# ansom . yers ( 

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State-Space Moded for Movement and Habitat Use


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## Imperial Mathematician




## Kepler's elliptical orbit for Mars..



## Imperial Mathematician



## Argos Satellite Telemetry Data

## Getting more out of the data

Goals of State-Space analysis

- Infer true locations from noisy data
- Account for error w/out loss of information
- Infer behaviour, test hypotheses



## Argos Satellite Telemetry Data

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- Infer true locations from noisy data
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- Infer behaviour, test hypotheses



## Data Filtering \& State Estimation

Jonsen et al. 2005. Ecology 86:2874-2880


Jonsen, Flemming and Myers (2005) Ecology 86: 2874-2880


## Noisy Data: ad-hoc Filtering

Extreme values removed prior to analysis


## State-Space Filtering is Fundamentally Different

 Location estimates w Cls \& parameter estimation$$
\alpha_{1} \alpha_{2} \alpha_{3} \alpha_{4} \alpha_{5} \ldots \alpha_{T} ; \gamma, \sigma, \tau
$$

## State-Space Filtering is Fundamentally Different

 Location estimates w Cls \& parameter estimation$$
\begin{aligned}
& \mathbf{Y}_{1} \mathbf{Y}_{2} \mathbf{Y}_{3} \mathbf{Y}_{4} \mathbf{Y}_{5} \mathbf{Y}_{6} \mathbf{Y}_{7} \mathbf{Y}_{8} Y_{9} \mathbf{Y}_{10} \mathbf{Y}_{11} \mathbf{Y}_{12} \ldots \mathbf{Y}_{\mathbf{T}} \\
& \\
& \\
& \text { We also carried out } \\
& \text { likelihood analysis } \\
& \alpha_{1} \alpha_{2} \alpha_{3} \alpha_{4} \alpha_{5} \ldots \alpha_{T} ; \gamma, \sigma, \tau
\end{aligned}
$$

## State-Space Filtering is Fundamentally Different

 Location estimates w Cls \& parameter estimation$$
Y_{1} Y_{2} Y_{3} Y_{4} Y_{5} Y_{6} Y_{7} Y_{8} Y_{9} Y_{10} Y_{11} Y_{12} \ldots Y_{T}
$$



$$
\alpha_{1} \alpha_{2} \alpha_{3} \alpha_{4} \alpha_{5} \cdots \alpha_{T} ; \gamma, \sigma, \tau
$$

## What are State Space Models

- Analysis of sequential data observed with error
- Estimate unobservable states from error-prone observations
- Simultaneously deal with process variability \& estimation error
- Accomodates non-Gaussian errors, nonlinear dynamics, and other complexities in the data
- Accomodates missing observations


## Why State Space Models?

- Simply one of the key "right ways" to think about many modern problems
- Engineers, Economists, Oceanographers use this approach
- State-space models used for:

Tracking moving objects
Shooting down missiles
Predicting stock market trends
Predicting global circulation patterns
Speech recognition

## The First State-Space Model:

 the Kalman Filter$$
\text { Process Model : } \quad y_{k+1}=A_{k} y_{k}+u_{k}
$$

Measurement Model: $\quad x_{k}=M_{k} y_{k}+v_{k}$

- Used to estimate state variables, not dynamical parameters
- Can be applied to non-stationary processes.
- Measurement noise and process noise are white and Gaussian.
- Dynamics are linear.


## State-Space Concept



## State Space Models

## Measurement Equation

- Relates imperfect observations to true position
- Estimate ARGOS error with $\varepsilon$

Transition Equation

- Predicts next position from behavioral model


## Error function



$$
\alpha_{t}=f\left(\alpha_{t-1}, \eta_{t} ; \gamma\right)
$$

$$
y
$$

movement function

## What is important about the transition equation?

$$
\alpha_{t}=f\left(\alpha_{t-1}, \eta_{t} ; \gamma\right)
$$

The state variable is random variable, and should NOT be thought of as a simple number. The above equation can be better interpreted as the probability of a given state value $\alpha_{t}$ Thus, we write the state as a Greek letter, $\alpha_{t}$ Consider the simplest model where the mean for the next time period is a simple multiple of this years state.

$$
p\left(\alpha_{t} \mid \alpha_{t-1}\right)=\mathcal{N}\left(\alpha_{t-1} \gamma, \sigma\right)
$$

## What is important about the state equation?

$$
\alpha_{t}=f\left(\alpha_{t-1}, \eta_{t} ; \gamma\right)
$$

The state variable is random variable, and should NOT be thought of as a simple number. We write the state as a greek letter, $\alpha_{t}$

How is this programmed with BUGS

$$
\begin{aligned}
& \text { mean }[t]<-\quad f(\text { alpha }[t-1] ; \gamma) \\
& \text { alpha }[t] \sim \text { dlnorm (mean[t], sigma) }
\end{aligned}
$$

This symbol means "is distributed as", and implies that alpha[t] is a random variable.

