

Studying Evolutionary Ecology 3: Mathematical Models

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Biol 417: Evolutionary Ecology

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Review

So far we have covered experimentation and comparative methods as tools for studying evolutionary ecology.

Those approaches have proven highly informative, but there is an elephant in the room that limits their flexibility.

Experimentation and comparative methods rely on **observed** outcomes. What happens if we want to study the evolutionary consequences of conditions that haven't yet occurred in the Earth's history?

Today we will learn about mathematical and computational approaches for studying evolutionary ecology.

What is modelling?

Hypothesis: An idea, supposition, or otherwise unproven theory used as the basis for further investigation.

Model: A generalised description of some phenomenon.

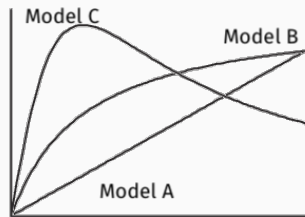
Model $\neq$ Hypothesis

A single hypothesis can be represented by multiple models.

Hypothesis: Number of offspring R increases with body size M

Models:

- $R = aM$ Model A: Number of offspring is proportional to mass
- $R = \frac{aM}{1+bM}$ Model B: Number of offspring saturates as mass increases
- $R = aMe^{-bM}$ Model C: Number of offspring first increases and then decreases as mass increases



Source: Hilborn & Mangel (1997)

The equation of a model is a very specific expression of the hypothesis. In other words, models help us clarify verbal descriptions of nature and the mechanisms involved.

Once we've transformed a verbal hypothesis into a mathematical model, the mathematical analysis maps the consequences of the assumptions.

This help us understand which parameters and processes are important, and which ones are not.

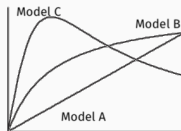
No model is correct ... but some models are useful.

Components of a model

Models are comprised of two main components:

Deterministic part: Describes the shape of the relationship (i.e., your hypothesis).

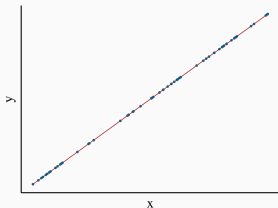
- Model A: $R = aM$
- Model B: $R = \frac{aM}{1+bM}$
- Model C: $R = aMe^{-bM}$



Stochastic part: Describes the randomness of the process (i.e., the noise in a system).

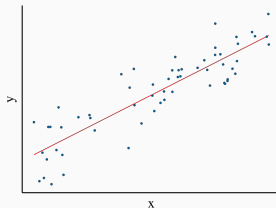
Deterministic models

- No components are uncertain
- Outcome is always the same
- $y_i = \beta_0 + \beta_1 x_i$



Stochastic models

- Some components are uncertain and characterised by probability distributions
- Outcome is variable
- $y_i = \beta_0 + \beta_1 x_i + \varepsilon_i$



Modelling in Evolutionary Ecology

Consider a population of individuals competing for resources, with two possible phenotypes: Doves (never fight) Hawks (always fight).

Questions: Which strategy is optimal? What proportions of the different strategies should we expect to see in a population?

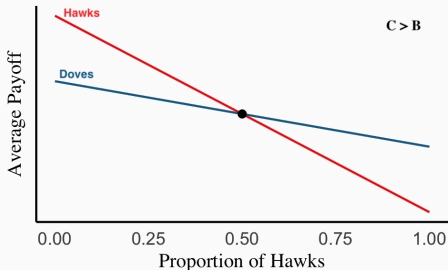
Assumptions:

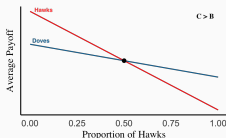
- When two doves meet, they will simply share the resource and the payoff to each dove is $\frac{B}{2}$.
- When a hawk meets a doves, the hawk always takes the resource and the payoffs are: 'hawk' $\rightarrow B$, dove is $\rightarrow 0$.
- When two hawks meet, they fight and the average payoff to each hawk is $\frac{B-C}{2}$.

	Hawk	Dove
Hawk	$\frac{B-C}{2}, \frac{B-C}{2}$	$B, 0$
Dove	$B, 0$	$\frac{B}{2}, \frac{B}{2}$

The optimal strategy will depend on who you are competing against, and the B and C .

We can calculate mean individual payoffs depending on the composition of the population, B , and C .





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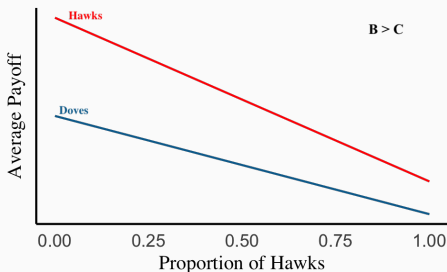
In a population of doves, no individual ever receives the full resource, B , so this system is always open to exploitation.

In a population of hawks, all of the animals suffer the cost of competing, C . If $C > B$, hawks costs outweigh benefits on average and doves can persist.

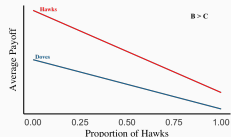
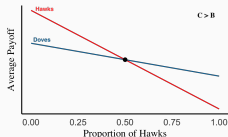
The ESS for the proportion of hawks and doves in a population ultimately depends on B and C .

