Quantitative Genetics Approaches to Modeling Adaptive Evolution

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Game Plan

- Quantitative genetics background
- Two approaches
  - Deterministic Gradient Equations (*sensu* Lande)
  - Stochastic Adaptive Dynamics (*sensu* Dieckmann)
- Pros and cons of these approaches
- Examples of theory applications
- Example of a real world system

Modeling Goals

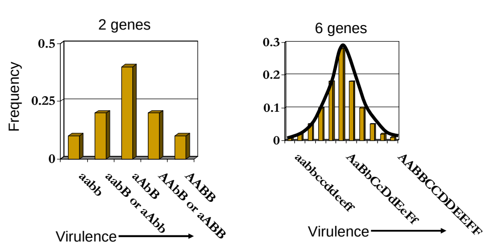
- Explore adaptive evolutionary processes underlying evolutionary patterns
- Explicitly link evolutionary consequences of ecological interactions
- Usually applied to theory problems (but not always)

Defining Quantitative Traits

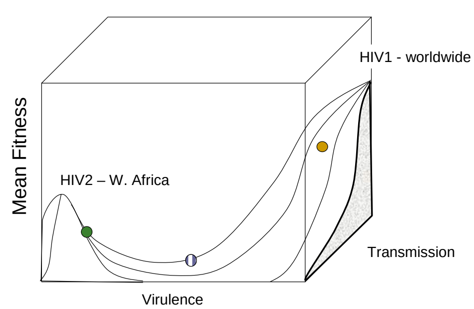
- Continuous, measurable, non-categorizable
- Genotypic and environmental effects determine trait value
- Usually follow phenotype
- Modeling at phenotypic level

Distribution of Quantitative Traits

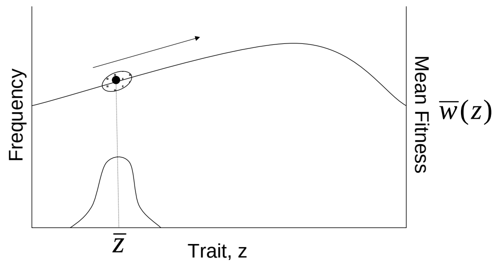
- It's Normal, Gaussian, Bell shaped



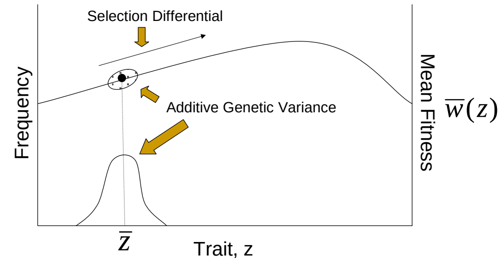
Adaptive Landscapes



Describing Movement across the Landscape



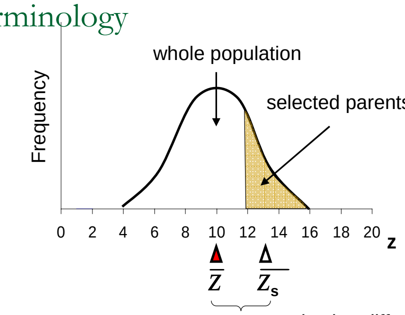
Describing Movement Depends on…



Deterministic Modeling Approaches

- Describe rate of change for mean value of a quantitative trait
- Based on Wright's work for discrete traits
- Lande 1976
- Breeder's Equation

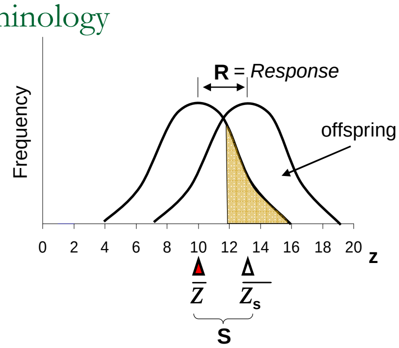
Terminology



$\bar{Z}$ is the mean of the whole population before selection

$\bar{Z}_s$ is the mean of the population after selection (the parents that get to reproduce)

Terminology



Putting It Together: The Breeder's Equation to Lande's Gradient Equation

$$\frac{d\bar{z}}{dt} \approx \Delta\bar{z}$$
$$= \bar{z}_{original} - \bar{z}_{offspring}$$
$$= R$$
$$= \left(\bar{z}_s(t) - \bar{z}(t)\right)h^2$$