$1^{\text {st }}$ location $=$ release point
eg. release location estimated with GPS

Apply dynamics (transition eqn)

Observe a location with error

Integrate over predicted \& observed densities (Bayes Rule)

Updated prediction becomes prior for next time step

## Software

WinBUGS: Bayesian Analysis Using Gibbs Sampling

Bayes Rule

$$
\begin{aligned}
& \text { R( } \left.\alpha_{t} \mid \mathrm{Y}_{t} ; \gamma\right)=\frac{p_{y}\left(\mathbf{y}_{t} \mid \alpha_{t}\right) p\left(\alpha_{t} \mid \mathrm{Y}_{t-1} ; \gamma\right)}{\int p_{y}\left(\mathbf{y}_{t} \mid \alpha_{t}\right) p\left(\alpha_{t} \mid \mathrm{Y}_{t-1} ; \gamma\right) d \mathbf{x}_{t}}
\end{aligned}
$$

This is the innovation likelihood

## Movement (Transition) Equation

- First difference correlated random walk
$\mathrm{d}_{\mathrm{t}}=\gamma \mathrm{T}(\theta) \mathrm{d}_{\mathrm{t}-1}+\mathrm{N}_{2}(0, \Sigma)$
$\alpha_{\mathrm{t}}=\alpha_{\mathrm{t}-1}+\mathrm{d}_{\mathrm{t}}$

Observation Equation
$y_{t}=t$-distribution $\left(\alpha_{t}, \sigma_{t}, v_{t}\right)$

Plus an algorithm to regularize estimated locations in time

## Movement (Transition) Equation

$$
\begin{aligned}
& \mathrm{d}_{\mathrm{t}}=\gamma \mathrm{T}(\theta) \mathrm{d}_{\mathrm{t}-1}+\mathrm{N}_{2}(0, \Sigma) \quad \boldsymbol{Z}_{0}, \quad \theta \text { (turn angle) }
\end{aligned}
$$

$$
\alpha_{t}=\alpha_{t-1}+d_{t}
$$

$\alpha_{\mathrm{t}} \quad \alpha_{\mathrm{t}-1}$

## Observation Equation

$y_{t}=\mathrm{t}$-distribution $\left(\alpha_{t}, \sigma_{t}, v_{t}\right)$
$\alpha_{t}$
$y_{t}$

## Dealing with Complex Data Argos telemetry data

- Observations made irregularly through time
- Observation errors non-Gaussian (extreme values)
- Observation errors vary through time


## "Ideal" Data

Regular time intervals with constant Gaussian errors, \& no missing data


## "Real" Data

Irregular time intervals with varying non-Gaussian errors, \& missing data


Time

## Sources of Uncertainty

- Estimation error
- Data observed with error
- Errors can be nonGaussian



Radio or acoustic telemetry

## Argos location errors


data from Vincent et al. 2002

## Argos errors follow $t$-distributions:



Jonsen, Flemming, Myers, Ecology, 2005


## Tag Precision

## $y_{t}=\mathrm{t}$-distribution $\left(\alpha_{t}, \mathrm{C} \sigma_{v}, v_{t}\right)$

O for each location class is assumed known (Vincent et al. 2002, Jonsen et al 2005)

C is an estimated parameter that scales the variance to each tag

Best tags are 1000's of times more precise than the worst tags

Best tags in a single lot can be 100's of times more precise than worst tags

 from a lot

State-space models allow you to think about things, that it is very difficult to think about otherwise
Navigation: Estimating the "Circle of Confusion"
Flemming et al. in press. Environmetrics


Regularized Track of Turtle 18284


Corresponding GC Route


Longitude

It is essential to treat groups of animals simultaneously for maximum utility of the data.

## Leatherback turtles are unique in that they expose their pineal spot to sunlight.

## Turtles are close to the surface during the day during migration



James et al. in review

# Examining Diel Migration Behaviour in Leatherbacks 



Jonsen, James Myers. in review. Journal of Animal Ecology


## Hierarchical Bayes State-Space Model (HB SSM)



## HB SSM



## Conventional Approaches Do Not Work



## Results are consistent with the hypothesis that the pineal spot improves navigation.

# Dynamics of behavior is very nonlinear, to determine hot spots and foraging 

- Solution: Markov switching models between behavioral modes
- Dynamics within a behavioral mode is linear


## State-Space Switching Models

## A. Unemployment


B. Probability of State 2

C. Probability of State 3


Federal Reserve Bank of St. Louis Review, July/August 2005, 87(4), pp. 435-52.


## Summary

- State-space models allow you to think about problems which have no conventional solution
- Fundamentally different approach to analysis of complex, error-prone data emphasis on estimation of "true" states, biological parameters and uncertainty
- Models can be fit to other types of sequential movement data (GPS, Archival tags)


## The Future

- Better incorporation of oceanographic data
- Model testing, statisticians do NOT know how to compare models with nonGaussian errors
- More "user friendly" (i.e. less "user angry" methods). This would include an easy to use library with a variety of possible behaviour.


