Population Genetics: Limits to Adaptation

# Introduction

Organisms are generally assumed to exhibit traits that are adaptive to the specifics of the environment in which they are found, as a result of natural selection. Some studies have indicated, however, that certain traits appear to be maladaptive, yet they are maintained within a population. This maladaptation may be a result of genetic constraints (such as a trait that is genetically correlated with another trait that is changing under selection), recent or fluctuating changes in selective pressures, conflicts between natural selection and sexual selection (for example, the long tail feathers of male peacocks), or gene flow (the movement of genes between two or more populations). The latter is the focus of this module.

# Importance

The role of gene flow in limiting adaptation has been debated by biologists. However, there is evidence from field and lab experiments to indicate that gene flow can be an important factor and may help explain the persistence of maladaptive traits in some populations.

# Questions

How is gene flow measured? What conclusions can be drawn from these measurements?

# Variables

|  |  |
| --- | --- |
| FST | fixation index |
| N | effective population size |
| m | effective proportion of immigrants |
| Nmest | estimate of gene flow |
| p(1) | average frequency of alleles observed in only one population |
| a | constant |
| b | constant |

# Methods

Dr. Susan Riechert has been working with a desert spider, *Agelenopsis aperta*, for over 30 years. Individuals of *A. aperta* exhibit genetically based behavioral traits that adapt them to the selective pressures of different environments. Aridlands spiders in Arizona and New Mexico are limited by prey availability but have minimal predation pressures. Spiders in these habitats exhibit high levels of aggression towards other spiders of the same species (i.e., they are very territorial), and show little discrimination among prey types of differing profitability. Individuals from a riparian woodland population in Texas, on the other hand, where prey is plentiful but predation pressures (from birds) are high, exhibit low levels of aggression toward other *A. aperta* individuals but discriminate between more and less profitable prey items. Finally, individuals from a riparian woodland population in Arizona, which is surrounded by aridlands populations, exhibit a mixture of aridlands and riparian behaviors.

These aridlands behaviors can be considered maladaptive in a riparian environment, where web-sites are plentiful, prey are abundant, and predation pressures are high. Territorial behavior not only requires energy but carries risks as well; if conflicts escalate spiders can be injured or even killed. Additionally, time spent out on the web (as opposed to within the funnel retreat), whether to engage in conflicts or to capture prey, is time that spiders are vulnerable to predation by birds. For both of these reasons, we would expect selection against aridlands behaviors in a riparian population. Riechert investigated the role of gene flow in maintaining these maladaptive behaviors in the Arizona riparian population (Riechert 1993) using electrophoretic techniques to analyze five local populations (the riparian woodland population plus four nearby populations from more arid habitats).

The following equation can be used to estimate gene flow:

|  |  |
| --- | --- |
|  | LaTeX Code: \[ Nm\_{est} = \frac{(1 / F\_{ST} - 1)}{4} \] |

where *N* is the effective population size (see EFFECTIVE POPULATION SIZE), *m* is the effective proportion of immigrants, and *FST* is the fixation index, which measures variation in allele frequencies among populations. If *Nm* > 1, there is enough gene flow to negate the effects of genetic drift, and if *Nm* > 4, then local populations belong to one panmictic (randomly mating) population (Wright 1931). We can use the *FST* values in the table below to estimate gene flow based on 14 loci.

**Table 1**

|  |  |
| --- | --- |
| Locus | FST |
| PGI1 | 0.020 |
| PGM1 | 0.023 |
| EST1 | 0.021 |
| MDH2 | 0.032 |
| IDH1 | 0.019 |
| GOT2 | 0.031 |
| GPD1 | 0.029 |
| SOD1 | 0.145 |
| LDH1 | 0.012 |
| MDH1 | 0.141 |
| GAM1 | 0.063 |
| HEX1 | 0.034 |
| GOT1 | 0.033 |
| FUM2 | 0.129 |
| Mean | 0.048 |

For the mean of all the loci, *FST* = 0.048. Plugging that value into our equation, we get

|  |  |
| --- | --- |
|  | LaTeX Code: \[ Nm\_{est} = \frac{(1 / 0.048 - 1)}{4} = 4.96\] |

Another approach to estimating gene flow involves using the average allele frequency of alleles unique to one population, across loci (*p*(1), or private alleles). In the equation below, *a* and *b* are constants equal to -0.505 and ó2.44, respectively, for sample sizes of 25:

|  |  |
| --- | --- |
|  | LaTeX Code: \[ \ln{p(1)} = a \ln{(Nm)} + b \] |

Riechert used this approach as well, starting with all five local populations, and at each step omitting the population farthest from the riparian woodland until the two populations being compared were the riparian woodland spiders and those from the immediately adjacent habitat.

