Advanced Topics in Population and Community Ecology and Conservation

Lecture 2

Ana I. Bento
Imperial College London
MRC Centre for Outbreak Analysis and Modelling
anabento02@imperial.ac.uk

II Southern-Summer School on Mathematical Biology
January 2013

Overview

Today we will...

- **What to do when replicated experimentation is not possible**

Imperial College London

Overview

Today we will...

- What to do when replicated experimentation is not possible
- **Matrices in conservation**

Overview

Today we will...

- What to do when replicated experimentation is not possible
- Matrices in conservation
- **The Soay sheep system as an example of use of a stochastic matrix**

Overview

Today we will...

- What to do when replicated experimentation is not possible
- Matrices in conservation
- The Soay sheep system as an example of use of a stochastic matrix
- **Integral projection models and the Yellowstone wolves system**

Overview

What to do when replicated experimentation is not possible

- There is only one St.Kilda and one Yellowstone National Park

Overview

What to do when replicated experimentation is not possible

- There is only one St.Kilda and one Yellowstone National Park
- So it is impossible to have experimental controls to investigate consequences of changes in plant phenology, or species reintroduction on ecosystem functioning, community structure and population dynamics of competitors or prey

Overview

What to do when replicated experimentation is not possible

- Insights into how environmental variation drives fluctuations in selection pressures, the additive genetic variance, and the response to selection in free-living populations requires detailed pedigrees, which can only be obtained through the study of marked individuals

Overview

What to do when replicated experimentation is not possible

- Currently the best we can do is to collect observational data, construct models from these data and analyse these models

Overview

What to do when replicated experimentation is not possible

- Currently the best we can do is to collect observational data, construct models from these data and analyse these models
- The analysis of models should provide insights into the workings of the system under study, but they should also allow the posing of hypotheses that themselves may suggest small-scale experiments or additional data that require collection

Matrices and conservation

Matrix models

- Matrix models are appropriate to study the dynamics of discrete characters, like age or genotype at a single locus

Matrices and conservation

Matrix models

- Matrix models are appropriate to study the dynamics of discrete characters, like age or genotype at a single locus
- Identifying key factors: association between demographic rate and population growth

Matrices and conservation

Matrix models

- Matrix models are appropriate to study the dynamics of discrete characters, like age or genotype at a single locus
- Identifying key factors: association between demographic rate and population growth
- Building a structured, stochastic model of population growth requires multiple steps.

Matrices and conservation

Matrix models

- Matrix models are appropriate to study the dynamics of discrete characters, like age or genotype at a single locus
- Identifying key factors: association between demographic rate and population growth
- Building a structured, stochastic model of population growth requires multiple steps.
- After the population has been split into a number of (st)ages with differing demographic rates, a series of environmental states needs to be identified

Matrices and conservation

Matrix models

- The environmental states might describe years when population growth is low, intermediate or high

Matrices and conservation

Matrix models

- The environmental states might describe years when population growth is low, intermediate or high
- The environmental states need to be linked to associated population transition matrices

Matrices and conservation

Matrix models

- The environmental states might describe years when population growth is low, intermediate or high
- The environmental states need to be linked to associated population transition matrices
- Elasticities (and sensitivities) are the tools to shed light upon the demographic rates that influence population growth in stochastic environments

Matrices and conservation

Matrix models

This machinery consists of three broad steps:

- Define environmental states

Matrices and conservation

Matrix models

This machinery consists of three broad steps:

- Define environmental states
- Construct a sequence of environmental states using a Markov chain

Matrices and conservation

Matrix models

This machinery consists of three broad steps:

- Define environmental states
- Construct a sequence of environmental states using a Markov chain
- Which is a mathematical system that undergoes transitions from one state to another, between a finite or countable number of possible states. It is a random process usually characterized as memoryless: the next state depends only on the current state and not on the sequence of events that preceded it

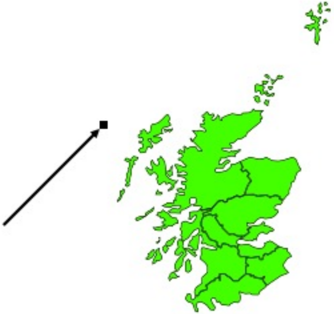
Matrices and conservation

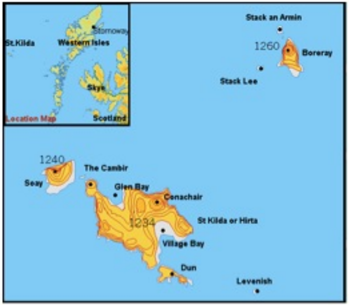
Matrix models

This machinery consists of three broad steps:

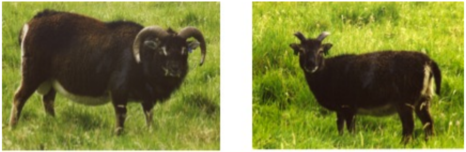
- Define environmental states
- Construct a sequence of environmental states using a Markov chain
- Which is a mathematical system that undergoes transitions from one state to another, between a finite or countable number of possible states. It is a random process usually characterized as memoryless: the next state depends only on the current state and not on the sequence of events that preceded it
- Perform perturbation analysis to calculate the influence of demographic rates on the long-run stochastic growth (λ)

Soay sheep in the St. Kilda archipelago



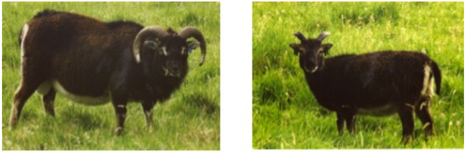


Soay sheep



- Wild, primitive breed, sexually dimorphic (females weigh up to 30kg, males 45kg), Sexually mature by six months, Females can mate with many males each oestrus

Soay sheep



- Wild, primitive breed, sexually dimorphic (females weigh up to 30kg, males 45kg), Sexually mature by six months, Females can mate with many males each oestrus
- Lambs born in April, animals gain condition in the summer, Rut in November, during winter they lose condition

Soay sheep

Why do we study them?

- Population fluctuates in an interesting way

Soay sheep

Why do we study them?

- Population fluctuates in an interesting way
- A simple system sheep and vegetation

Soay sheep

Why do we study them?

- Population fluctuates in an interesting way
- A simple system sheep and vegetation
- High population growth rate and population crashes

Soay sheep

How do we study them?

- Mark individuals, follow them throughout life and construct individual life-histories

Imperial College London

Soay sheep

How do we study them?