# Critical Spatial/Temporal Models Tools 

Ransom A. Myers (RAM) Dalhousie University, Canada


Pew Global Sharks Assessment FMAP (Future of Marine Animal Populations) Sloan Census of Marine Life
http://fish.dal.ca
Lenfest Foundation

What was the most common large animal in the world? (perhaps this one was)


## Loss of sharks in the Gulf of Mexico

300 fold_decline - no_nene noticed


Oceanic Whitetip captures per 10,000 hooks

Circumstantial evidence of
oceanic whitetip sharks being common in the Gulf of Mexico


## Critical Modeling Tools

- Generalized linear models with negative binomial error
- Generalized linear mixed effects models to standardize old and new surveys

a. Northern Gulf of Mexico bottom shrimp trawl survey
b. NMFS offshore bottom trawl survey
c. NMFS inshore bottom trawl survey
d. Southeast U.S. SEAMAP bottom shrimp trawl survey
e. North Carolina Institute of Marine Sciences longline survey
f. Crooke commericial longline data
$\mu$. Meta-analytic mean


## Loss of Dusky Sharks in the Eastern US








## Consequences of "protection" since 1993: Rate of decline has increased:




Instantaneous rate of change in abundance
Change in trend since 1993

## Critical Modeling Tools

Surveys vary in time, and the sharks move seasonally up and down the coast

We used a generalized linear mixed effect model with negative binomial errors to describe the seasonal movement up and down the coast by allowing the seasonal harmonics to be an interaction, i.e. latitude and harmonics.

## Reduce fishing mortality for sensitive species for survival of the species

Dusky
Silky
Blacktip
Bigeye thresher
Common thresher
Scalloped hammerhead
White
Mako
Tiger
Blue
Oceanic whitetip



Proportional reduction of fishing mortality

## Critical Modeling Tools

- Calculus
- Generalized linear models


## Hammerhead sharks

## Sphyrna lewini




Science. Jan. 2003. J.K. Baum, R.A. Myers, D.G. Kehler, B. Worm, S.J. Harley, P.A. Doherty

## Results



## Critical Modeling Tools

- Development of a new regression model that does not use "zeros" (we believe the fishermen sometimes lie).
- Robustness analysis that show results are robust to alternative assumptions


| 1 Caribbean | 6 NE Coastal |
| :--- | :--- |
| 2 Gulf of Mexico | 7 NE Distant |
| 3 Florida | 8 Sargasso |
| 4 S Atlantic Bight | 9 S America |
| 5 Mid Atlantic Bight |  |



## Same results for trawl surveys in Gulf of <br> Mexico <br> Scalloped hammerhead



## Same results for trawl surveys in Gulf of Mexico

Great hammerhead


Shepherd and Myers Ecology Letters 2005

## Decline of Mediterranean Sharks

By catch associated with a Tuna Trap
In Ligurian Sea
"Tonnara di Camogli"


## Decline of Hammarhead sharks



Boero F. \& A. Carli 1979 - Boll. Mus. Ist. Biol. Univ. Genoa (47)

## Decline of Mediterranean Sharks

## By catch associated with a Tuna Trap

In Tirrenian Sea

"Tonnarella di Baratti"


Hammerhead shark


School shark


Smooth-hound


## Critical Modeling Tools

- Repeat analysis world wide using a metaanalytic approach



## Critical Modeling tools:

- Generalized linear models to standardize historical surveys, e.g. diurnal differences
- Mapping historical surveys on recent Stratified Random design


Catch Per Hundred Hooks, Year $=1952$


Catch Per Hundred Hooks, Year $=1953$


Catch Per Hundred Hooks, Year $=1954$


Catch Per Hundred Hooks, Year $=1955$


Catch Per Hundred Hooks, Year $=1956$


Catch Per Hundred Hooks, Year $=1957$


Catch Per Hundred Hooks, Year $=1958$


Catch Per Hundred Hooks, Year $=1959$


Catch Per Hundred Hooks, Year $=1960$


Catch Per Hundred Hooks, Year $=1961$


Catch Per Hundred Hooks, Year $=1962$


Catch Per Hundred Hooks, Year $=1963$


Catch Per Hundred Hooks, Year $=1964$


Catch Per Hundred Hooks, Year $=1965$


Catch Per Hundred Hooks, Year $=1966$


Catch Per Hundred Hooks, Year $=1967$


Catch Per Hundred Hooks, Year $=1968$


Catch Per Hundred Hooks, Year $=1969$


Catch Per Hundred Hooks, Year $=1970$


Catch Per Hundred Hooks, Year $=1971$


Catch Per Hundred Hooks, Year $=1972$


Catch Per Hundred Hooks, Year $=1973$


Catch Per Hundred Hooks, Year $=1974$


Catch Per Hundred Hooks, Year $=1975$


Catch Per Hundred Hooks, Year $=1976$


Catch Per Hundred Hooks, Year $=1977$


Catch Per Hundred Hooks, Year $=1978$


Catch Per Hundred Hooks, Year $=1979$


Catch Per Hundred Hooks, Year $=1980$


## Critical Modeling Tools

- Plot the data and think for yourself


## Common patterns of decline



## Critical Modeling tools:

- Nonlinear Mixed Effect Models to Describe Common Patters


## Totally Stupid Reasons for not Believing the Obvious

- You ignore research surveys.
- Removing Large Predators Couldn't Possibly Affect Survival of Other Fish.
- Fishing Couldn't Possibly Affect the Size of Tuna.
- Fishermen are so stupid they cannot use satellite data to find tuna.
- Fishermen are so stupid that they don't improve their gear.

