A trait, or integrated set of traits, that increases the fitness of an organism. The process of improving the fit of phenotype to environment through natural selection.

Generally speaking, adaptations are traits or characters that appear to be too well-fitted to their environment to have arisen by chance. That is, they must be the result of selection. Adaptations may involve morphological, physiological or behavioural traits. They arise through the accumulation of a series of small improvements over time.

"If it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous successive slight modifications, my theory would absolutely break down." — Darwin

Examples of adaptations:
- The eye
- Bird wings
- The human brain
- Homeothermic temperature regulation
- Human language
In order to identify a trait as an adaptation, we must first hypothesize its use or function, and then test that hypothesis. As we saw in the Gould & Lewontin article, it is important to test the hypothesis of adaptation against a variety of null and alternative hypotheses.

Why do polar bears have white coats?

- **Adaptive hypothesis:** white coat is an adaptation for camouflage
  - **Test:** observe hunting behaviour and assay use of camouflage
  - **Result:** camouflage not usually important in hunting
- **New adaptive hypothesis:** white coat is an adaptation for trapping solar heat
  - **Test:** hairs are actually clear and translucent, and trap 16% of incident light energy – better than most hair types.

Results don't support our first adaptive hypothesis.

What's missing?
Testing adaptive hypotheses

Identifying adaptations

The polar bear example shows that ecological and physiological patterns are consistent with one particular adaptive hypothesis – but it doesn’t show that fur color evolved via a process of adaptation.

We’ve compared alternative hypotheses of adaptation – but we haven’t tested the biological null hypothesis: that no adaptation has occurred.

The primary null hypothesis is that traits have evolved due to drift (according to the neutral model).

Testing adaptive hypotheses

Approaches to testing adaptive hypotheses

There are various experimental and theoretical ways to test hypotheses of adaptation. Each has its benefits and drawbacks:

- Observational studies (e.g., the polar bear study)
- Experiments
- Theoretical models
- Comparative method
- Molecular evidence

Testing adaptive hypotheses

Experimental approaches: example

Tephritid flies have dark bands on their wings. When disturbed, they wave their wings in a manner reminiscent of the territorial behavior of their predator (leg waving in jumping spiders).

- Do the flies mimic their predators?
- Does this mimicry deter predators?
- Does it deter jumping spiders in particular?
Testing Adaptive Hypotheses

Conclusion:

The evidence suggests that the morphology and behavior of the flies increases their fitness in the face of their primary predator.

Unlike the observational approach, this gives direct evidence of a fitness advantage.

However, experiments like this still don’t directly test the hypothesis that the traits evolved due to the process of adaptation.

Testing adaptive hypotheses

Experimental approaches: example

Two classes of models predict how a trait should evolve under a specific set of environmental circumstances (usually ignoring genetics altogether).

- Optimality models assume that a trait will evolve to impart the highest possible fitness.
- Evolutionarily Stable Strategy (ESS) models assume that the fitness of a phenotype depends on what other phenotypes are present. This doesn’t always lead to maximal fitness.

Testing adaptive hypotheses

Theoretical approaches – example

We might do an ESS model to explore the possibility that lekking behavior in birds is an adaptation to predation risk (because the risk of predation gets spread out among large numbers of males).

The model would predict the number of males we should see on a lek as a function of the risk of predation and the likelihood of mating.

We could then measure whether the number of males we observe in nature is consistent with the predictions of the model, given our observations of predation and mating probabilities.
Testis size in bats
Male bats vary from species to species in the size of their testes.

Adaptive hypothesis: Larger testes produce more sperm, which provides an advantage if sperm from multiple males competes for fertilization in a female.

Prediction: Species with larger social groups should have males with larger testes (because more males are competing for reproductive access to females).

Testing adaptive hypotheses
The comparative method – Example

These models offer quantitative predictions for observational or experimental studies.

However, they seldom compare predictions to alternative hypotheses (either adaptive or non-adaptive).

Also, the quantitative predictions might not take into account constraints on adaptation – any failure of observations to match predictions might be due to such constraints.

Testing adaptive hypotheses
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Testing adaptive hypotheses
The comparative method

If we have an adaptive hypothesis for a trait, then we might expect to see a correlation between the explanatory variable (X) and the trait itself (Y).

However, another possible explanation for such a correlation is the process of evolution itself: organisms whose common ancestors had both X and Y are also likely to have X and Y.
Testing adaptive hypotheses
The comparative method – Example

Null hypothesis: Closely related species might have similar group size and testis size simply because they share a common ancestor.

Controlling for common ancestry, males in species with larger group sizes still have larger testes.

Evidence that phylogenetically independent contrasts of a trait (e.g., testis size) are correlated with a hypothesized explanatory variable (e.g., group size) suggests that:

- The trait has evolved in the absence of (or despite) phylogenetic constraint
- Not all evolution of the trait has been neutral (because there is evidence of directionality)

The comparative method explicitly tests adaptive hypotheses against a null hypothesis.
“Correlation is not causation.”
Still not a direct rejection of the neutral model.