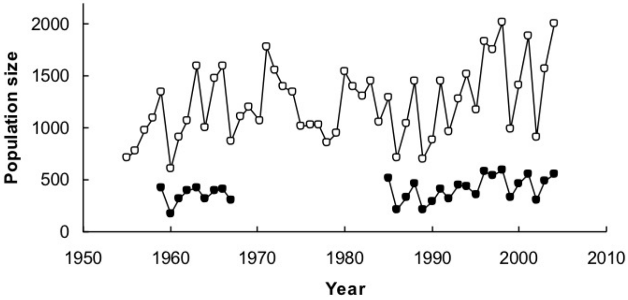
- Mark individuals, follow them throughout life and construct individual life-histories
- Collect data on population size, food availability and climate

Soay sheep

Since 1985 - capture and mark lambs with unique ear tag. >95% of animals in study area are marked

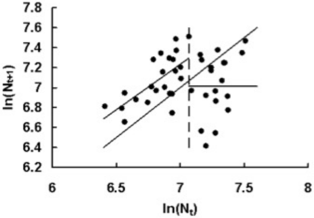
Imperial College London

Time series of Soay sheep counts



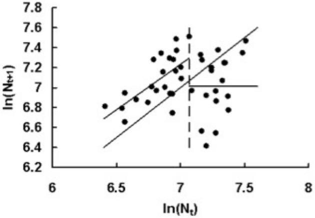
Imperial College London

Density dependence and stochasticity



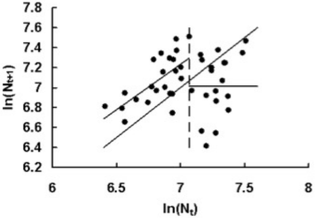
- Threshold = c = 7.066 or 1170 sheep. Below c the slope of the regression line is not significantly different from unity. The growth rate is not density dependent

Density dependence and stochasticity



- Threshold = c = 7.066 or 1170 sheep. Below c the slope of the regression line is not significantly different from unity. The growth rate is not density dependent
- Above c the slope is significantly different from unity. The growth rate is density-dependent

Density dependence and stochasticity



- Threshold $= c = 7.066$ or 1170 sheep. Below c the slope of the regression line is not significantly different from unity. The growth rate is not density dependent
- Above c the slope is significantly different from unity. The growth rate is density-dependent
- Storms at the end of winter explained some of the variation around the regressions (Bento PhD thesis - 2012)

Survival rates vary with age and sex

Significant time variation in survival

Figure. Female survival with age (left). Male survival with age (right)

Imperial College London

Factors associated with survival

Different demographic classes respond in contrasting ways to density and climate

	Females	**Males**
Lambs	Density, NAO	Density, NAO
Yearlings	February rainfall	NAO
2-6 year olds	March rainfall	
>6 year olds	Density, NAO	Constant

Why contrasting responses?

Caused by life-history differences

- Males: cost of reproduction in the rut (Autumn)

Why contrasting responses?

Caused by life-history differences

- Males: cost of reproduction in the rut (Autumn)
- Females: cost of reproduction in late winter / early spring

Fertility

- Fertility rates influenced by density and climate in different ways in different demographic classes

Imperial College London

Fertility

- Fertility rates influenced by density and climate in different ways in different demographic classes
- December-April temperature influences recruitment rates

A stochastic matrix model for Soay sheep

- One matrix for females, one matrix for males

A stochastic matrix model for Soay sheep

- One matrix for females, one matrix for males
- Density calculated as sum of male and female matrix

A stochastic matrix model for Soay sheep

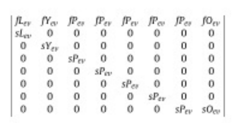
- One matrix for females, one matrix for males
- Density calculated as sum of male and female matrix
- Survival and fecundity functions include density-dependent and climatic effects

A stochastic matrix model for Soay sheep

- One matrix for females, one matrix for males
- Density calculated as sum of male and female matrix
- Survival and fecundity functions include density-dependent and climatic effects
- Climatic effects drawn from mutually correlated, serially independent normal distributions

Stochastic, density-dependent structured model

$n_t + 1 = A_t n_t$



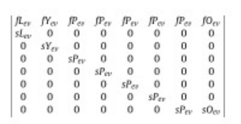
$$\begin{vmatrix} fL_{ev} & fY_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fO_{ev} \\ sL_{ev} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY_{ev} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP_{ev} & sO_{ev} \end{vmatrix}$$

- where f represents fecundity and s survival, L lambs, Y yearlings, P prime-aged, O oldest individuals

For details on how to implement a markov chain see Ezard and Coulson 2010

Stochastic, density-dependent structured model

$n_t + 1 = A_t n_t$



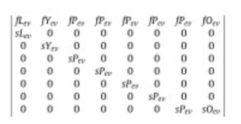
$$\begin{vmatrix} fL_{ev} & fY_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fO_{ev} \\ sL_{ev} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY_{ev} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP_{ev} & sO_{ev} \end{vmatrix}$$

- where f represents fecundity and s survival, L lambs, Y yearlings, P prime-aged, O oldest individuals
- Environmental variability is implemented using a markov chain (set of numbers generated by transition rules)

For details on how to implement a markov chain see Ezard and Coulson 2010

Stochastic, density-dependent structured model

$n_t + 1 = A_t n_t$



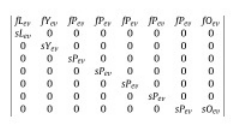
$$\begin{vmatrix} fL_{ev} & fY_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fO_{ev} \\ sL_{ev} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY_{ev} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP_{ev} & sO_{ev} \end{vmatrix}$$

- where f represents fecundity and s survival, L lambs, Y yearlings, P prime-aged, O oldest individuals
- Environmental variability is implemented using a markov chain (set of numbers generated by transition rules)
- Population transition matrix at time t ontains demographic rates drawn from a specific environmental state ev (which is a year or specific type of year)

For details on how to implement a markov chain see Ezard and Coulson 2010

Stochastic, density-dependent structured model

$n_t + 1 = A_t n_t$



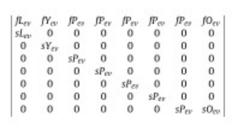
$$\begin{vmatrix} fL_{ev} & fY_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fO_{ev} \\ sL_{ev} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY_{ev} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP_{ev} & sO_{ev} \end{vmatrix}$$

- Describe the probability of moving from one number to another

For details on how to implement a markov chain see Ezard and Coulson 2010

Stochastic, density-dependent structured model

$n_t + 1 = A_t n_t$



$$\begin{vmatrix} fL_{ev} & fY_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fP_{ev} & fO_{ev} \\ sL_{ev} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY_{ev} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP_{ev} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP_{ev} & sO_{ev} \end{vmatrix}$$

- Describe the probability of moving from one number to another
- Different markov chains generate different environmental dynamics

For details on how to implement a markov chain see Ezard and Coulson 2010

Stochastic, density-dependent structured model

Perturbation

- Unlike deterministic analysis (when there is only one number to perturb, in stochastic perturbation analysis we have distributions

Stochastic, density-dependent structured model

Perturbation

- Unlike deterministic analysis (when there is only one number to perturb, in stochastic perturbation analysis we have distributions
- We perturb by varying amounts to ensure that either the coefficient of variation, mean or the variance of the distribution of demographic rates remains fixed.