These estimates are conservative: Fishermen are smarter (GPS, satellite information, ACDP (Acoustic Current Doppler Profiler)).



Locations of a leatherback turtle over a two week period tagged by my student Mike James that maintains its position within a cold core ring (somehow).

## Study area



# Analysis repeated using independent research data 



Change in biomass or abundance
Ward and Myers 2005 Ecology

These estimates are conservative:
(fish are smaller)


Size (kg)

## Change in body size



Ward and Myers 2005 Ecology


Ward and Myers 2005 Ecology


## Critical Modeling tools:

- Generalized linear mixed effects models to standardize historical surveys for depth and soak time


## Loss of sharks in the Gulf of Mexico 300 fold decline - no one noticed



Oceanic Whitetip captures per 10,000 hooks

## What about prey fish?



Illustration taken from the book "Encyclopedia of Canadian Fishes" by Brian W. Coad with Henry Waszczuk and Italo Labignan, 1995,

## Explosion of Pomfrets in the Gulf of Mexico $\sim 1000$ fold increase - no one noticed



Pomfret captures per 10,000 hooks

## The Rise of the Marine Mesopredators



Pelagic Sting Ray Pteroplatytrygon violacea


## Explosion of Pelagic Stingrays in the Gulf of Mexico ~1000 fold increase - no one noticed



Pelagic stingray captures per 10,000 hooks


## Major shrimp stocks in the North Atlantic



## Cod and shrimp biomass in the North Atlantic:

 time seriesLabrador


Northern Newfoundland




Flemish Cap




Worm and Myers, Ecology 2003

## Step 2: Random-effects metaanalysis



## Critical Modeling Tools

- Random effects meta-analysis
- Corrections for temporal autocorrelations
- Corrections for spatial autocorrelaitons
- Modeling of environmental (bottom up) effects



## Blue marlin (Makaira nigricans)



## Sailfish <br> (Istiophorus albicans)








## Critical Modeling Tools

- Hierarchical Bayes State-Space Models


## Loss of species density per decade

- Displayed is the number of tuna and billfish species that are found on a standard longline with 1000 hooks
- The time series runs from 1952-1999
- It shows how large hotspots are disappearing over time and how few concentrations of diversity remain today

After data from: Worm B, Sandow M, Oschlies A, Lotze HK, Myers RA (2005) Global patterns of predator diversity in the open oceans. Science Aug. 2005.

## 1950s



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-1369

## 1960s



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-13

## 1970s



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-136

## 1980s



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-13

## 1990s



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-13

## Critical Modeling Tools: Rarefaction diversity

-Compare diversity between cells with different sample size

- Species richness: Expected number of species per 50 individuals
-Species density: expected number of species per 1000 hooks







|  |  |  |  |  |  |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |



| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |

## Tagging also shows bluefin restricted to N Atlantic



Source: Block et al. 2005. Nature 434: 1121-1127

## Global decline in ocean predator diversity

- Increasing catches
- Decreasing diversity
- Long-term decline linked to fishing
- Yearly variability linked to climatic changes

Worm, Sandow, Oschlies, Lotze, Myers 2005.



# ENSO affects diversity across entire Pacific <br> Species richness <br> Blue marlin catch rates 



| -0.15 | -0. | -0.05 | 0 | 0.05 | 0.1 | 0.15 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |


$-0.42-0 . \quad 0 \quad 0.1 \quad 02 \quad 0.3$

Slope of $\Delta_{t}$ with ENSO
Source: Worm, Sandow, Oschlies, Lotze, Myers 2005.
Science 309:1365-1369

# Understand oceanographic drivers of diversity 

Patterns of diversity were explained by

- Mean temperature
- Fronts and eddies
- Oxygen



## Critical Modeling Methods

- Spatial regression with anisotropic spatially correlated errors
- We used SAS Proc MIXED (and the generalized linear model additions) which are very fast, and easy to use.


## Use remaining hotspots for global conservation

- Consistent patterr of species richnes and density
- Five major hotspo
- U.S. east coast
- Hawaiian chain
- Southeast Pacific
- Australian east co
- Sri Lanka


## Protect diversity hotspots in national waters

- Special places where many species aggregate
- Key habitats



## Validate hotspots across species groups




Source: Worm et al. 2005.
Science: 309:1365-1369

## Simulating area closures

- Hotspot closure reduces catch of threatened species
- Displacement issues must be considered
- Fishing effort needs to be reduced as well



## Critical Modeling Method

- Simulation methods

The First Collective Act of Humanity was to save the great whales -
despite massive denial

- we can do
the same for the remaining virgin areas of the oceans and for the great sharks.


