

Integrated models

A scenic photograph of a grassy field with a large tree on the left, a path leading towards a building with two chimneys in the background, and a modern light pole in the foreground. The scene is lush with greenery and trees, suggesting a park or campus setting.

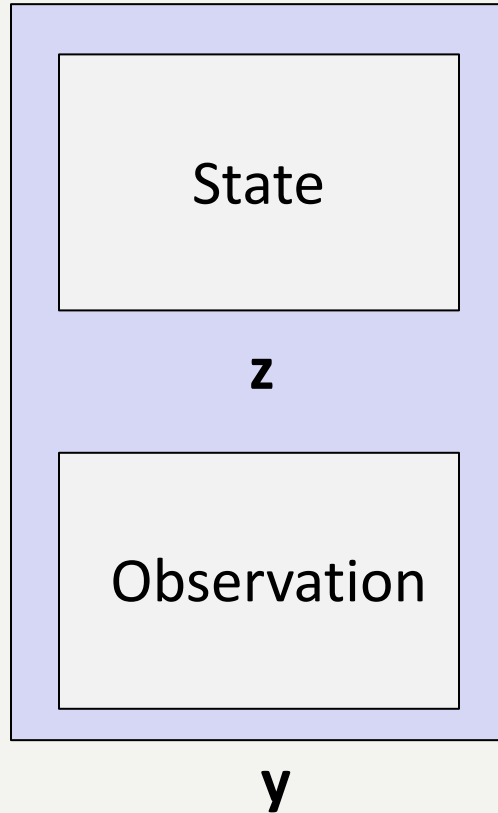
Marc Kéry

AHM Workshop
MSU, East Lansing
22–26 July 2024

The greatness of hierarchical models



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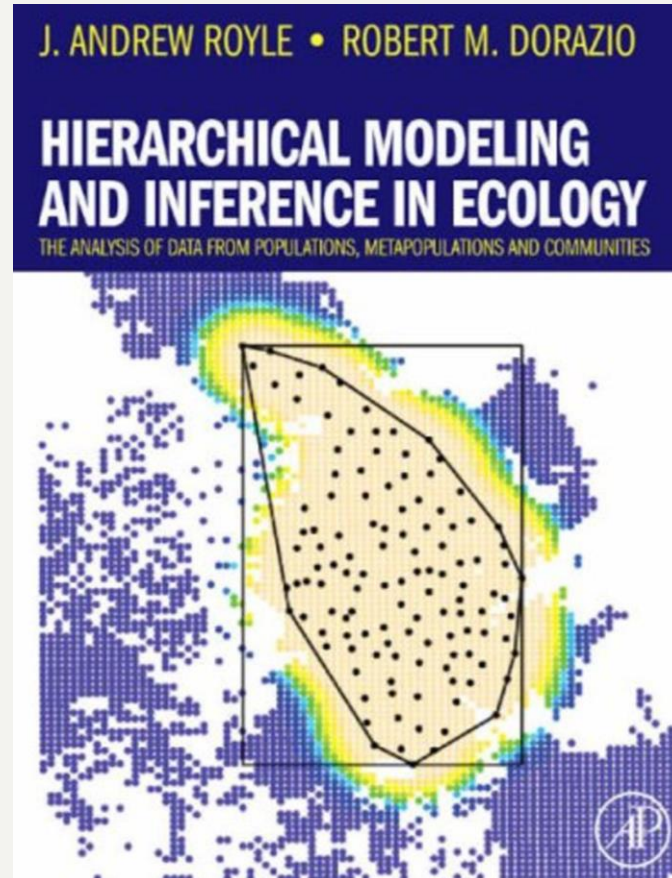


The greatness of hierarchical models



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THE SOURCE !