Stochastic, density-dependent structured model

Perturbation

- Unlike deterministic analysis (when there is only one number to perturb, in stochastic perturbation analysis we have distributions
- We perturb by varying amounts to ensure that either the coefficient of variation, mean or the variance of the distribution of demographic rates remains fixed.
- The stochastic elasticity of λ with respect the rate we will perturb is the proportional change in λ for a proportional change in that rate

Imperial College London

Stochastic, density-dependent structured model

Perturbation

- Unlike deterministic analysis (when there is only one number to perturb, in stochastic perturbation analysis we have distributions
- We perturb by varying amounts to ensure that either the coefficient of variation, mean or the variance of the distribution of demographic rates remains fixed.
- The stochastic elasticity of λ with respect the rate we will perturb is the proportional change in λ for a proportional change in that rate
- Different age-classes respond in different ways to environmental stochasticity such that we might want to quantify the responses of life-history stages to disturbances within and between different environmental states

Stochastic, density-dependent structured model

Perturbation

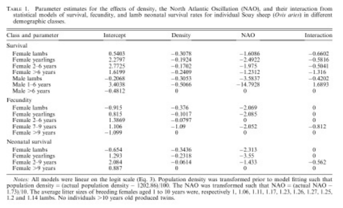


Table 1. Parameter estimates for the effects of density, the North Atlantic Oscillation (NAO), and their interaction from statistical models of survival, fecundity, and lamb neonatal survival rates for individual Soay sheep (*Ovis aries*) in different demographic classes.

Class and parameter	Intercept	Density	NAO	Interaction
Survival				
Female lambs	0.5403	−0.3078	−1.6086	−0.6602
Female yearlings	2.2797	−0.1924	−2.4922	−0.5816
Female 2–6 years	2.7725	−0.1702	−1.975	−0.5041
Female >6 years	1.6199	−0.2409	−1.2312	−1.316
Male lambs	−0.2068	−0.3053	−3.5837	−0.4202
Male 1–6 years	3.4038	−0.5066	−14.7928	1.6893
Male >6 years	−0.4812	0	0	0
Fecundity				
Female lambs	−0.915	−0.376	−2.069	0
Female yearlings	0.815	−0.1017	−2.085	0
Female 2–6 years	1.3869	−0.0797	0	0
Female 7–9 years	1.106	−1.09	−2.052	−0.812
Female >9 years	−1.099	0	0	0
Neonatal survival				
Female lambs	−0.654	−0.3436	−2.313	0
Female yearlings	1.293	−0.2318	−3.55	0
Female 2–9 years	2.084	−0.0614	−1.433	−0.562
Female >9 years	0.887	0	0	0

Notes: All models were linear on the logit scale (Eq. 3). Population density was transformed prior to model fitting such that population density = (actual population density − 1202.86)/100. The NAO was transformed such that NAO = (actual NAO − 1.73)/10. The average litter sizes of breeding females aged 1 to 10 years were, respectively 1, 1.06, 1.11, 1.17, 1.23, 1.26, 1.27, 1.25, 1.2 and 1.14 lambs. No individuals >10 years old produced twins.

Why does this model perform well?

Model performance

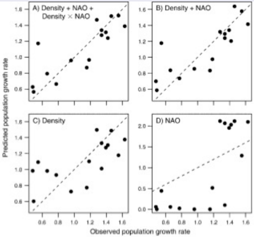


Fig. 3. Model checking plots comparing observed and predicted values for the four time series models (Eq. 13) summarized in Table 5. (A) The behavior of the full model with main effects of weather and density and their interaction; (B) main effects for density and weather; (C) the main effect of density alone; (D) the behavior of the model containing a main effect of weather alone. Dashed lines represent $y = x$. Note that the y-axis scale differs in (D), the model for the NAO.

Why does this model perform well?

- Strength of density dependence and climatic affects differ across demographic classes

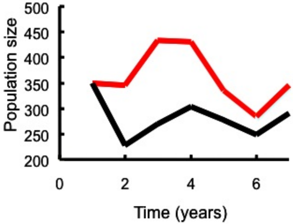
Why does this model perform well?

- Strength of density dependence and climatic affects differ across demographic classes
- Population size at time t independent of population size at time t

Why does this model perform well?

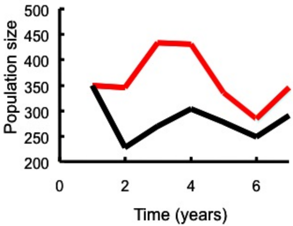
- Strength of density dependence and climatic affects differ across demographic classes
- Population size at time t independent of population size at time t
- Need to consider total density, population structure and climate

Predicting a crash



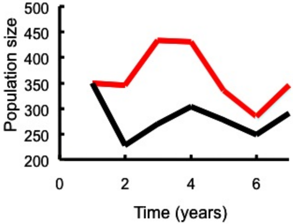
- The distribution of weather is associated with the frequency and severity of a crashes over a period of time

Predicting a crash



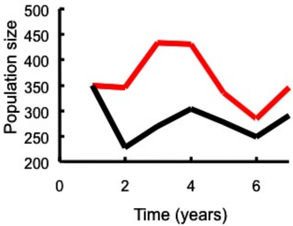
- The distribution of weather is associated with the frequency and severity of a crashes over a period of time
- Each line represents one simulation.

Predicting a crash



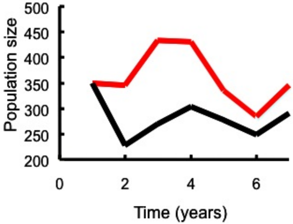
- The distribution of weather is associated with the frequency and severity of a crashes over a period of time
- Each line represents one simulation.
- Initial population size identical, but different population structures. Age structure drawn from data

Predicting a crash



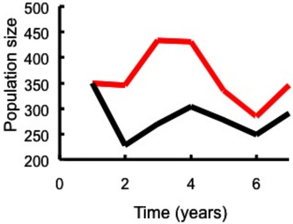
- Two identical population sizes experiencing the same weather conditions (but with different initial structures) can experience very different trajectories.

