3 Canalization

Today I will introduce you to an old topic in evolutionary developmental biology.

3.1 Basics

Before we begin, we must clarify a few concepts[1,2].

Variability The genetic propensity to vary. It has two components:

- **Mutational variance** The change in phenotypic variance of a trait caused by mutation. Can be measured using mutation accumulation experiments (e.g. body size in *Caenorhabditis elegans*[3]).
- **Environmental variance** Component of the phenotypic variance caused by variation in the environment. In isogenic lines, the phenotypic variance equals the environmental variance.

Phenotypic plasticity Response of the mean phenotype to changes in the environment (e.g. seasonal polyphenism in *Bicyclus anynana*). Special case:

- **Reaction norm** The response curve of a quantitative trait (e.g. body size) over a continuous environmental gradient (e.g. temperature).

Canalization Genetic capacity to buffer the phenotype against perturbations. There are two types of canalization:

- **Genetic canalization** Genetic capacity to buffer the phenotype against mutation
- **Environmental canalization** Genetic capacity to buffer the phenotype against environmental perturbations

Adaptation A feature that promotes fitness and has evolved through natural selection for its current function. Particular instances of phenotypic plasticity and canalization may or may not be adaptive.

These concepts are interrelated. For example, canalization is reduced variability, and phenotypic plasticity is a special kind of environmental variance.

3.2 Two examples of canalization

For the rest of the lecture we shall concentrate on two case studies of canalization from *Drosophila melanogaster*, originally studied by C. H. Waddington[4,5,6]. Here are some major points:

- Waddington noticed that when flies from certain wild strains were submitted to specific environmental perturbations they developed particular morphological abnormalities.
- To test whether the variability had a genetic basis, he selected for and against the appearance of the defects (i.e. on the sensitivity to the environmental perturbation); these selection regimes corresponded to decreasing and increasing environmental canalization, respectively.
- The traits responded in both directions, confirming that these instances of environmental canalization had a genetic basis and could evolve.
- In addition, the defects were "genetically assimilated" in the lines selected for increased sensitivity to the environmental perturbation (i.e. the abnormalities developed in the absence of the environmental stimulus). Waddington proposed that this mechanism could account for instances of apparent inheritance of acquired characters[7].
- Initial genetic analyses revealed that environmental canalization was polygenic. Gibson & Hogness (1996) showed that canalization of the bithorax phenotype was largely caused by a polymorphism in the homeotic gene *Ubx*.

3.3 Next Lecture

In the next lecture we will consider one molecular mechanism for canalization: heat-shock proteins. Required reading is the paper by Rutherford & Lindquist (1998)[8].

3.4 Literature Cited

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