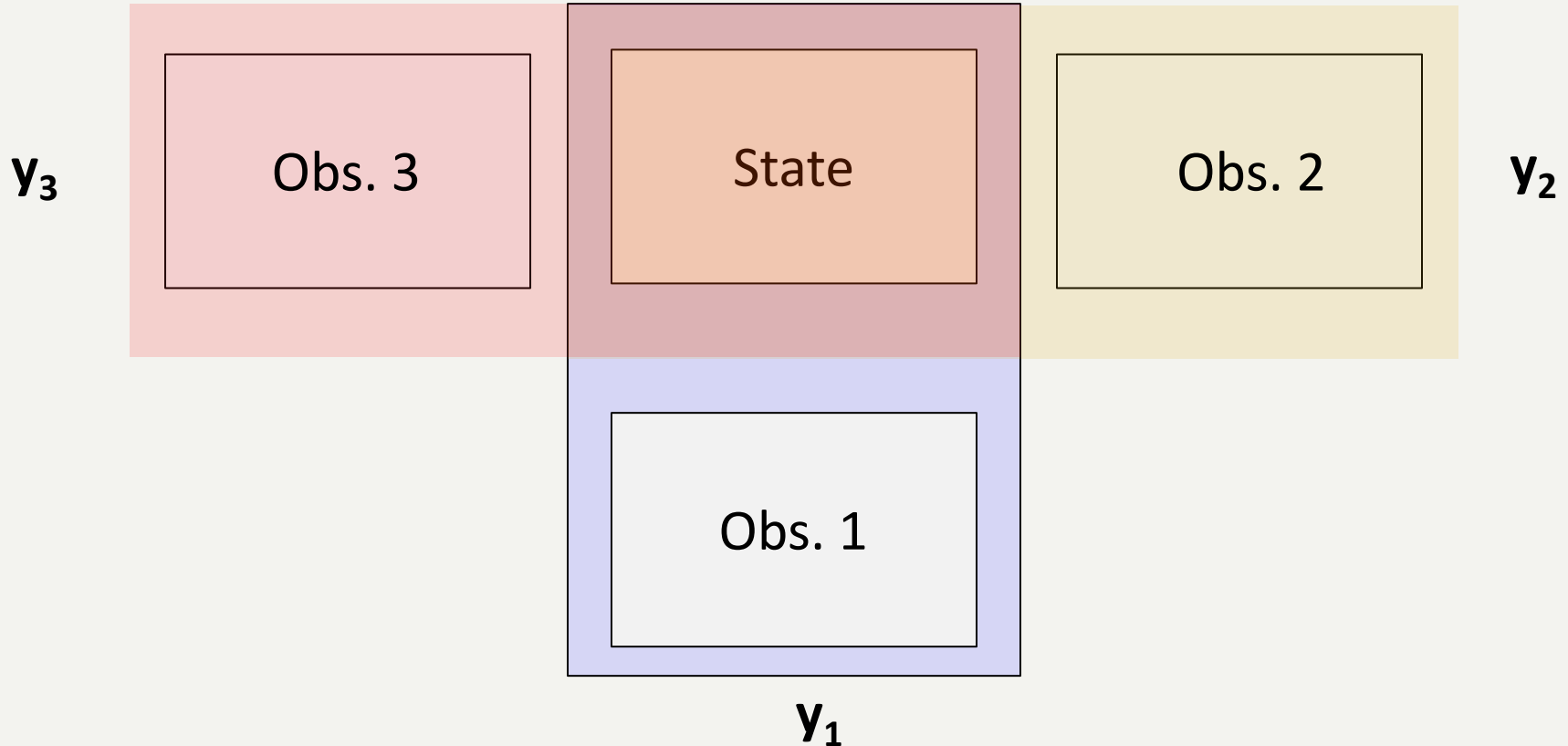


R&D 2008

The even greater greatness of integrated models



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Outline



- What ? (“use all info“ principle in statistical modeling)
- Why ? (“makes a lot of sense", + precision, + estimable params)
- How ? (joint density/likelihood = product when data independent)
- When ? / When not ? (not always !)
- Showcase a very simple integrated SDM to demonstrate the principles

What are IMs ?



- Integrated models: statistical method to share information about some underlying process by combining in a single analysis two or more data sets
- Mega-trend in statistical ecology during last 30 years
- Typically, data sets are disparate, i.e., of somewhat different kinds
- Form joint likelihood with shared parameters among likelihoods of each data set
- Joint likelihood is NOT only approach to combining information, see Pacifici et al., *Ecology*, 2017, who distinguish three methods: “sharing“, “correlation“, “covariate“
- Joint likelihood most “direct“, creates strongest link between data sets
- This is what we here define as an integrated model: joint likelihood for two or more disparate data sets with at least one shared parameter
- See Chapter 10 in AHM2: *“Integrated models for multiple types of data“*
- See Chapter 20 in Kéry & Kellner (2024 = “ASM book”), in the AHM workshop handouts

