

BIOL2007 - ARTIFICIAL SELECTION

Summary

Examine how artificial selection (**AS**) experiments can be exploited by evolutionary biologists, especially quantitative geneticists.

In essence, the method involves **1)** application of selection (of a known strength) to field or laboratory populations over a shortened evolutionary timescale and **2)** assays of outcomes of selection in terms of changes in phenotypes/genotypes.

AS yields information on quantitative traits in terms of their underlying genetic variability, the relationships between traits and their effects on performance (fitness).

We use an illustrative example, in the context of mate choice, to assess the advantages and disadvantages of the use of **AS** to resolve debates about the true pattern of evolutionary changes in key traits in nature.

The underlying logic of **AS** is that by manipulating the process of natural selection in a controlled way (e.g. in the laboratory), we can gain a deeper understanding of evolution. Selection experiments are intended as mimics of natural selection allowing observation of evolutionary dynamics under controlled conditions.

Background: For fundamentals of **AS**, see my lecture on the evolution of quantitative characters. In each generation, researchers allow only certain individuals to breed - usually by selecting individuals with extreme phenotypes for the trait of interest.

If the variation in the character has a genetic basis then, over time, **AS** can alter the value of the mean phenotype expression of the character. An **AS** experiment can be used to provide an estimate of h^2 and so quantify the degree of response of a trait in a selection experiment.

Potentially, **AS** allows us to measure the consequences for laboratory or field populations of varying patterns of selection where the selective forces are applied over a shortened timescale. We can determine the variability of traits and their relationship to fitness.

Key features of AS experiments

1) May see asymmetric response in UP and DOWN directions.

Depending on the history of the population under selection, it may or may not respond equally in each direction.

- 2) Selected populations can reach a selection limit beyond which further progress is difficult or impossible. These limits may arise because the additive genetic variance present in the initial population has become fixed by selection.
- 3) After reaching the limit, what happens if selection is relaxed? Often the tendency is for populations to revert to their original state. May reflect presence of non-additive genetic variance for the trait. Also could reflect counter-balancing of AS by natural selection.
- 4) Usually researchers are interested not only in the response of the trait that is under selection (the "**direct response**") but also in the values of other traits in the selected populations (the "**indirect or correlated responses**").

Correlated responses may be caused by pleiotropic effects of the selected alleles, or by linkage disequilibrium between the selected alleles and loci affecting other traits. In general, the former are of more interest to researchers.

- 5) AS experiments are often carried out with relatively small population sizes so that chance random associations may well be present. One check on this is to use replicated lines within each selection regime. If replicates show a similar suite of direct and correlated responses, this indicates that they reflect genuine rather than spurious associations. And hence of likely general applicability.

EXAMPLE - MATE CHOICE

AS has been used to test models of sexual selection and mate choice. In Jim's lecture on sexual selection, he discussed female choice, in which males compete for the favours of females. The problem is how to explain the evolution of characters such as male ornamental traits (e.g. the peacock's tail). Much debate is around models of "Indirect Selection" in mating systems where females receive only gametes from their mate.

“Good genes” and “Runaway/Fisherian” models seek to explain that female choice can only have spread through the indirect benefits associated with being present in fitter progeny. Both models predict that female preferences co-evolve with male ornaments and require strong genetic correlations between genes for choosiness and genes for male ornaments to achieve this. Evidence for such correlations is rare. However, recent work on laboratory populations of stalk-eyed flies has

used AS to show that selection on male ornaments causes a correlated response in female preferences.

In the context of sexual selection, stalk-eyed flies are interesting because they possess an exaggerated male trait subject to female choice. The basic biology is that females show high rates of multiple mating at nocturnal mating aggregations (leks), mating several times with the resident male.

Wilkinson's group (USA) has used a genetic approach - applying AS to male stalk-eyed flies. He tested whether a) whether both female preference and male eyespan are genetically variable and b) they genetically covary in a direction consistent with mate choice.

What was already known?

- 1) *male eyespan can be greater than body length*
- 2) *in the wild, males with longer eyespans are found in larger aggregations of females than is true for short eyespan males*
- 3) *male-male competition also occurs - males attempt to displace each other from favoured mating sites (largest eye span usually wins)*

The experiment

Three selection regimes maintained for up to 13 generations

- for large eyespan relative to body size
- for small eyespan relative to body size
- control (unselected)

In effect AS was on allometric shape of the flies. There were two replicates for each selection regime.

Results

DIRECT RESPONSE to selection?

Relative eyespan increased in the high lines and decreased in the low lines.

CORRELATED RESPONSES?

Are there any changes in female preference? Used choice chambers to give females from each selection regime choice between a short (S) and a large (L) eye span male. Unselected females showed strong preference, on average, for L males. Females from L lines similarly preferred, on average, L males. However S line females preferred, on average, S males - a complete reversal of the preference usually observed.

This experiment provides **strong evidence for genetic covariance between female preference and a sexually selected trait.**

The lack of any increase in preference between control and long eye span selected lines suggests **that preference in natural populations is already exaggerated as far as possible.**

Experiment confirms the genetic predictions of good genes and runaway models but doesn't unambiguously support one or the other. In both models, females with stronger preferences mate with better-ornamented males, so both predict positive correlations between preference and ornament genes.

The genetic correlation observed by Wilkinson is probably due to linkage disequilibrium (association of alleles at preference and ornament loci). However, can't rule out pleiotropy (alleles with effects on both traits) or physical linkage - although these explanations appear unlikely.