

# Laws of Adaptation

Lectures on Long Term Evolution

October 2006

Département de Mathématiques et de Statistique

Université de Montréal

by Carlo Matessi

Istituto di Genetica Molecolare - Consiglio Nazionale delle Ricerche

Via Abbiategrosso 207, Pavia, Italy

## Summary

*Lecture 1 [The short term dynamic approach].* Darwin's finches. Biological adaptation. Natural selection. Fitness (reproductive success). A moderately general equation of short term evolution driven by natural selection. Maximization of mean fitness when constant selection acts on many variants (alleles) of a single gene. "Lotka-Volterra" equations of population dynamics under competition for limited resources. A biological model for the competition parameters. Short term evolution driven by density-frequency dependent selection due to competition. A functional maximized by selection of this type in the case of one gene with many alleles.

*Lecture 2 [The static optimization approach].* Solutions to complex adaptation problems in evolutionary ecology are predicted starting from the postulate that fitness is maximized by natural selection. Classical examples (with constant or variable environment): seed dormancy in annual plants; clutch size in birds and other animals that invest in parental care. Adaptation problems in animal behavior (e.g., conflicts among individuals) often imply context (frequency) dependent fitness. Population games and the concept of "Evolutionary Stable Strategy": a substitute of optimization in case of frequency dependent fitness. A classical example: the "Hawk-Dove" game.

*Lecture 3 [The long term dynamic approach. Part I].* Short term evolution driven by constant selection on two genes with two alleles. Interference of genetic recombination with natural selection and failure of fitness maximization. Two time scales of evolutionary dynamics: short term evolution (fast dynamics), driven by selection; long term evolution (slow dynamics), driven by mutations. Invading mutations. Long Term Equilibria.

*Lecture 4 [The long term dynamic approach. Part II].* Maximization of fitness at monomorphic LTE under constant selection. Mutations must increase fitness in order to invade. Polymorphic LTE cannot exist under constant selection. Stability of (convergence to) monomorphic LTE under constant selection.

*Lecture 5 [The long term dynamic approach. Part III].* Monomorphic LTE under frequency dependent selection. Equivalence of the LTE condition with the ESS condition for continuous strategies. The "Continuous stability" condition. Stability of (convergence to) monomorphic LTE under frequency

dependent selection. Polymorphic LTE cannot exist in the neighborhood of monomorphic LTE under frequency dependent selection.

*Lecture 6 [Monomorphic LTE: examples in the evolution of sex-ratio, I].* Sex-ratio. Why the 1:1 sex-ratio prevails in nature. Exceptions and their adaptive nature: female biased SR in parasitoid wasps; sex-ratio conflicts in social Hymenoptera (wasps, bees, ants). Analysis of long term evolution driven by mutations of both queen and workers behaviors in SR control; identification of the long term equilibria.

*Lecture 7 [Polymorphic LTE, Part I].* Adaptive polymorphisms in nature and their selective agents. Short term evolution, driven by frequency dependent selection, of a discrete (qualitative) character with two types, controlled by one gene with several alleles; functionals that are maximized in this process; long term evolution of traits of this type and polymorphic LTE.

*Lecture 8 [Polymorphic LTE, Part II].* Long term evolution of continuous traits under frequency dependent selection and monomorphic states that can be invaded by *any* mutation. Frequency dependent disruptive selection in the vicinity of such states. A simple general model of frequency dependent disruptive selection; long term evolution and polymorphic LTE for continuous traits controlled by one gene: non-additive alleles; additive alleles. Long term evolution of modifiers of variability of expression of the trait. "Genetic-free" polymorphic LTE.