IMs as shared-process models

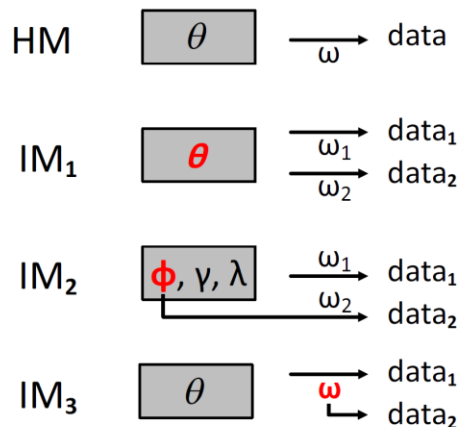


FIGURE 10.1

Schematic of hierarchical models and three variants of integrated models (IMs). In hierarchical models, we distinguish between a hidden process (the *gray box*, with one or more parameters θ) and the observations (“data”). They are linked by *arrows* representing the observation process, with one or more associated parameters ω . The shared parameter in the IMs is shown in *red*. Data sets in almost all IMs are linked through a shared parameter in the process model, as in IM₁ and IM₂. Linkage through a parameter in the observation model, as in IM₃, occurs more rarely.

(AHM2)

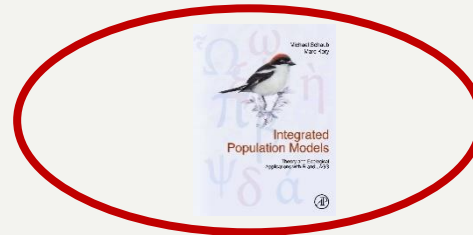
- However, not all IMs are hierarchical models (HMs); see e.g. ASM: chapter 20

Not all IMs are IPMs, or IMs and IPMs



- Integrated population models (IPMsor “the real IPMs”)
- IPMs (Besbeas et al., *Biometrics*, 2002; with independent, and earlier, developments in fisheries, starting with Archibald & Fournier 1982) have become the most highlighted example of an IM in population ecology; see also our recent book (Schaub & Kéry, AP, 2022).

IPMs



Not all IMs are IPMs, or IMs and IPMs



- Integrated population models (IPMsor “the real IPMs”)
- IPMs (Besbeas et al., *Biometrics*, 2002; with independent, and earlier, developments in fisheries, starting with Archibald & Fournier 1982) have become the most highlighted example of an IM in population ecology; see also our recent book (Schaub & Kéry, AP, 2022).
- But principles of IPMs extend to vastly more classes of models than “just” population models



The real IPMs

- e.g., have time-series of counts, capture-recapture data, productivity data (e.g., nestling counts) -> Integration vehicle typically a matrix population model
- Dail-Madsen can serve, too; see Chap. 20 in the IPM book ("Kestrel" case study), also Jimenez *et al.* 2023
- (For individual-based IPMs see Chandler & Clark, MEE, 2014, & Chap. 21 in IPM book)

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KESTREL	
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<p>IPM ingredients: time series of counts (monitoring data), capture-recapture data (data sets), dead-recovery data</p> <p>Location: Switzerland</p> <p>Spatio-temporal scale: 16,000 km², 19 years</p>	
<p>20.1 INTRODUCTION</p> <p>Space can safely be predicted to become a big topic for integrated population models (IPMs) as it has in many other branches of ecological statistics over the last 20 years or so. In the case of IPMs, one reason for space becoming more important, of course, is that its inclusion increases our understanding of population dynamics—populations are typically spatially structured, and hence, their dynamics can be better understood when space is included. However, the main reasons for the use of space that can be predicted for IPMs are arguably the increasing availability of spatially replicated data and great progress in computational power and understanding in the treatment of space in statistics. Hence, we now see increasing numbers of locations from which data on the demography of a species become available. While most</p>	

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The Cantabrian capercaillie: A population on the edge

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^k Swiss Ornithological Institute, Sempach, Switzerland

HIGHLIGHTS

- Cantabrian capercaillie population has recently been classified as "critically endangered" by Spanish Government.
- To develop management plans, information on demographic parameters are necessary to understand population dynamics.
- In 2019 we estimated the size of population at 191 individuals.
- Since the 1970s, we estimated a shrinkage of the population range by 85%.
- Annual survival was estimated at 0.707 and post-recruitment at 0.223.