Predicting a crash



- Two identical population sizes experiencing the same weather conditions (but with different initial structures) can experience very different trajectories.
- In red:age-structure dominated by animals not susceptible to density

Predicting a crash



- Two identical population sizes experiencing the same weather conditions (but with different initial structures) can experience very different trajectories.
- In red:age-structure dominated by animals not susceptible to density
- In black: age-structure dominated by animals susceptible to density

Model performance and conclusions

- The detail matters

Model performance and conclusions

- The detail matters
- The probability of any one crash occurring is determined by the population density, the weather and the population structure

Model performance and conclusions

- The detail matters
- The probability of any one crash occurring is determined by the population density, the weather and the population structure
- Different models from the same system can generate different predictions

Integral projection models (IPMs)

Overview

- What is an IPM

Integral projection models (IPMs)

Overview

- What is an IPM
- Devise a model that allows quantities of interest to be calculated

Integral projection models (IPMs)

Overview

- What is an IPM
- Devise a model that allows quantities of interest to be calculated
- Perturb model; how quantities change?

Integral projection models (IPMs)

Overview

- What is an IPM
- Devise a model that allows quantities of interest to be calculated
- Perturb model; how quantities change?
- What to model?

Integral projection models (IPMs)

Overview

- What is an IPM
- Devise a model that allows quantities of interest to be calculated
- Perturb model; how quantities change?
- What to model?
- Temporal dynamics of multivariate distribution of individual characters (genotypes and phenotypes)

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

- A relatively new, extremely powerful model that examines the behaviour of numerous aspects of a system is the integral projection model (IPM) (Easterling et al. 2000).

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

- A relatively new, extremely powerful model that examines the behaviour of numerous aspects of a system is the integral projection model (IPM) (Easterling et al. 2000).
- IPMs allow the dynamics of continuous phenotypic character distributions to be tracked

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

- A relatively new, extremely powerful model that examines the behaviour of numerous aspects of a system is the integral projection model (IPM) (Easterling et al. 2000).
- IPMs allow the dynamics of continuous phenotypic character distributions to be tracked
- Individuals in different positions along the continuum have different rates of survival, reproduction and development

Imperial College
London

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

- Ellner and Rees (Ellner and Rees 2006, 2007, Rees and Ellner 2009) have conducted most of the fundamental research on analysing these models

VOL. 167, NO. 3 THE AMERICAN NATURALIST MARCH 2006

Integral Projection Models for Species
with Complex Demography

Stephen P. Ellner[1,*] and Mark Rees[1,†]

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

- Ellner and Rees (Ellner and Rees 2006, 2007, Rees and Ellner 2009) have conducted most of the fundamental research on analysing these models
- But they are yet to be widely used, although a growing number of researchers have begun to construct and analyse IPMs (Metcalf et al. 2008, Ozgul et al. 2010).

VOL. 167, NO. 3 THE AMERICAN NATURALIST MARCH 2006

Integral Projection Models for Species
with Complex Demography

Stephen P. Ellner[1,*] and Mark Rees[2,†]

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

There are 4 quantities to take into consideration:

- Population dynamics: population growth rate, variance in population growth rate, long run stochastic growth rate and population age-structure

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

There are 4 quantities to take into consideration:

- Population dynamics: population growth rate, variance in population growth rate, long run stochastic growth rate and population age-structure
- Life history: generation length, dispersion of reproduction, mean and variance in life reproductive success (LRS) and mean and variance in longevity

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

There are 4 quantities to take into consideration:

- Population dynamics: population growth rate, variance in population growth rate, long run stochastic growth rate and population age-structure
- Life history: generation length, dispersion of reproduction, mean and variance in life reproductive success (LRS) and mean and variance in longevity
- Quantitative genetics: additive genetic (co)variances, heritabilities and selection via LRS

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

There are 4 quantities to take into consideration:

- Population dynamics: population growth rate, variance in population growth rate, long run stochastic growth rate and population age-structure
- Life history: generation length, dispersion of reproduction, mean and variance in life reproductive success (LRS) and mean and variance in longevity
- Quantitative genetics: additive genetic (co)variances, heritabilities and selection via LRS
- Population genetics: allele frequencies, growth rates of alleles or genotypes, variation in allele frequencies and strength of selection

London

Integral projection models (IPMs)

Linking population dynamics, life history, population and quantitative genetics

- If immigration and emigration are ignored, IPMs (and matrix models) consist of four fundamental functions that describe the associations between discrete or continuous characters (or both) and the individual 1) survival, 2) development, 3) recruitment, and 4) inheritance rates (Easterling et al. 2000).

Integral projection models (IPMs)

How are these quantities related?

To find out we need to track:

- Allele frequencies to address population genetic questions

Integral projection models (IPMs)

How are these quantities related?

To find out we need to track:

- Allele frequencies to address population genetic questions
- Phenotypic traits to address quantitative genetic questions

Integral projection models (IPMs)

How are these quantities related?

To find out we need to track:

- Allele frequencies to address population genetic questions
- Phenotypic traits to address quantitative genetic questions
- Population size to address population dynamics

Integral projection models (IPMs)

How are these quantities related?

To find out we need to track:

- Allele frequencies to address population genetic questions
- Phenotypic traits to address quantitative genetic questions
- Population size to address population dynamics
- Survival and fertility rates to address life history questions

Integral projection models (IPMs)

The data more specifically

To find out we need to record:

- Survival from time t to t+1,

For a step by step guide on the construction of models see Coulson's paper (Oikos 2012)

Integral projection models (IPMs)

The data more specifically

To find out we need to record:

- Survival from time t to t+1,
- The character value of surviving individuals at time t+1

For a step by step guide on the construction of models see Coulson's paper (Oikos 2012)

Integral projection models (IPMs)

The data more specifically

To find out we need to record:

- Survival from time t to t+1,
- The character value of surviving individuals at time t+1
- The number of offspring produced between t and t+1 that recruit to the population at time t+1

For a step by step guide on the construction of models see Coulson's paper (Oikos 2012)

Integral projection models (IPMs)

The data more specifically

To find out we need to record:

- Survival from time t to t+1,
- The character value of surviving individuals at time t+1
- The number of offspring produced between t and t+1 that recruit to the population at time t+1
- The character values of offspring at time t+1 when they recruit to the population

For a step by step guide on the construction of models see Coulson's paper (Oikos 2012)

Integral projection models (IPMs)

The functions- Survival

- The survival function determines the number of individuals (and their character values) that remain in the population between time t and t+1

Integral projection models (IPMs)

The functions- Survival

- The survival function determines the number of individuals (and their character values) that remain in the population between time t and t+1
- The aim is to identify an equation that describes how a specific trait (e.g. body weight) influences survival.

