we might expect to.

**Issue #1:** Geographic variation might not reflect local adaptation.

A. Variation due to **genetic drift**
   defined as random changes in allele frequencies from one generation to next

B. Variation due to **founder effect**
   defined as founding of a new population by a non-representative subset of genotypes from source population

**Example.** Song dialects in island populations of some birds appear to reflect a founder effect.

**Issue #1 cont’d:** Geographic variation might not reflect local adaptation.

C. When there exist multiple ‘solutions’ to the same ‘problem’.

**Example**
Jumping spiders have many ornaments and diverse courtship.

southwest species, *Habronattus pugillis*, varies strikingly within populations, from one sky island population to the next.

*Mating in jumping spiders involves visual and...*

*Habronattus* species of jumping spiders show tremendous diversity of courtship displays.

Damian Elias

peacock spider

http://www.youtube.com/watch?v=BMjniVovzI8
http://www.youtube.com/watch?v=gBOkV04kF54
**Hypotheses**

1. Habitats differ on different ranges. Some agent of selection related to habitat generates differences between males. Perhaps different signals transmit better on the different ranges. **THIS IS A LOCAL ADAPTATION HYPOTHESIS, but there is no evidence for it...**

2. Sexual selection favors males with 'extravagant' traits. But exactly what trait is not so important. Different mutations arise in different populations, resulting in evolution of different signals, each of which are attractive. **NOT A LOCAL ADAPTATION HYPOTHESIS** Some limited evidence for this...

**Issue #2: Why no geographic variation where expected?**

**Possible Explanations**

- no genetic variation in trait
- migration (gene flow)
- historical lag
- constraints on selection

**Example**

Population comparisons of hostplant learning in pipevine swallowtails

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In East Texas, pipevine swallowtail lays eggs on 2 host species that differ in leaf shape (narrow v. broad)

Female learns the leaf shape of host that is currently most abundant and suitable for young.
In Appalachian mountains of Virginia, *pipevine swallowtail* lays eggs on just 1 host species with 1 leaf shape (broad). Yet females in this population learn leaf shape in common garden experiments as well as East Texas females.

**In other words, NO LOCAL ADAPTATION**

**Summary: WHY NO LOCAL ADAPTATION?**

1. Learning not costly? Not likely.
2. No genetic variation in trait? Not likely either.
3. Gene flow erodes population differences? **Maybe!**
5. Constraints on selection. **Maybe!**

The need to learn other tasks may maintain ability to learn leaf shape. Selection is **constrained**.

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**Less than ideal traits in nature:**

1. Imperfect mimicry
2. Imperfect lens camera eye

And...

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**Stomach brooding of young in *Rheobatrachus* frogs**

Seems less than ideal, but good enough!

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**The Panda Principle**

“The panda’s thumb provides an elegant zoological counterpart to Darwin’s orchids. An engineer’s best solution is debarred by history. The panda’s true thumb is committed to another role, too specialized for a different function to become an opposable, manipulating digit. So the panda must use parts on hand and settle for an enlarged wrist bone and a somewhat clumsy, but workable solution. The sesamoid thumb wins no prize in an engineer’s derby.”

— Stephen Jay Gould
Panda Principle suggests that what evolves is not what is the best solution to a problem, but the most workable solution. Natural selection takes path of least resistance. (but why ‘resistance’?)

Bolas spider makes a ‘minimalist web’. At end of the hanging line is a small drop of glue.

Bad design? No, works great, capturing lots of… male moths. drop of glue contains chemicals that mimic sex pheromone of certain moths.

Why don’t moths evolve to stop responding?

In Sonoran desert, some whiptail lizard populations reproduce without sex but not without courtship.

Sonoran spotted whiptail (Cnemidophorus sonorae) populations consist of parthenogenetic females (= females lay unfertilized eggs that hatch into viable females). Females engage in pseudocopulation with each other. Pseudocopulation triggers hormonal changes necessary for ovulation and egg laying.

Wasted time… extra predation risk… why does natural selection not remove it?

Loss of copulation presumed to require a gradual process of many, small genetically-based changes. Process may be constrained by an adaptive valley where intermediates have reduced fitness.