

CUMULATIVE SELECTION GRADIENTS IN A GARTER SNAKE¹

THE PROBLEM

Arnold studied variation in the number of body vertebrae and the number of tail vertebrae in populations of *Thamnophis elegans* from two regions of central California. He found relatively little vertebral variation within populations, but there were considerable differences in vertebral number between populations on the coast side of the Coast Ranges and populations on the Central Valley side of the Coast Ranges. The consistent difference suggested that selection might have produced these differences, and Arnold attempted to determine the amount of selection necessary to produce these differences.

THE DATA

Arnold collected pregnant females two local populations in each of two sites in northern California 282 km apart from one another. Females were collected over a ten-year period and returned to the University of Chicago. Dam-offspring regressions were used to estimate additive genetic variances and covariances of vertebral number.² Mark-release-recapture experiments in the California populations showed that females with intermediate numbers of vertebrae grow at the fastest rate, at least at the inland site, although no such relationship was found in males. This is the genetic variance-covariance matrix he obtained:

$$\begin{array}{cc} & \begin{array}{cc} \textit{body} & \textit{tail} \end{array} \\ \begin{array}{c} \textit{body} \\ \textit{tail} \end{array} & \begin{pmatrix} 35.4606 & 11.3530 \\ 11.3530 & 37.2973 \end{pmatrix} \end{array}$$

THE METHOD

We know from Lande and Arnold's results that the change in multivariate phenotype from one generation to the next, $\Delta\bar{\mathbf{z}}$, can be written as

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\boldsymbol{\beta} \quad ,$$

where \mathbf{G} is the genotypic variance-covariance matrix, $\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{s}$ is the set of partial regression coefficients describing the direct effect of each character on relative fitness.³ If we are willing to assume that \mathbf{G} remains constant, then the total change in a character subject to selection for n generations is

$$\sum_{k=1}^n \Delta\bar{\mathbf{z}} = \mathbf{G} \sum_{k=1}^n \boldsymbol{\beta} \quad .$$

¹ drawn from Arnold, in *Proceedings of the Second International Conference on Quantitative Genetics*, ed. B. S. Weir, E. J. Eisen, M. M. Goodman, and G. Namkoong, pp. 619–636; Sinauer Associates.

² 1000 progeny from 100 dams.

³ \mathbf{P} is the phenotypic variance-covariance matrix and \mathbf{s} is the vector of selection differentials.

Thus, $\sum_{k=1}^n \beta$ can be regarded as the cumulative selection differential associated with a particular observed change, and it can be estimated as

$$\sum_{k=1}^n \beta = \mathbf{G}^{-1} \sum_{k=1}^n \Delta \bar{z} \quad .$$

THE RESULTS

The overall difference in vertebral number between inland and coastal populations can be summarized as:

$$\begin{array}{l} \textit{body} \left(16.21 \right) \\ \textit{tail} \left(9.69 \right) \end{array}$$

Given the estimate of \mathbf{G} already obtained, this corresponds to a cumulative selection gradient between inland and coastal populations of

$$\begin{array}{l} \textit{body} \left(0.414 \right) \\ \textit{tail} \left(0.134 \right) \end{array}$$

Applying the same technique to looking at the differences between populations within the inland site and within the coastal site we find cumulative selection gradients of

$$\begin{array}{l} \textit{body} \left(0.035 \right) \\ \textit{tail} \left(0.038 \right) \end{array}$$

for the coastal site and

$$\begin{array}{l} \textit{body} \left(0.035 \right) \\ \textit{tail} \left(-0.004 \right) \end{array}$$

for the inland site.

THE CONCLUSIONS

“To account for divergence between inland and coastal California, we must invoke cumulative forces of selection that are 7 to 11 times stronger than the forces needed to account for differentiation of local populations.”

Furthermore, recall that the selection gradients can be used to partition the overall response to selection in a character into the portion due to the direct effects of that character alone and the portion due to the indirect effects of selection on a correlated character. In this case the overall response to selection in number of body vertebrae is given by

$$\mathbf{G}_{11}\beta_1 + \mathbf{G}_{12}\beta_2 \quad ,$$

where $\mathbf{G}_{11}\beta_1$ is the direct effect of body vertebral number and $\mathbf{G}_{12}\beta_2$ is the indirect effect of tail vertebral number. Similarly, the overall response to selection in number of tail vertebrae is given by

$$\mathbf{G}_{12}\beta_1 + \mathbf{G}_{22}\beta_2 \quad ,$$

where $\mathbf{G}_{22}\beta_2$ is the direct effect of tail vertebral number and $\mathbf{G}_{12}\beta_1$ is the indirect effect of body vertebral number. Using these equations it is straightforward to calculate that 91% of the total divergence in number of body vertebrae is a result of direct selection on this character. In contrast, only 51% of the total divergence in number of tail vertebrae is a result of direct selection on this character, i.e., 49% of the difference in number of tail vertebrae is attributable to indirect selection as a result of its correlation with number of body vertebrae.

THE CAVEATS

- This approach cannot distinguish strong selection that happened over a short period of time from weak selection that happened over a long period of time.
- This approach *assumes* that the observed differences in populations are the result of selection, but populations isolated from one another will diverge from one another even in the absence of selection simply as a result of genetic drift.
 - Small amount of differentiation between populations within sites could reflect relatively recent divergence of those populations from a common ancestral population.
 - Large amount of differentiation between populations from inland versus coastal sites could reflect a more ancient divergence from a common ancestral population.