## USA Bay Scallops Landings











Meta-analysis of cownose ray trends



Southeast US SEAMAP trawl survey




## Increase in small sharks: sharpnose shark



NMFS offshore trawl survey


Southeast US SEAMAP trawl survey




Strong, W.R. Jr; Snelson, F.F. Jr; Gruber, S.H. Copeia 1990, 836-839

## GREAT HAMMERHEAD SHARK PREDATION UPON SPOTTED EAGLE RAY

by Demian Chapman

## Loss of hammerheads from surveys



Shepherd and Myers, 2005, Ecology Letters


Generalized linear model results

|  | Estimate | StdErr | p | $\mathrm{k} /$ scale |
| :--- | ---: | ---: | ---: | ---: |
| Abundance | -0.169 | 0.0171 | $5.67 \mathrm{e}-23$ | 4.28 |
| Length | -0.0105 | $1.4 \mathrm{e}-3$ | $8.85 \mathrm{e}-14$ | 18.8 |

## Great hammerhead





Generalized linear model results

|  | Estimate | StdErr | p | $\mathrm{k} /$ scale |
| :--- | ---: | ---: | ---: | ---: |
| Abundance | -0.143 | 0.0812 | 0.079 | 1.96 |
|  |  |  |  |  |
| Length | $-7.19 \mathrm{e}-3$ | 0.0707 | 0.919 | 1 |



Generalized linear model results

|  | Estimate | StdErr | p | $\mathrm{k} / \mathrm{scale}$ |
| :--- | ---: | ---: | ---: | ---: |
| Abundance | -0.172 | 0.0443 | $9.99 \mathrm{e}-5$ | 4.28 |
| Length | -0.0136 | $5 . \mathrm{e}-3$ | $6.69 \mathrm{e}-3$ | 63.2 |





Relative abundance





Instaneous rate of change in abundance with time

## Experimental Results of Pete Peterson and Sean Powers in North Carolina



Legend

- Experimental site
- Before/after density
$\Delta$ Sampled but no scallops


# Loss of Bay Scallops with Cownose Ray Fall Migration 



# Mortality of almost 100\% during fall migration of cownose rays 



August bay scallop density

## Excluding cownose rays allow the survival of bay scallops.




## Trophic Cascades: Consequences of the loss of top predators may be greater than we think

The First Collective Act of Humanity was to save the great whales -
despite massive denial

- we can do
the same for the remaining virgin areas of the oceans and for the great sharks.


# Past use of State-Space Models for Movement 

- Models by David Brillinger in 1998 showed migration across oceans using a directional random walk on a sphere.
- John Sibert used "almost linear" Kalman filter models to improve popup tags locations (see U. of Hawaii website)
- Morales, Haydon, Friar, Holsinger, Fryxell (Ecology 2004) used hidden Markov models



## Blue marlin (Makaira nigricans)



## Sailfish <br> (Istiophorus albicans)








Not only have large predators declined by at least a fact 10, but mesopredators have often increased by at least a factor of 10 .


FMAP (Future of Marine Animal Populations) part of the Sloan Census of Life http://www.fmap.ca Pew Global Sharks Assessment
Species Group Time (yr) Source

Not only have large predators declined by at least a fact 10, but mesopredators have often increased by at least a factor of 10 .


FMAP (Future of Marine Animal Populations) part of the Sloan Census of Life http://www.fmap.ca Pew Global Sharks Assessment

## Special Case of State-Space Models: Hidden Markov Model



- one discrete hidden node and one discrete or continuous observed node per time slice.
- $\alpha$ : hidden variables
- Y: observations
- Structures and parameters remain same over time
- Three parameters in a HMM:
- The initial state distribution $\mathrm{P}\left(\alpha_{1}\right)$
- The transition model $P\left(\alpha_{t} \mid \alpha_{t-1}\right)$
- The observation model $P\left(Y_{t} \mid \alpha_{t}\right)$


## Error function

## State Space Models

Maximize likelihood to estimate model parameters
$\gamma$ observed location

Use Markov Chain
Monte Carlo methods in WinBugs

$$
\alpha_{t}=f\left(\alpha_{t-1}, \eta_{t} ; \gamma\right)
$$

movement function

## State-Space Models

> Process model
> true location $\alpha_{t+1}=f$ (true location $\alpha_{t}$, parameters, process variability)

## Observation model

observed location $\mathbf{y}_{\boldsymbol{t}}=h\left(\right.$ true location $\alpha_{t}$, observation error)

## State-Space Models

## Process model

true location $\alpha_{t+1}=f$ (true location $\alpha_{t}$, parameters, process variability)

Observation model
observed location $\mathbf{y}_{t}=h\left(\right.$ true location $\alpha_{t}$, observation error)

## Location Estimates



## This represents a different way of thinking

## How are animals different from particles?

- They have free will
- They have "inertia", they tend to keep going the same direction.
- They have different behaviours


## Why State Space Models

- This is simply one of the key "right ways" to think about many key modern problems:
- Engineers, economists, oceanographers, and speech recognition scientists, use modifications of this idea;
- If you want to shoot down a missile, you use a state space model.

Depth (m)
Dive duration (min)
Temperature (C)
When migrating leatherbacks spend more time close to the surface during the day.


From James, Ottensmeyer, and Myers (in review)






## Economometrics:

## How our analysis differs:

- We use a large amount of prior information on the accuracy of locations, i.e. they are described by "heavy tailed" distributions.
- We model the performance of each transmitter, because there are very clear differences among transmitters.
- We use the first state-space model of switching for movement implemented for an ecological problem.
- First meta-analytic approach which combines information from different tracts using a hierarchical random-effects meta-analytic approach.