Imperial College London

Integral projection models (IPMs)

The functions- Survival

- There is a large literature on how best to do this, with markrecapture analysis widely used for cases when not all living individuals are seen at each population census (Lebreton et al. 1992).

Imperial College London

Integral projection models (IPMs)

The functions- Survival

- There is a large literature on how best to do this, with markrecapture analysis widely used for cases when not all living individuals are seen at each population census (Lebreton et al. 1992).
- Or you can use classic linear regression techniques: e.g. binomial error structure and a logit link function because individuals either survive (1) or die (0) over each time step

Imperial College London

Integral projection models (IPMs)

The functions- Survival

- There is a large literature on how best to do this, with markrecapture analysis widely used for cases when not all living individuals are seen at each population census (Lebreton et al. 1992).
- Or you can use classic linear regression techniques: e.g. binomial error structure and a logit link function because individuals either survive (1) or die (0) over each time step
- So we then get S(z, t): the predicted probability of survival given a specific character value z

Integral projection models (IPMs)

The functions- Recruitment

- The recruitment function describes the number of new individuals that are added to the population at time t+1 in other words the number of offspring produced between time t and t+1 that survive to t+1.

Imperial College London

Integral projection models (IPMs)

The functions- Recruitment

- The recruitment function describes the number of new individuals that are added to the population at time t+1 in other words the number of offspring produced between time t and t+1 that survive to t+1.
- The analysis focuses on identifying the expected number of offspring produced by a female of a given value of a specific trait (e.g. body weight)

Integral projection models (IPMs)

The functions- Recruitment

- The recruitment function describes the number of new individuals that are added to the population at time t+1 in other words the number of offspring produced between time t and t+1 that survive to t+1.
- The analysis focuses on identifying the expected number of offspring produced by a female of a given value of a specific trait (e.g. body weight)
- Again you can use classic linear regression techniques: e.g. binomial error structure and a logit link function because individuals either successfully produce a recruit (1) or not (0) over each time step

Integral projection models (IPMs)

The functions- Recruitment

- The recruitment function describes the number of new individuals that are added to the population at time t+1 in other words the number of offspring produced between time t and t+1 that survive to t+1.
- The analysis focuses on identifying the expected number of offspring produced by a female of a given value of a specific trait (e.g. body weight)
- Again you can use classic linear regression techniques: e.g. binomial error structure and a logit link function because individuals either successfully produce a recruit (1) or not (0) over each time step
- So we then get R(z, t): the predicted probability of producing offspring given a specific character value z

Integral projection models (IPMs)

The functions- Development

- The development function describes how the character value (e.g. body weight) changes among surviving individuals from time t to t+1.

Integral projection models (IPMs)

The functions- Development

- The development function describes how the character value (e.g. body weight) changes among surviving individuals from time t to t+1.
- We need to bear in mind that not all surviving individuals that had the same body weight at time t will have identical body weights at time t+1. This means that for each body weight at time t we require a probability distribution of possible body weights at time t+1.

Integral projection models (IPMs)

The functions- Development

- The development function describes how the character value (e.g. body weight) changes among surviving individuals from time t to t+1.
- We need to bear in mind that not all surviving individuals that had the same body weight at time t will have identical body weights at time t+1. This means that for each body weight at time t we require a probability distribution of possible body weights at time t+1.
- The aim is to work out the expected distribution of body weights at time t+1 among survivors given their distribution of body weights at time t.

Integral projection models (IPMs)

The functions- Development

- Working out the distribution of expected body weights at time t+1 for each observed body weight at time t before adding these distributions together.

Integral projection models (IPMs)

The functions- Development

- Working out the distribution of expected body weights at time t+1 for each observed body weight at time t before adding these distributions together.
- The mathematical notation to describe this is G(z'| z, t). Here the z is body weight at time t and z is body weight at time t+1. The | symbol means 'given' or 'conditional on'.

Integral projection models (IPMs)

The functions- Development

- A body weight distribution for time t + 1 is obtained by summing this function over all body weights at time t

Integral projection models (IPMs)

The functions- Development

- A body weight distribution for time t + 1 is obtained by summing this function over all body weights at time t
- First, it assumes that the probability distribution of character values at t +1 for any given character value at t is Guassian (see details in Easterling et al. (2000))

Integral projection models (IPMs)

The functions- Development

- A body weight distribution for time t + 1 is obtained by summing this function over all body weights at time t
- First, it assumes that the probability distribution of character values at t +1 for any given character value at t is Guassian (see details in Easterling et al. (2000))
- G(z'| z, t) is consequently a function describing how body weight at time t maps to body weight at time t +1 among those individuals that survive.

Integral projection models (IPMs)

The functions- Inheritance

- Identical logic to that used to construct the function G(z'| z, t) is used to identify D(z'| z, t)

Integral projection models (IPMs)

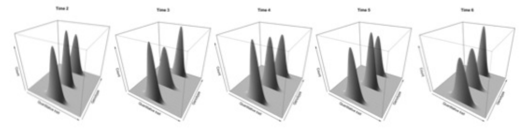
The functions- Inheritance

- Identical logic to that used to construct the function G(z‘| z, t) is used to identify D(z‘| z, t)
- Regress the body weights of recruits that enter the population at time t + 1 against that of parents (in this case the mother) at time t.

Imperial College London

Integral projection models (IPMs)

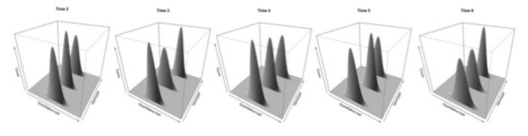
Why do distributions change? And what are the biological processes?



Integral projection models (IPMs)

Why do distributions change? And what are the biological processes?

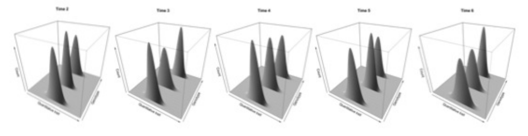
- Mass removed by mortality and emigration



Integral projection models (IPMs)

Why do distributions change? And what are the biological processes?

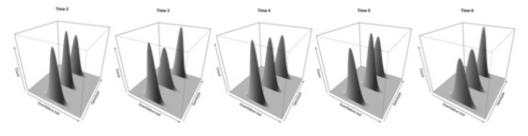
- Mass removed by mortality and emigration
- Mass added by reproduction and immigration



Integral projection models (IPMs)

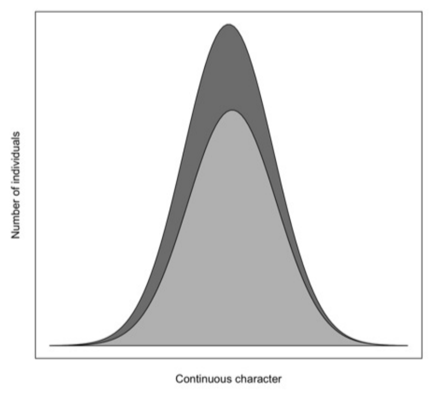
Why do distributions change? And what are the biological processes?