GRAPHICAL ABSTRACT

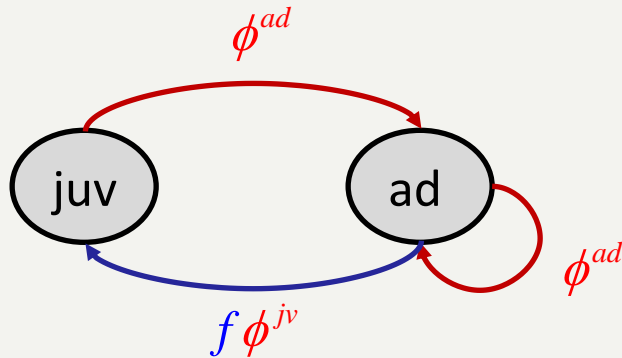
Distribution map for the 1970s (from Castrovieja et al., 1974) and current range of the Cantabrian capercaillie. In the inset, location of the study area in Spain.



Real IPMs in a nutshell



- Matrix model is the usual integration vehicle (e.g., Caswell bible)
- Imagine a time-series of counts of adults such as $C = c(10, 18, 5, 12, \dots)$
- Decision on when you observe, e.g., pre- or post-breeding "census"
- What life-stages do you want to distinguish ? Which are there during that time point ?
- Draw the life-cycle graph, deduce equations from that & translate into BUGS



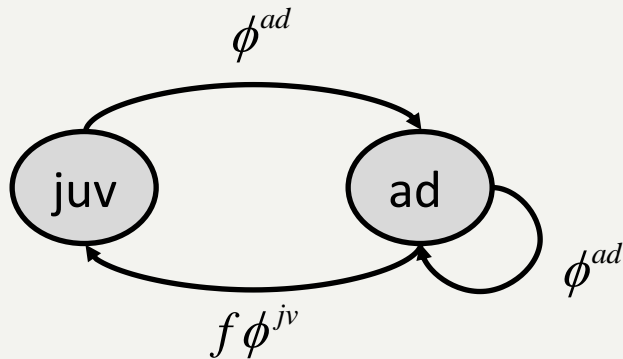
$$\begin{pmatrix} N_{t+1}^{juv} \\ N_{t+1}^{ad} \end{pmatrix} = \begin{bmatrix} 0 & f\phi^{juv} \\ \phi^{ad} & \phi^{ad} \end{bmatrix} \begin{pmatrix} N_t^{juv} \\ N_t^{ad} \end{pmatrix}$$

$$\begin{aligned} N[t+1,1] &= 0*N[t,1] + f*\phi1*N[t,2] \\ N[t+1,2] &= \phi2*N[t,1] + \phi2*N[t,2] \end{aligned}$$

Real IPMs in a nutshell



- But can't estimate parameters from time-series of counts alone :(
- (remember the data : $C = c(10, 18, 5, 12, \dots)$)

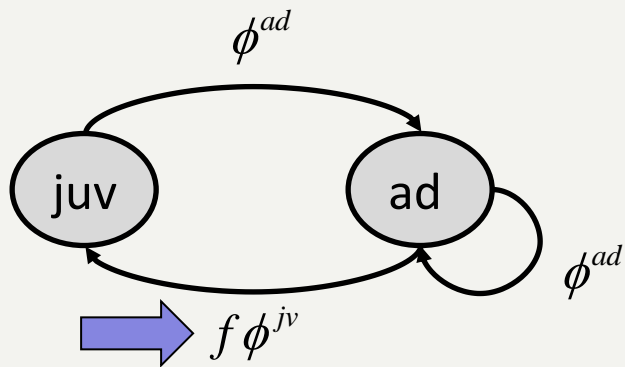


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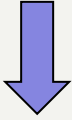
Real IPMs in a nutshell