## Making Switching Models Work

- Meta-analysis greatly improves the estimates because relative few transitions are observed for each track.
- In the Bayesian approach, both the parameters ?? and the values of the states $\left(\alpha_{1}, \alpha_{2}, \ldots, \alpha_{T}\right)$ are viewed as random variables.


## What is Kalman Filtering Used For?

- What is it used for?
- Tracking missiles
- Tracking heads/hands/drumsticks
- Extracting lip motion from video
- Lots of computer vision applications
- Economics
- Navigation


## First Measurement

$$
\begin{gathered}
z_{1}, \sigma_{z_{1}}^{2} \\
\hat{X}_{1}=z_{1} \\
\hat{O}_{1}^{2}=\sigma_{z_{1}}^{2}
\end{gathered}
$$

Conditional Density Function


## Second Measurement

$$
z_{2}, \sigma_{z_{2}}^{2}
$$

## Conditional Density Function



## Combine Estimates

$$
\hat{x}_{2}=\hat{x}_{1}+K_{2}\left(z_{2}-\hat{x}_{1}\right)
$$

$$
K_{2}=\frac{\sigma_{1}^{2}}{\sigma_{1}^{2}+\sigma_{z_{2}}^{2}}
$$

## Combine variances



## Combined Estimates

Conditional Density Function

$$
\begin{aligned}
\hat{x} & =\hat{x}_{2} \\
\hat{\sigma}^{2} & =\sigma_{2}^{2}
\end{aligned}
$$

## But suppose we're moving



- Not all the difference is error
- Some may be motion
- KF can include a motion model
- Estimate velocity and position


## Switching Models

- Does not work well on one animal
- Works well if animals have the same switching parameters (this is the same as a fixed effect meta-analysis).
- We would like to have a hier. model, where parameters are random variables.


## Applications



GPS


Satellite orbit computation


Active noise control


Tracking

## Examples - Target tracking

The state process consists of the position, velocity, and acceleration coördinates (9 dimensions in all) of a ballistic or steered target (i.e rocket or missle); randomness in the state process may come from interactions with the atmosphere, or from evasive maneuvers. Observations consist of data from radar and infrared sensors, and prior knowledge of the initial location of the target; observation noise comes from background noise sources such as clutter, or internal thermal noise in the sensor.

## Examples: Weather and Ocean Prediction

Nonlinear filtering theory allows new data to be assimilated into the differential equations which drive a numerical model of the ocean and/or atmosphere.

## Examples

- Asset Pricing - Each component of the state is the value of some asset or derivative, or else an underlying interest rate; the observations consist of data on specific sale prices of related assets at a sequence of times.


## Different short behavors

## Why state-space models?

- Only method that models time series structure with missing values.
- Models estimation error.
- Models non Gaussian errors.
- Models nonlinear relationships.


## Further advantages

- Switching models


# What about Levy flights? Heuristic, but not mechanistic. 



## State space models

- State variables
- parameters
- forcing functions
- rules of change
- the state variables in the future depend upon the current state, the parameters (constants), any external perturbations (the forcing functions), and the rules of change


## State variables

- The complete description of the current state of the system -- complete enough that you can "rebuild" the system with this amount of information
- examples - the number of animals in the population - the age structure of a population, the presence or absence of species in a community matrix ....


## Parameters

- Do not change over time and are the constants that describe the rates or limits
- intrinsic rates of growth, carrying capacity, survival rates, fecundity rates etc.


## Forcing functions

- Natural or anthropogenic factors that affect the state
- weather impacts on survival or reproduction
- harvesting
- These are "external" to the model -- that is we don't attempt to describe the dynamics of these factors


## Rules of change

- The equations that describe how the state variables change over time in relation to the current values of the state, the parameters, the the forcing functions.
- $S_{t+1}=f\left(S_{t}, p, u_{t}\right)$


## A simple state space model Logistic growth

- Numbers next year are number this year + net production, minus removals
- $\mathrm{N}_{\mathrm{t}+1}=\mathrm{N}_{\mathrm{t}}+\mathrm{r} \mathrm{N}_{\mathrm{t}}\left(1-\mathrm{N}_{\mathrm{t}} / \mathrm{k}\right)-\mathrm{C}_{\mathrm{t}}$
- N is the population size
- $r$ is the intrinsic rate of increase
- $k$ is the carrying capacity
- $C$ is the catch


## Quiz \#1

- Take a piece of paper
- From this logistic growth model
- 1 - what are the state variable(s)
- 2 - what are the parameter(s)
- 3 - what are the forcing function(s)
- 4 - what are the rules of change


## The answer

- The state variable is the population size
- The parameters are the intrinsic rate of increase $r$, and the carrying capacity $k$
- The forcing function is the catch
- The rules of change is the equation


## Components of rules of change

- Logical relationships
- statements that are true by definition
- numbers next year = numbers this year + births - deaths + immigration - emigration
- also known as tautologies
- Functional relationships
- specify the relationship between a rate and a state variable or something related to a state variable (survival as a function of density)


## For logistic growth model

- A logical relationship
- number alive next year is number alive this year plus net production minus catch
- The functional relationship
- net production $=\mathrm{rN}_{\mathrm{t}}\left(1-\mathrm{N}_{\mathrm{t}} / \mathrm{k}\right)$
- STATE PROCESS
- The primary object of study is a Markov process, X, whose probability law is known, but which cannot be observed directly. It serves as a model for the true state of the system under study; hence $X$ is called the state process. The simulation below shows a real-valued process; in practice $X$ may be high-dimensional, with values in a manifold or metric space.
- OBSERVATIONS
- At certain times t[1],t[2],... (perhaps continuously), some function of the state, corrupted by noise, is observed. For example, observations might be of the form
- $Y t[n]=h[X t[n], V t[n]]$
- where h is a continuous function, and $\mathrm{Vt}[1], \mathrm{Vt}[2], \ldots$ are independent random variables, independent of $X$.