- Mass removed by mortality and emigration
- Mass added by reproduction and immigration
- Mass is transformed by ontogenetic development



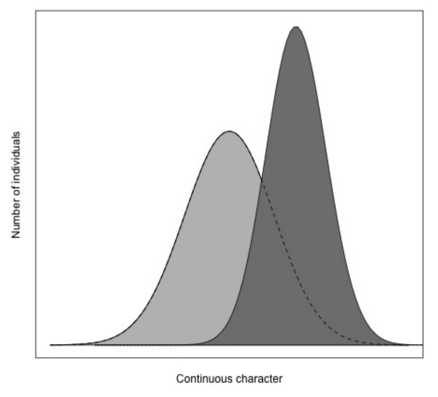
Integral projection models (IPMs)

Mass removal- Mortality



Integral projection models (IPMs)

Transformation- Ontogenic development



Integral projection models (IPMs)

Mass addition- fertility

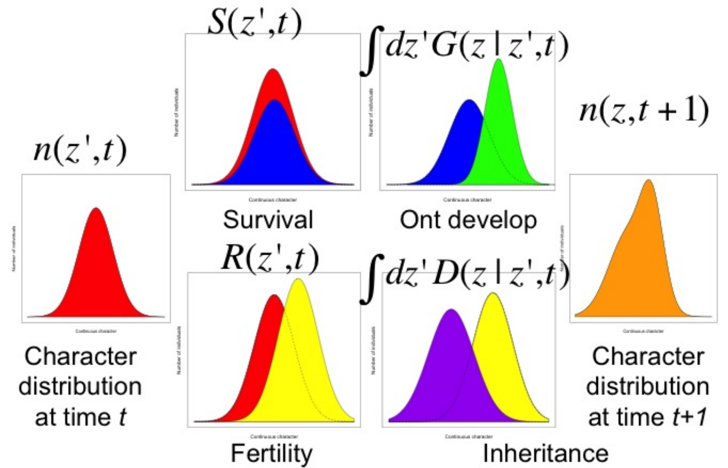
Integral projection models (IPMs)

Mass addition- Inheritance

Integral projection models (IPMs)

Putting it all together

- The model will project a distribution of the character (e.g.body weight) at time t to a new distribution at t+1 (Easterling et al. 2000)



Integral projection models (IPMs)

Putting it all together

$$n(t+1,z) = \int \left\{ \begin{matrix} G(t,z \mid z')S(t,z') + \\ D(t,z \mid z')R(t,z) \end{matrix} \right\} n(t,z')dz$$

Integral projection models (IPMs)

Calculation of quantities

- Annual population growth

Integral projection models (IPMs)

Calculation of quantities

- Annual population growth
- Age-structure

Integral projection models (IPMs)

Calculation of quantities

- Annual population growth
- Age-structure
- Distribution of body sizes

Imperial College London

Integral projection models (IPMs)

Calculation of quantities

- Annual population growth
- Age-structure
- Distribution of body sizes
- Genotype and allele frequencies

Integral projection models (IPMs)

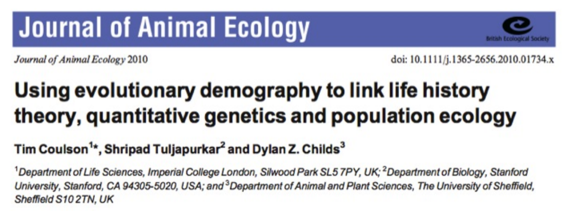
Calculation of quantities

- Annual population growth
- Age-structure
- Distribution of body sizes
- Genotype and allele frequencies
- Covariance between parent and offspring characters

Integral projection models (IPMs)

Calculating quantities

Calculation of some quantities too involved to provide derivations in this lecture, but see...



Journal of Animal Ecology

Journal of Animal Ecology 2010 doi: 10.1111/j.1365-2656.2010.01734.x

Using evolutionary demography to link life history theory, quantitative genetics and population ecology

Tim Coulson[1]*, Shripad Tuljapurkar[2] and Dylan Z. Childs[3]

[1]Department of Life Sciences, Imperial College London, Silwood Park SL5 7PY, UK; [2]Department of Biology, Stanford University, Stanford, CA 94305-5020, USA; and [3]Department of Animal and Plant Sciences, The University of Sheffield, Sheffield S10 2TN, UK

Integral projection models (IPMs)

Calculating quantities

- The easiest way to work with the IPM is to take the continuous distribution, N(z, t), and to discretise it. In other words, choose a sequence of values (closely spaced) that start below the smallest value of the character observed, and above the largest value.

Integral projection models (IPMs)

Calculating quantities

- The easiest way to work with the IPM is to take the continuous distribution, N(z, t), and to discretise it. In other words, choose a sequence of values (closely spaced) that start below the smallest value of the character observed, and above the largest value.
- Write model in matrix form. The larger the number of bins, the greater the number of calculations required.

Imperial College London

Integral projection models (IPMs)

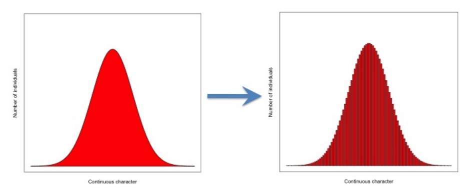
Calculating quantities

- Having identified the range of character values to encompass, and chosen a number of bins, next calculate the midpoint value of each bin, and then evaluate each of the four functions at each midpoint value.