- So bring in the other data



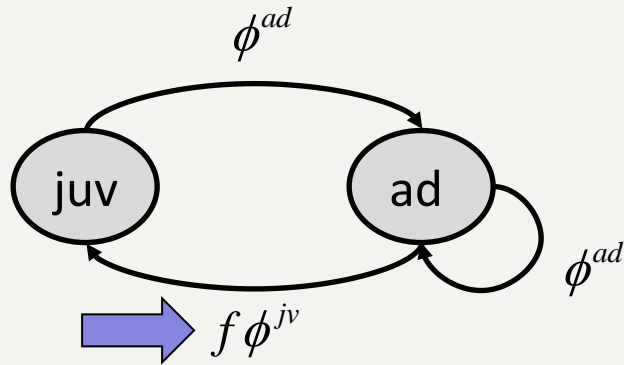
Counts of young


$$\begin{pmatrix} N_{t+1}^{juv} \\ N_{t+1}^{ad} \end{pmatrix} = \begin{bmatrix} 0 & f\phi^{juv} \\ \phi^{ad} & \phi^{ad} \end{bmatrix} \begin{pmatrix} N_t^{juv} \\ N_t^{ad} \end{pmatrix}$$

Real IPMs in a nutshell



- So bring in the other data



Counts of young

Cap-recap data (CJS)

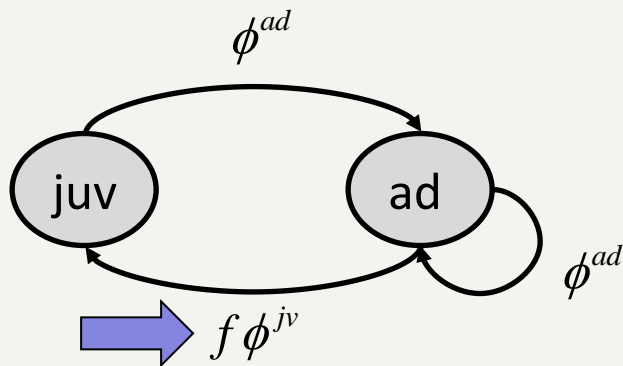
$$\begin{pmatrix} N_{t+1}^{juv} \\ N_{t+1}^{ad} \end{pmatrix} = \begin{bmatrix} 0 & f\phi^{juv} \\ \phi^{ad} & \phi^{ad} \end{bmatrix} \begin{pmatrix} N_t^{juv} \\ N_t^{ad} \end{pmatrix}$$

A blue arrow points down to the top-right element of the matrix, $f\phi^{juv}$. A red arrow points down to the bottom-left element of the matrix, ϕ^{ad} . A red arrow points up to the bottom-left element of the matrix, ϕ^{ad} .

Real IPMs in a nutshell



- So bring in the other data



$$\begin{pmatrix} N_{t+1}^{juv} \\ N_{t+1}^{ad} \end{pmatrix} = \begin{bmatrix} 0 & f\phi^{juv} \\ \phi^{ad} & \phi^{ad} \end{bmatrix} \begin{pmatrix} N_t^{juv} \\ N_t^{ad} \end{pmatrix}$$

A blue arrow points down to the top-right element $f\phi^{juv}$ of the matrix. A red arrow points up to the bottom-left element ϕ^{ad} of the matrix.

..... And suddenly you can !

IPMs, informative priors, and sequential analyses



- Analysis of all data sets at once

$$\mathbf{y}^* = \mathbf{y}_1, \mathbf{y}_2, \mathbf{y}_3$$

$$p(\boldsymbol{\theta}^* | \mathbf{y}^*) = \frac{p(\mathbf{y}^* | \boldsymbol{\theta}^*) p(\boldsymbol{\theta}^*)}{p(\mathbf{y}^*)}$$

IPMs, informative priors, and sequential analyses



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- ... yields same posterior as is the final posterior of a sequential analysis

$$p(\boldsymbol{\theta}_1 | \mathbf{y}_1) = \frac{p(\mathbf{y}_1 | \boldsymbol{\theta}_1) p(\boldsymbol{\theta}_1)}{p(\mathbf{y}_1)}$$

IPMs, informative priors, and sequential analyses



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IPMs, informative priors, and sequential analyses



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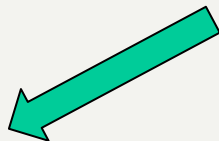
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IPMs, informative priors, and sequential analyses



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That is,

$$p(\boldsymbol{\theta}_3 | \mathbf{y}_3) = p(\boldsymbol{\theta}^* | \mathbf{y}^*)$$

Very incomplete overview of IMs (from AHM2)



Table 10.1 An incomplete overview of integrated models (IMs) for inference about distribution, abundance, demography, and movement. SCR denotes spatial capture-recapture. Combination types printed in boldface are illustrated in this chapter.