## Structural Equation Modelling (SEM)

Minimise the difference between the observed (S) and implied ( $($ ) covariances by adjusting the path coefficients (B)

$$
\begin{array}{ll}
x & =x . B+z \\
x & =z .(1-B)^{-1}
\end{array}
$$

$x$ : matrix of time-series of Regions 1-3
B: matrix of unidirectional path coefficients

Variance-covariance structure:

$$
\begin{array}{ll}
X^{\top} \cdot x=\Sigma & =(I-B)^{-\top} \cdot C \cdot(I-B)^{-1} \\
\text { where } C & =z^{\top} z
\end{array}
$$


$x^{\top} . x$ is the implied variance covariance structure
$C$ contains the residual variances ( $u, v, w$ ) and covariances

The free parameters are estimated by minimising a [maximum likelihood]

## Modeling Sequential Data

- Sequential data arises in many areas of science \& engineering
- Types of data sources:
-Time series, generated by a dynamical system
- Sequence generated by one-dimensional spatial process
- On- line analysis vs. Off-line analysis


## Classical Solutions

- Classic approaches to time-series prediction
- Linear models: ARIMA(auto-regressive integrated moving average), ARMAX(autoregressive moving average exogenous variables model)
- Nonlinear models: neural networks, decision trees
- Problems with classic approaches
- prediction of the future is based on only a finite window
- it's difficult to incorporate prior knowledge
- difficulties with multi-dimensional inputs and/or outputs


## State-Space Models

- Assumptions:
- There is some underlying hidden state of the world (query) that generates the observations (evidence), and evolves in time, possibly as a function of our inputs
- Models are first-order Markov, i.e.,

$$
P\left(X_{t} \mid X_{1: t-1}\right)=P\left(X_{t} \mid X_{t-1}\right)
$$

- observations are conditional first-order Markov

$$
P\left(Y_{t} \mid X_{t}, Y_{t-1}\right)=P\left(Y_{t} \mid X_{t}\right)
$$

- Time-invariant or homogeneous
- The goal: computing of the belief state:

The belief on the hidden state of the world given the observations up to the current time y1:t and inputs u1:t to the system, $\mathrm{P}(\mathrm{X} \mid \mathrm{yS} 1: \mathrm{t}$, u1:t )

- State-space model must define a prior $P\left(X_{1}\right)$, a state-transition function, $P\left(X_{t} \mid X_{t-1}\right)$, and an observation function, $P\left(Y_{t} \mid X_{t}\right)$


## SSM: Representation

Hidden Markov Models (HMMs):
$\mathrm{X}_{\mathrm{t}}$ is a discrete random variables
Kalman Filter Models (KFMs):
$\mathrm{Xt}_{\mathrm{t}}$ is a vector of continuous random variables
Dynamic Bayesian Networks (DBNs): more general and expressive language for representing state-space models

## SSM: Inference

- A state-space model defines how $X_{t}$ generates $Y_{t}$ and $X_{t}$.
- The goal of inference is to infer the hidden states (query) $X_{1: t}$ given the observations (evidence) $Y_{1: t}$.



## 

- Inference tasks:
- Filtering (monitoring): recursively estimate the belief state using Bayes' rule
- prediction: computing $\mathrm{P}\left(\mathrm{X}_{\mathrm{t}} \mid \mathrm{y}_{1: \mathrm{t}-1}\right)$
- updating: computing $P\left(X_{t} \mid y_{1: t}\right)$
- throw away the old belief state once we have computed the prediction ("rollup")
- Smoothing: estimate the state of the past, given all the evidence up to the current time
- Fixed-lag smoothing (hindsight): computing $P\left(X_{t-1} \mid y_{1: t}\right)$ where $\mathrm{I}>0$ is the lag
- Fixed-interval smoothing (offline): computing $P\left(X_{t} \mid y_{1: T}\right)$ for all
- Prediction: predict the future
- Lookahead: computing $\mathrm{P}\left(\mathrm{X}_{\mathrm{t}+\mathrm{h}} \mid \mathrm{y}_{1: \mathrm{t}}\right)$ where $\mathrm{h}>0$ is how far we want to look ahead

$$
1 \leq t \leq T
$$

- Viterbi decoding: compute the most likely sequence of hidden states given the data
- MPE (abduction): $\mathrm{x}_{1: \mathrm{t}}^{*}=\operatorname{argmax} \mathrm{P}\left(\mathrm{x}_{1: \mathrm{t}} \mid \mathrm{y}_{1: \mathrm{t}}\right)$