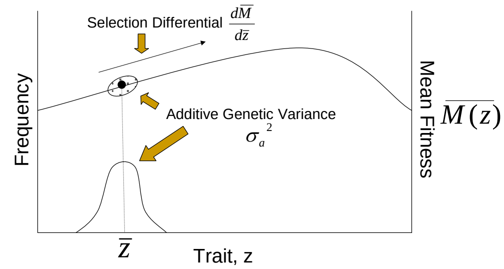
Breeder's Equation

$$= \frac{\sigma_p^2}{\bar{w}} \frac{d\bar{w}}{d\bar{z}} h^2$$

Magic
(i.e., Lande 1976)

$$= \sigma_a^2 \frac{1}{\bar{w}} \frac{d\bar{w}}{d\bar{z}}$$
$$= \sigma_a^2 \frac{d \ln(\bar{w})}{d\bar{z}}$$
$$= \sigma_a^2 \frac{d\bar{M}}{d\bar{z}}$$

Describing Movement Depends on…



Lande's Equation Combines These…

$$\frac{d\bar{z}}{dt} = \sigma_a^{\ 2} \frac{d\overline{M}(z)}{d\bar{z}}$$

- Lots of assumptions
- User beware
- Assumptions mostly reasonable
- Most accurate under weak selection

Stochastic Simulation Approaches

- Adaptive Dynamics
  - Dieckmann, Geritz, others
- Simulates "mutational stochasticity"
- Based on ESS theory
- Underlying fitness function

ESS Theory in One Slide!

- Compare the fitness of a rare mutant to a resident type to see if the mutant can invade
- We compare fitness(mutant|resident) to fitness(resident|resident)
- If fitness(mutant|resident) is greater than fitness(resident|resident) then, mutant invades
- Somewhat simplified!

Adaptive Dynamics Simulation

- Mutants appear in the population stochastically
- Fitnesses compared
- Type in population is updated

- These approaches have different assumptions and the potential to give quite different results, but in practice they frequently give similar results

Deterministic Approaches

- Pros
  - Analytical approach makes it easy to understand dynamics
  - Tries to realistically mimic mutation and selection processes
- Cons
  - Constant variance assumption and disruptive selection
  - Applicability to frequency dependent selection?
  - Standing variance vs. mutation-selection balance

Stochastic Approaches

- Pros
  - Can use any type of fitness function
  - Relatively easy to analyze
  - Models of speciation
- Cons
  - Potentially computationally intensive
  - Mutation-selection process unnatural

Fitness Functions Are Everything

- Measure fitness function experimentally
- Pull fitness function from underlying ecological model (most common)
  - $$\frac{dx}{dt} = f(x,z)x$$
  - f describes per capita growth rate, which is a measure of fitness

Making Ecology Explicit

- Usual assumption is that underlying ecological model is at equilibrium
- Ecology can be made explicit
  - Deterministic model with interaction between ecological and evolutionary timescales
  - Stochastic model with both mutational and demographic stochasticity

Applications

- Most often used in theoretical systems, but can be applied to real systems
- Two theory examples
  - Darwinian Extinction/Evolutionary Suicide
  - Evolutionary Branching (underlying phylogenetic patterns)
- Real system example
  - Plague in prairie dogs

Darwinian Extinction

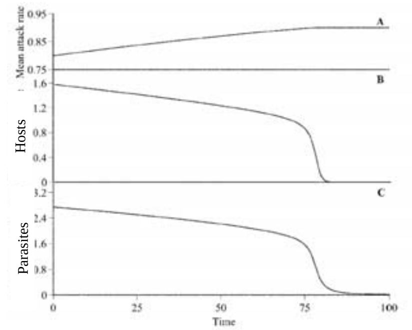
- Lande's approach with explicit ecology

$$\frac{dx}{dt} = x(-1 + rx - x^2 - zy)$$

$$\frac{dy}{dt} = y\left(-d - y + (z+1)x\right)$$

$$\frac{dz}{dt} = \sigma_a^2 \frac{df}{dz} = \sigma_a^2 x$$

Webb 2003



Webb 2003

Evolutionary Branching

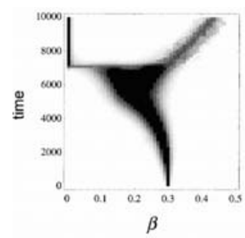
- Adaptive Dynamics

$$\frac{dx_i}{dt} = r(\beta_i)x_i - q\left(\sum x_i + y\right)x_i - \beta_i x_i y$$