Data Types Combined	Reference
Capture-recapture, dead-recovery data	Burnham (1993), Lebreton et al. (1995), Catchpole et al. (1998)
Capture-recapture, dead-recovery data, incidental observations	Barker (1997, 1999)
Capture-recapture, telemetry	Nasution et al. (2001)
Unmarked counts, capture-recapture	Besbeas et al. (2002, 2003)
Capture-recapture, carcass examination data	Goodman (2004)
Age-at-harvest data, tag recovery data	Conn et al. (2008)
Occupancy, capture-recapture	Conroy et al. (2008)
Counts, telemetry, capture-recapture	Johnson et al. (2010b)
Two different sign counts (burrows, pellets)	Wilson et al. (2010)
Occupancy, counts	Pagel and Schurr (2012), Pagel et al. (2014)
Noninvasive genetic SCR data, telemetry data	Sollmann et al. (2013a,b)
Mark-resight, telemetry	Sollmann et al. (2013b)
SCR data, telemetry	Royle et al. (2013), Linden et al. (2018)
Occurrence data at two different spatial grains	Keil et al. (2013, 2014), Pacifici et al. (2019)

Very incomplete overview of IMs (from AHM2)



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Capture-recapture, dead-recovery data	Burnham (1993), Lebreton et al. (1995), Catchpole et al. (1998)
Closed and open capture-recapture data	Pollock's robust design (Pollock 1982, Kendall et al. 1997)
Capture-recapture, dead-recovery data, incidental observations	Barker (1997, 1999)
Capture-recapture, telemetry	Nasution et al. (2001)
Unmarked counts, capture-recapture	Besbeas et al. (2002, 2003)
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Very incomplete overview of IMs (from AHM2), ctd.



Distance sampling, time removal

Noninvasive SCR data, count data

Opportunistic point pattern data, replicated counts

Capture-recapture, counts, age-at-harvest data

Telemetry, counts

Capture-recapture, counts

SCR data, occupancy data

Opportunistic presence-only data, occupancy data

SCR data, opportunistic point pattern, telemetry

Occupancy data, count data

Noninvasive SCR data, occupancy data

Camera-trapping, live trapping, telemetry

Counts, distance sampling, time-to-detection

SCR data, distance sampling

Counts, telemetry

SCR data, telemetry

Counts, telemetry, capture-recapture, reproductive data

Various combinations

Very various combinations

Amundson et al. (2014)

Chandler and Clark (2014)

Dorazio (2014), Miller et al. (2019)

Lee et al. (2015)

Schmidt et al. (2015)

Ahrestani et al. (2017), Zhao et al. (2019)

Clare et al. (2017)

Koshkina et al. (2017), Fletcher et al. (2019)

Tenan et al. (2017b)

Zipkin et al. (2017)

Dey et al. (2017)

Jiménez et al. (2017)

Péron and Garel (2019), Hostetter et al. (2019)

Chandler et al. (2018)

Ketz et al. (2018)

Augustine et al. (2018b), Murphy et al. (2019)

Regehr et al. (2018)

2019 Special Feature in *Ecology*: Fletcher et al. (2019), Pacifici et al. (2019), Plard et al. (2019), Saunders et al. (2019), Van Schmidt et al. (2019), Zipkin et al. (2019); and also Gamble et al. (2020)
The IPM book (Schaub and Kéry, 2021)

The why and how of IMs, or: a fresh look at IMs



- IMs represent simply the same old principle of a parametric statistical model: formulate the joint density of all observed data (and possibly latent variables, too)
 - Use of all available data make sense
 - More data is better: more precision, perhaps more params estimable
 - Not all data points (=random variables) have the same distribution
 - For each datum, specify density as a function of parameters that are shared among data
- Look at this in two trivially simple examples