Integral projection models (IPMs)

Calculating quantities

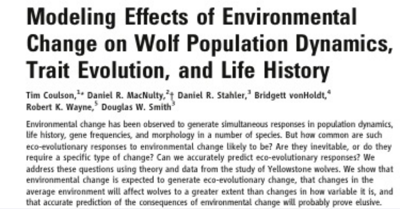
- Having identified the range of character values to encompass, and chosen a number of bins, next calculate the midpoint value of each bin, and then evaluate each of the four functions at each midpoint value.
- Generate four matrices, one describing predicted transition rates from each function of the functions



Imperial College London

Integral projection models (IPMs)

The wolves in Yellowstone as an example



Modeling Effects of Environmental Change on Wolf Population Dynamics, Trait Evolution, and Life History

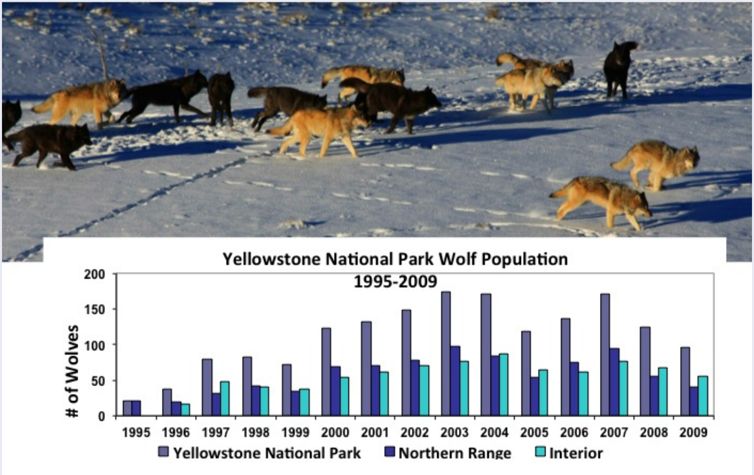
Tim Coulson,[1*] Daniel R. MacNulty,[2†] Daniel R. Stahler,[3] Bridgett vonHoldt,[4]
Robert K. Wayne,[5] Douglas W. Smith[3]

Environmental change has been observed to generate simultaneous responses in population dynamics, life history, gene frequencies, and morphology in a number of species. But how common are such eco-evolutionary responses to environmental change likely to be? Are they inevitable, or do they require a specific type of change? Can we accurately predict eco-evolutionary responses? We address these questions using theory and data from the study of Yellowstone wolves. We show that environmental change is expected to generate eco-evolutionary change, that changes in the average environment will affect wolves to a greater extent than changes in how variable it is, and that accurate prediction of the consequences of environmental change will probably prove elusive.

Science 2011

Integral projection models (IPMs)

The wolves in Yellowstone as an example



Integral projection models (IPMs)

Coat colour variation

- Yellowstone wolf population has been extensively monitored since its introduction in 1995

Imperial College London

Integral projection models (IPMs)

Coat colour variation

- Yellowstone wolf population has been extensively monitored since its introduction in 1995
- Grey and black wolves co-exist (only in North America)

Integral projection models (IPMs)

Coat colour variation

- Yellowstone wolf population has been extensively monitored since its introduction in 1995
- Grey and black wolves co-exist (only in North America)
- Grey allele ancestral

Integral projection models (IPMs)

Coat colour variation

- Yellowstone wolf population has been extensively monitored since its introduction in 1995
- Grey and black wolves co-exist (only in North America)
- Grey allele ancestral
- Coat colour caused by genotype at one locus

Integral projection models (IPMs)

Model assumptions and stucture

- Sexes have identical demography

Integral projection models (IPMs)

Model assumptions and stucture

- Sexes have identical demography
- No age structure and random mating

Integral projection models (IPMs)

Model assumptions and stucture

- Sexes have identical demography
- No age structure and random mating
- Mendelian inheritance for coat colour locus

Integral projection models (IPMs)

Model assumptions and stucture

- Sexes have identical demography
- No age structure and random mating
- Mendelian inheritance for coat colour locus
- Demographic stochasticity can be ignored

Imperial College London

Integral projection models (IPMs)

Model assumptions and stucture

- Sexes have identical demography
- No age structure and random mating
- Mendelian inheritance for coat colour locus
- Demographic stochasticity can be ignored
- Discrete time

Integral projection models (IPMs)

Analysis

- Run simulation and calculate quantities

Integral projection models (IPMs)

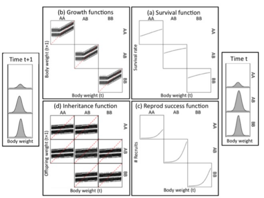
Analysis

- Run simulation and calculate quantities
- Perturb environment by altering values in variance-covariance matrix

Integral projection models (IPMs)

Putting it all together

Graphical representation of the IPM that maps the bivariate distribution of genotype and body weight at time t to a new distribution at time t + 1. Functions (b) and (d) are probability density functions showing the range of y values for each x value; both of these functions are identical across genotypes. Associations between body weight and both survival and reproductive success varied with genotype, whereas growth rates and inheritance did not. The body weight and genotype distributions at times t and t + 1 are, respectively, on the right and left of the functions to provide a graphical representation of the mathematical structure of the



IPM

Integral projection models (IPMs)

Predictions

- The model performed well in predicting key features of the wolf population

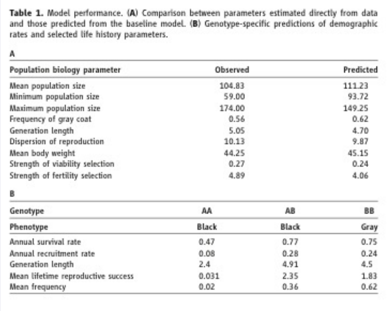


Table 1. Model performance. (**A**) Comparison between parameters estimated directly from data and those predicted from the baseline model. (**B**) Genotype-specific predictions of demographic rates and selected life history parameters.

A

Population biology parameter	Observed	Predicted
Mean population size	104.83	111.23
Minimum population size	59.00	93.72
Maximum population size	174.00	149.25
Frequency of gray coat	0.56	0.62
Generation length	5.05	4.70
Dispersion of reproduction	10.13	9.87
Mean body weight	44.25	45.15
Strength of viability selection	0.27	0.24
Strength of fertility selection	4.89	4.06

B

Genotype	AA	AB	BB
Phenotype	**Black**	**Black**	**Gray**
Annual survival rate	0.47	0.77	0.75
Annual recruitment rate	0.08	0.28	0.24
Generation length	2.4	4.91	4.5
Mean lifetime reproductive success	0.031	2.35	1.83
Mean frequency	0.02	0.36	0.62

Integral projection models (IPMs)

Predictions

- The model performed well in predicting key features of the wolf population
- Provided insight into the dynamics of the coat color genotype.

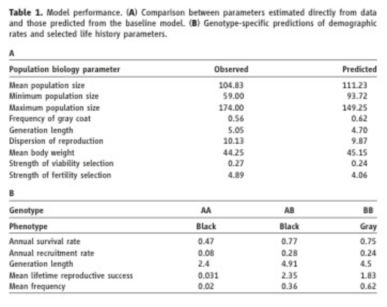


Table 1. *Model performance.* (**A**) Comparison between parameters estimated directly from data and those predicted from the baseline model. (**B**) Genotype-specific predictions of demographic rates and selected life history parameters.