**Table 2**

|  |  |  |
| --- | --- | --- |
| p(1) | Average sample size | Number of Populations |
| 0.0607 | 31.9 | 5 |
| 0.0540 | 30.8 | 4 |
| 0.0483 | 31.9 | 3 |
| 0.0484 | 34.9 | 2 |

Given *p*(1) for the two nearest populations we can calculate the gene flow among them (*Nm*) by rearranging:

|  |  |
| --- | --- |
|  | LaTeX Code: \[ \frac{\ln{p(1)} - b}{a} = \ln{(Nm)} \] |

Substituting our known values, we get

|  |  |
| --- | --- |
|  | LaTeX Code: \[ \frac{\ln{p(1)} - (-2.44)}{-0.505} = \ln{(Nm)} = 1.1649 \] |

and we can exponentiate

|  |  |
| --- | --- |
|  | LaTeX Code: \[ Nm = e^{1.1649} = 3.2059 \] |

However, because the values of the constants are based on a sample size of 25 and our average sample size for the two populations is 34.9, we need to make the following correction:

|  |  |
| --- | --- |
|  | LaTeX Code: \[ Nm^\* = Nm \times \frac{N}{25} \] |

The actual level of gene flow among these populations is

|  |  |
| --- | --- |
|  | LaTeX Code: \[ Nm^\* = 3.2059 \times \frac{34.9}{25} = 4.475 \] |

# Interpretation

The value obtained for *Nmest* based on the mean *FST* (*Nmest* = 4.96) indicates extensive gene flow among these five populations of *A. aperta* (since *Nmest* > 4). Based on private alleles for the riparian woodland and its closest neighbor, the value for *Nm*\* (4.475) also suggests that gene flow is exerting a significant influence (*Nm*\* > 4). Riechert also set up drift fence barriers with pitfall traps between the riparian woodland habitat and adjacent habitats to investigate actual movement of spiders between habitats, and found that there was indeed regular population exchange, although more spiders were moving into the riparian woodland habitat than out of it.

# Conclusion

We would expect that in populations of riparian woodland spiders, where aridlands behaviors are maladaptive, these traits would be selected against and would not persist in the population. This expectation is borne out in the population of riparian woodland *A. aperta* in Texas, but not in the Arizona riparian woodland population. What makes the two populations different? The population in Texas is isolated from surrounding *A. aperta* populations, and therefore does not experience gene flow between itself and more aridlands populations. The Arizona population, however, experiences considerable gene flow from surrounding populations. As a result, genes for behavioral traits that are maladaptive in the woodland are continually introduced into the population, thus effectively swamping the action of natural selection.

# Additional Questions

1) Use the *FST* values from Table 1 to calculate *Nmest* for each locus (recall that these *FST* values are based on all five populations). Do these values support the conclusion we made based on the mean *FST*?

2) Use the *p*(1) values from Table 2 to calculate *Nm*\*. What trend in the estimate of gene flow (*Nm*\*) do you observe as more distant populations are included in the analysis? Does this estimate of gene flow for all five populations (based on the mean frequency of alleles found in only one population [private alleles]) lead to the same conclusion as the estimate of gene flow for all five populations based on the mean value of *FST*?

# Source

Futuyma, D. J. 1986. *Evolutionary Biology, 2nd ed*. Sinauer Associates, Inc. Sunderland, MA.

Riechert, S. E. 1993. Investigation of potential gene flow limitation of behavioral adaptation in an aridlands spider. *Behavioral Ecology and Sociobiology 32*:355-363.

Wright, S. 1931. Evolution in Mendelian populations. *Genetics 16*:97-159.

# About this Resource

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This material is now being revised as part of the “Resources for Improving Quantitative Skills in Community College Biology[[2]](#endnote-2)” project. As part of that project is also aligned with the OpenStax Biology Textbook[[3]](#endnote-3).

It is published using the QUBES Open Education Resources publishing platform[[4]](#endnote-4).

1. http://www.tiem.utk.edu/~gross/bioed/ [↑](#endnote-ref-1)
2. https://qubeshub.org/community/groups/quantbioatcc/ [↑](#endnote-ref-2)
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