The why and how of IMs, or: a fresh look at IMs



- Joint likelihood/density for all data in an analysed data set:
-> basic principle of likelihood-based statistical inference with either maximum likelihood or Bayesian posterior inference
- Express probability of data set as a joint density, then view that as a function of the unknown parameters = likelihood function
- Imagine very simple case: have observed species richness at five sites and want to infer mean and spatial variation of species richness at a statistical “population” of sites from which our sample of 5 sites stems from
- Ignore discreteness of data and imperfect detection and assume Normal distribution is suitable model
- See Example 1 R code

Joint density in statistical inference (Ex. 1)



- Example 1:
- [1] 44 52 42 66 53

$$y_1 \sim \text{normal}(\mu, \sigma)$$

$$y_2 \sim \text{normal}(\mu, \sigma)$$

$$y_3 \sim \text{normal}(\mu, \sigma)$$

$$y_4 \sim \text{normal}(\mu, \sigma)$$

$$y_5 \sim \text{normal}(\mu, \sigma)$$

- Likelihood = joint density: product of densities of each random variable (= datum)

$$L(\mu, \sigma \mid y_{1\dots 5}) = \text{dnorm}(y_1, \mu, \sigma) \times \text{dnorm}(y_2, \mu, \sigma) \times \\ \text{dnorm}(y_3, \mu, \sigma) \times \text{dnorm}(y_4, \mu, \sigma) \times \text{dnorm}(y_5, \mu, \sigma) =$$

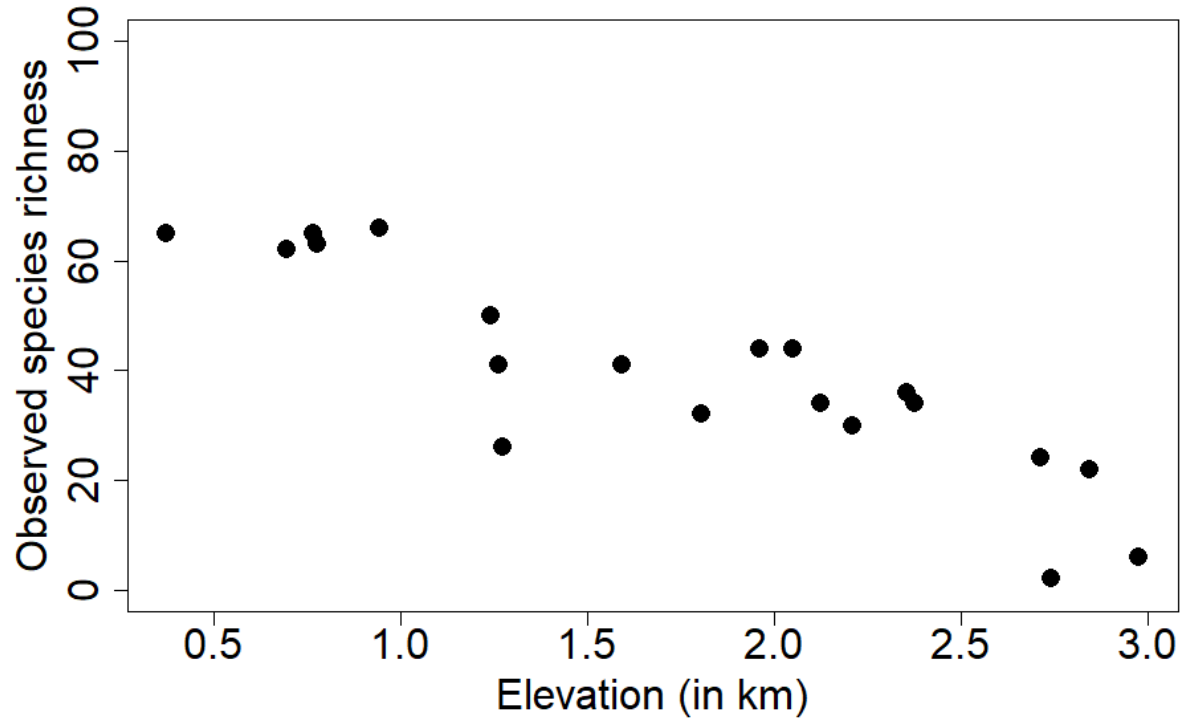
$$\prod_{i=1}^5 \text{dnorm}(y_i, \mu, \sigma)$$

Joint density in statistical inference (Ex. 1)