$$\frac{dy}{dt} = \sum \beta_i x_i y - \Gamma y$$

Boots and Haraguchi 1999

Tradeoffs and Evolutionary Impacts



Boots and Haraguchi 1999

Plague and Prairie Dogs

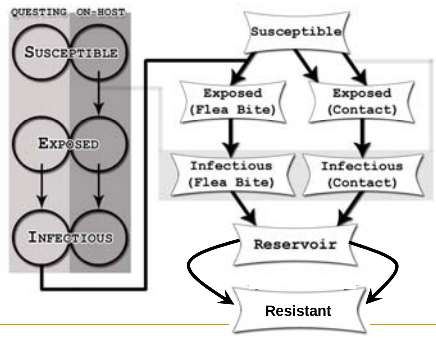
with Brandon Goodell and Mike Antolin

- Highly virulent with 95-100% mortality
- It's been this way for a long time

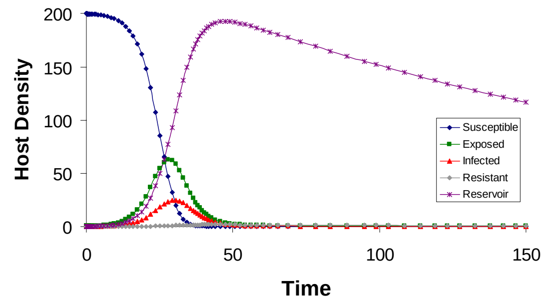
Motivation

- Variation in levels of resistance among hosts
- In prairie dogs: Strong selection pressure, weak response – What's up?

Fleas	Prairie Dogs



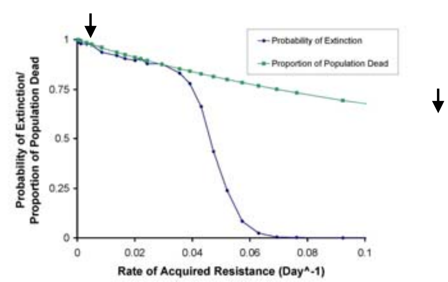
Validating Ecological Model



Quantitative Validation

	Model	Field Data
Probability of Extinction	98%	12 of 12 epizootics
Time to Extinction	~ 14 weeks	~ 6-8 weeks

A Resistance Threshold



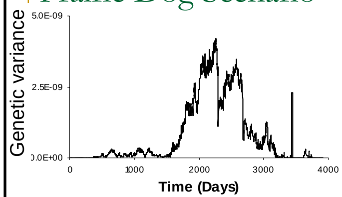
Adding Genetic Variation

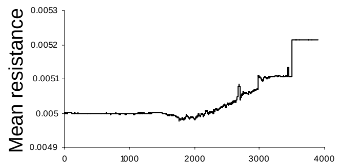
- Simulation model
- Stochastic births and deaths (demographic stochasticity)
- When birth occurs, offspring has probability of slightly different resistance (mutational stochasticity)

Adding Selection

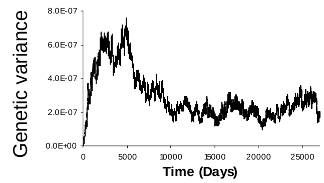
- Plague returns to a town approximately every 7 years
- Pulsed plague from the distribution of plague return times

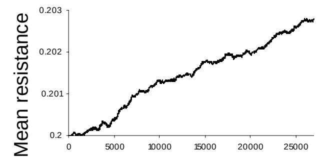
Prairie Dog Scenario





Great Gerbil Scenario





When is demographic stochasticity important?

- Race between evolutionary and demographic stochasticity processes
- Theory suggests critical population size is 10-100 individuals
- Prairie dog models - about 6 resistant individuals usually survive
- Great gerbil models – many individuals survive

Gomulkiewicz and Holt 1995
Lande 1993

Initial conditions matter

- Different initial conditions (i.e., levels of resistance) is what drives differences in population persistence
- Threshold exists such that some populations/species are unable to maintain evolutionary response despite strong selection pressure

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