A

Population biology parameter	Observed	Predicted
Mean population size	104.83	111.23
Minimum population size	59.00	93.72
Maximum population size	174.00	149.25
Frequency of gray coat	0.56	0.62
Generation length	5.05	4.70
Dispersion of reproduction	10.13	9.87
Mean body weight	44.25	45.15
Strength of viability selection	0.27	0.24
Strength of fertility selection	4.89	4.06

B

Genotype	AA	AB	BB
Phenotype	**Black**	**Black**	**Gray**
Annual survival rate	0.47	0.77	0.75
Annual recruitment rate	0.08	0.28	0.24
Generation length	2.4	4.91	4.5
Mean lifetime reproductive success	0.031	2.35	1.83
Mean frequency	0.02	0.36	0.62

Integral projection models (IPMs)

Predictions

- The model performed well in predicting key features of the wolf population
- Provided insight into the dynamics of the coat color genotype.
- The IPM predicts that black heterozygotes have higher annual survival rates and annual reproductive rates, longer generation times, and greater lifetime reproductive success than either of the homozygotes

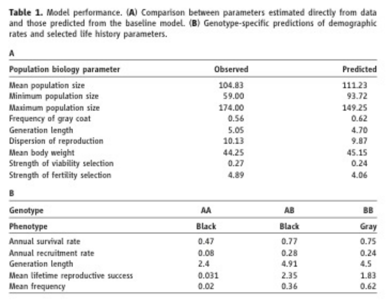


Table 1. Model performance. (**A**) Comparison between parameters estimated directly from data and those predicted from the baseline model. (**B**) Genotype-specific predictions of demographic rates and selected life history parameters.

A

Population biology parameter	Observed	Predicted
Mean population size	104.83	111.23
Minimum population size	59.00	93.72
Maximum population size	174.00	149.25
Frequency of gray coat	0.56	0.62
Generation length	5.05	4.70
Dispersion of reproduction	10.13	9.87
Mean body weight	44.25	45.15
Strength of viability selection	0.27	0.24
Strength of fertility selection	4.89	4.06

B

Genotype	AA	AB	BB
Phenotype	Black	Black	Gray
Annual survival rate	0.47	0.77	0.75
Annual recruitment rate	0.08	0.28	0.24
Generation length	2.4	4.91	4.5
Mean lifetime reproductive success	0.031	2.35	1.83
Mean frequency	0.02	0.36	0.62

Integral projection models (IPMs)

Results

- Alter mean environment ecological and evolutionary parameters inevitably change together

Integral projection models (IPMs)

Results

- Alter mean environment ecological and evolutionary parameters inevitably change together
- Alter environmental variance small impact

Imperial College London

Integral projection models (IPMs)

Results

- Alter mean environment ecological and evolutionary parameters inevitably change together
- Alter environmental variance small impact
- Rapid eco-evolutionary dynamics primarily shuffling of existing variance rather than adaptation

Integral projection models (IPMs)

Results

- Alter mean environment ecological and evolutionary parameters inevitably change together
- Alter environmental variance small impact
- Rapid eco-evolutionary dynamics primarily shuffling of existing variance rather than adaptation
- On average years will get worse for wolves (less snow, fewer prey, more disease); will hit survival and fertility

Imperial College London

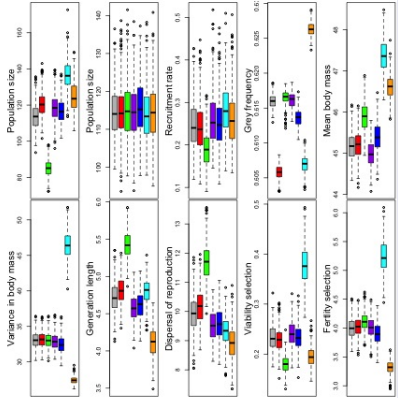
Integral projection models (IPMs)

Results

- Alter mean environment ecological and evolutionary parameters inevitably change together
- Alter environmental variance small impact
- Rapid eco-evolutionary dynamics primarily shuffling of existing variance rather than adaptation
- On average years will get worse for wolves (less snow, fewer prey, more disease); will hit survival and fertility
- increase in year-to-year variance in survival and fertility

Integral projection models (IPMs)

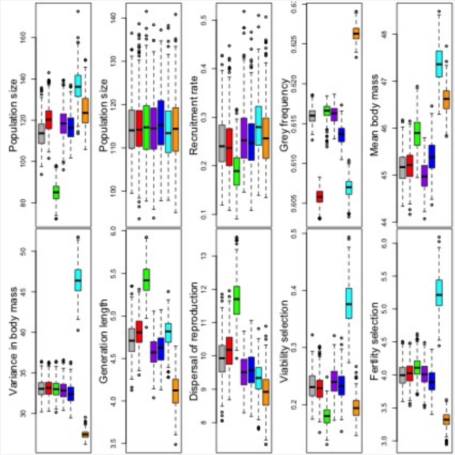
Results



- Consequences of perturbing the mean value of function intercepts (A) and (C to J) and the standard deviation of the intercept distribution (B) on the distribution of various population biology parameters

Integral projection models (IPMs)

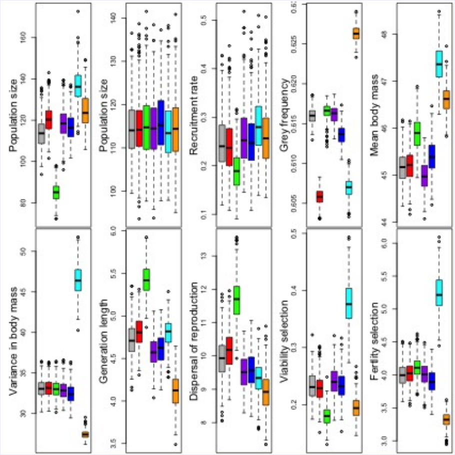
Results



- The gray distributions represent values from a simulation with no function perturbed

Integral projection models (IPMs)

Results



- The coloured distributions are from simulations in which one intercept distribution was perturbed

Summary

- When IPMs are useful in that they have a very general way to combine theory from population ecology, population genetics, quantitative genetics and life history

Summary

- When IPMs are useful in that they have a very general way to combine theory from population ecology, population genetics, quantitative genetics and life history
- Their strength not only comes from the ease with which they can be parameterized, but also from the observation that all fundamental population parameters describe a summary statistic of a character distribution or its dynamics

Summary

- When IPMs are useful in that they have a very general way to combine theory from population ecology, population genetics, quantitative genetics and life history
- Their strength not only comes from the ease with which they can be parameterized, but also from the observation that all fundamental population parameters describe a summary statistic of a character distribution or its dynamics
- Prediction requires an understanding of which parts of the life cycle environmental change will impact