- What we see in example 1:
 - we can't estimate anything with a single datum,
 - without sharing some information, nothing can be estimated
 - but we can with 2 or more data point
 - more data means:
 - more information
 - less estimation error (point estimates closer to target)
 - more precision (asymptotic SEs become smaller)
- Parameters μ and σ are shared among all random variables/data and estimated jointly from the data
- But note: this is NOT an integrated model, but simply meant to illustrate the principle of a joint density, which will also be basis for joint likelihood in an IM

Joint density in statistical inference (Ex. 2)



Joint density in statistical inference (Ex. 2)



- Example 2 (where density depends on some covariate x):

$$y_1 \sim \text{normal}(\mu_1, \sigma) \quad , \text{ where } \mu_1 = \alpha + \beta * x_1$$

$$y_2 \sim \text{normal}(\mu_2, \sigma) \quad , \text{ where } \mu_2 = \alpha + \beta * x_2$$

$$y_3 \sim \text{normal}(\mu_3, \sigma) \quad , \text{ where } \mu_3 = \alpha + \beta * x_3$$

....

$$y_{20} \sim \text{normal}(\mu_{20}, \sigma) \quad , \text{ where } \mu_{20} = \alpha + \beta * x_{20}$$

- Likelihood = joint density: product of densities of each random variable (= datum)

$$\begin{aligned} L(\alpha, \beta, \sigma \mid y, x) &= d\text{norm}(y_1, \alpha + \beta x_1, \sigma) \times d\text{norm}(y_2, \alpha + \beta x_2, \sigma) \times \\ &\quad d\text{norm}(y_3, \alpha + \beta x_3, \sigma) \times \dots \times d\text{norm}(y_{20}, \alpha + \beta x_{20}, \sigma) = \\ &\quad \prod_{i=1}^{20} d\text{norm}(y_i, \alpha + \beta x_i, \sigma) \end{aligned}$$

Joint density in statistical inference (Ex. 2)



- What we see in example 2: same really as in example 1
- Now, parameters α , β and σ are shared among all random variables/data and estimated jointly from all the data
- This is again NOT an integrated model, but is meant to illustrate the principle of a joint density, or (similarly) a joint likelihood

Summary on why and how of IMs



- By analogy with any likelihood we can say this about IMs:
- **HOW:** formulate the likelihood as a product of the densities of all random variables (= data points, which now are in different data sets !), as in any statistical inference
- **WHY:** Similarly as in any likelihood, using all the information on some estimation problem means:
 - It makes more sense to use all pieces of information we have
 - We get better estimates (e.g., more accurate, more precise)
 - Sometimes we can estimate a parameter that we cannot with less information

Example of a very simple IM in an SDM context

- See Chapter 20 from ASM book (handout)



Fig. 20–2: A flock of common swifts (*Apus apus*) above the village of Glovelier, Swiss Jura mountains (Photo Alain Georgy).

Normally, our preference would be for an SDM that contains an explicit representation of the false-negative errors that always occur when collecting such data in the field. That is, for a



When/when not integrate ?



- When have multiple pieces of information that bear on the same inference problem, then it probably always makes sense to at least consider exploitation of all that information in a formal way.
- This is an integrated model, and you may expect to get all the advantages associated with it

When/when not integrate ?



- However, there are costs, too, to using an integrated model:
 - Model more complex, to understand, to build, to fit, and to explain to others
 - Costs of added complexity must be more than compensated for by the benefits of increased precision and/or ability to estimate more params
 - Adding rubbish data may make things worse
- Decision should also depend on the **objective of the modeling**
- e.g., when have counts + CMR + fecundity data,
- ... but interest in population trend, then perhaps don't fit a full IPM,
but just use GL(M)M on counts
- ... but interest on survival, perhaps just use CMR data and fit a CJS

Future research in integrated models



- Where does the information come from ?
- Contributions of different data sets to estimate a parameter in the model ?
- Goodness-of-fit
- Independence: meaning, diagnosis and consequences of non-independence
- More mechanistic observation models for the count data in an IPM
(Normal strange choice really for discrete integers....)
- Specifically, combine IPMs with more regular estimation models for abundance, such as Jolly-Seber, closed-population abundance, Nmix Problem there !
---- in BUGS implementation, leads to N being both a derived (= deterministic) quantity and a stochastic one.... Not possible