The ESS for the proportion of hawks and doves in a population ultimately depends on B and C .

When $B > C$, doves are never favoured on average.



	Hawk	Dove
Hawk	$\frac{B-C}{2}, \frac{B-C}{2}$	$B, 0$
Dove	$B, 0$	$\frac{B}{2}, \frac{B}{2}$



Based on this simple model of competition we were able to understand what resources are worth fighting for.

It also lets us predict what proportions of phenotypes might be expected in any given population.

We were able to do this without any empirical data.

Stochastic Simulation

Experimentation and comparative methods can be seen as *'inverse'* modelling (i.e., we have the data and we try to identify the process that generated it).

Simulation can be seen as *'forward'* modelling. If we pick/build a model, what patterns can we expect to see in data.

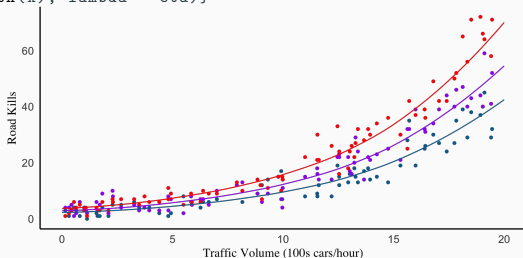
Evolutionary ecologists often use simulation in order to explore patterns that would emerge from a given model(s).

If we chain together simulations from multiple models we can generate rich and complex descriptions of evolutionary systems.

Stochastic simulations rely on computer algorithms to randomly sample values from probab. distribns. to emulate real systems.

E.g., We can use sims. to explore the effects of climate change in a system where traffic and temperature influence road kills.

```
Road_Kills <- function(x, x_2) {  
  B_0 <- 0.01 #Intercept  
  B_1 <- 0.15 #Traffic effect  
  B_2 <- 0.05 #Temp effect  
  eta = exp(B_0 + B_1*x + B_2*x_2)  
  rpois(n = length(x), lambda = eta)}  
  
X <- runif(80, 0, 20)  
Deaths_15C <- Road_Kills(X, 15)  
Deaths_20C <- Road_Kills(X, 20)  
Deaths_25C <- Road_Kills(X, 25)
```



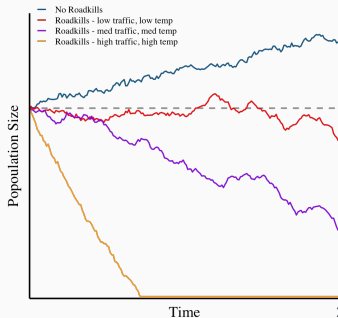
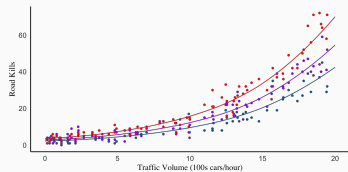
If we chain together simulations from multiple models we can generate rich descriptions of complex systems.

```
POP <- as.vector(200)
for(i in 1:200){
  Births <- rpois(1, 40)
  Deaths <- rpois(1, 38)
  POP[i+1] <- POP[i] + Births - Deaths}
```

```
POP2 <- as.vector(200)
for(i in 1:200){
  Births <- rpois(1, 40)
  Deaths <- rpois(1, 38)
  RK_Deaths <- Road_Kills(2, 15)
  POP2[i+1] <- POP2[i] + Births - Deaths - RK_
    Deaths}
```

```
...
  RK_Deaths <- Road_Kills(5, 20)
...

...
  RK_Deaths <- Road_Kills(10, 25)
...
```



With simulation studies you can easily manipulate any ingredient in your models (model params, data, params of the distributions). This makes simulations a very **powerful** tool for exploring evolutionary ecology.

With simulation studies you can easily manipulate any ingredient in your models (model params, data, params of the distributions). This makes simulations a potentially **dangerous** tool for exploring evolutionary ecology.

Always approach simulation studies with care and make sure the computational system you put together matches the ecological reality of the question you are trying to study.

Limitations of Modelling

Models allow us to circumvent real-world complications, but their utility depends on how they are structured and the assumptions that they rely on.

Models alone can't 'prove' anything, for that we need data.

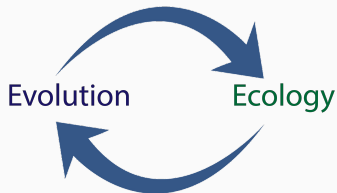
Highly complex models can accurately describe the real world, but may be uninterpretable, simple models may be interpretable, but often provide poor predictions, so where is the happy medium?

Models force us to be explicit about verbal hypotheses and are themselves are tests of whether verbal descriptions are sound.

Models have the ability to advance the field by introducing new predictions.

Models can outline the parameter space in which an evolutionary phenomenon can occur (e.g., hawks/doves).

Models allow us to circumvent real-world complications in order to tackle virtually any problem.



	Dynamic	Static
Proximate (How)	Ontogeny (development)	Mechanism (causation)
Ultimate (Why)	Phylogeny (evolution)	Function (adaptation)

References

Hilborn, R. & Mangel, M. (1997). *The ecological detective: confronting models with data*. vol. 28. Princeton University Press.