## SSM: Learning

- Parameters learning (system identification) means estimating from data these parameters that are used to define the transition model $P\left(X_{t} \mid X_{t-1}\right)$, the observation model $P\left(Y_{t} \mid X_{t}\right)$ \& the prior $P\left(X_{1}\right)$
- The usual criterion is maximum-likelihood(ML)
- The goal of parameter learning is to compute
- $\theta_{\text {ML }}^{*}=\operatorname{argmax}_{\theta} \mathrm{P}(\mathrm{Y} \mid \theta)=\operatorname{argmax}_{\theta} \log \mathrm{P}(\mathrm{Y} \mid \theta)$, where

$$
\log P(Y \mid \theta)=\log \prod_{m=1}^{N_{\text {tan }}} P\left(y_{1: T}^{m} \mid \theta\right)=\sum_{m=1}^{N_{\text {tami }}} \log P\left(y_{1: T}^{m} \mid \theta\right)
$$

- Or $\theta^{*}{ }_{\text {MAP }}=\operatorname{argmax}_{\theta} \log \mathrm{P}(\mathrm{Y} \mid \theta)+\log \mathrm{P}(\theta)$ if we include a prior on the parameters
- Two standard approaches: gradient ascent and EM(Expectation Maximization)
- Problem: Hidden variables complicate finding of the globally optimal parameters
- Structure learning: more ambitious


## HMM: Hidden Markov Model



- one discrete hidden node and one discrete or continuous observed node per time slice.
- X : hidden variables
- Y: observations
- Structures and parameters remain same over time
- Three parameters in a HMM:
- The initial state distribution $\mathrm{P}\left(\mathrm{X}_{1}\right)$
- The transition model $P\left(X_{t} \mid X_{t-1}\right)$
- The observation model $P\left(Y_{t} \mid X_{t}\right)$


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- The observation model $P\left(Y_{t} \mid X_{t}\right)$
- HMM is the simplest DBN
- a discrete state variable with arbitrary dynamics and arbitrary measurements


## Special Case of State-space Models: Hidden Markov Model



- one discrete hidden node and one discrete or continuous observed node per time slice.
- $\alpha$ : hidden variables
- Y: observations
- Structures and parameters remain same over time
- Three parameters in a HMM:
- The initial state distribution $\mathrm{P}\left(\alpha_{1}\right)$
- The transition model $P\left(\alpha_{t} \mid \alpha_{t-1}\right)$
- The observation model $P\left(Y_{t} \mid \alpha_{t}\right)$


## HMM: Hidden Markov Model



## KFM: Kalman Filter Model

- KFM has the same topology as an HMM
- all the nodes are assumed to have linear-Gaussian distributions

$$
\begin{aligned}
x(t+1) & =A^{*} x(t)+v(t), \\
v & \sim N(0, Q): \text { process noise, } x(0) \sim N(X(0), V(0)) \\
y(t) & =C^{\star} x(t)+w(t), \\
w & \sim N(0, R): \text { measurement noise }
\end{aligned}
$$

- Also known as Linear Dynamic Systems (LDSs)

- a partially observed stochastic process
- with linear dynamics and linear observations: $f(a+b)=f(a)+f(b)$
- both subject to Gaussian noise
- KFM is the simplest continuous DBN
- a continuous state variable with linear-Gaussian dynamics and measurements


## All Roads Lead From Gauss 1809

"... since all our measurements and observations are nothing more than approximations to the truth, the same must be true of all calculations resting upon them, and the highest aim of all computations made concerning concrete phenomenon must be to approximate, as nearly as practicable, to the truth. But this can be - accomplished in no other way than by suitable combination of more

- observations than the number absolutely requisite for the determination of
- the unknown quantities. This problem can only be properly undertaken
- when an approximate knowledge of the orbit has been already attained,
- which is afterwards to be corrected so as to satisfy all the observations
- in the most accurate manner possible."
- From Theory of the Motion of the Heavenly Bodies Moving about the Sun in Conic Sections, Gauss, 1809


## What does a Kalman filter do ?

- The Kalman filter propagates the conditional density in time.





## How does it do it?

- The Kalman filter iterates between two steps - Time Update (Predict)
- Project current state and covariance forward to the next time step, that is, compute the next a priori estimates.
- Measurement Update (Correct)
- Update the a priori quantities using noisy measurements, that is, compute the a posteriori estimates.

$$
\hat{y}_{k}=\hat{y}_{k}^{-}+K_{k}\left(X_{k}-M_{k} \hat{X}_{k}^{-}\right)
$$

- Choose $K_{k}$ to minimize error covariance


## You can ask questions and think about questions you can not otherwise.

- Circle of confusion
- Turtle speed at night
- Are there modes, or "behavioural states" in their behaviour.


## Random Effect Model

No random effects


Random intercept


Random intercept and slope



## Weights in Canadian waters



Nesting female morphometrics: St. Croix, U.S.V.I.
Boulon et al. 1996. Chelonian Conserv, Biol. 2:141-147.
Lines fit by constant slope analysis of covariance after log transformation.

Male leatherback movements

- not previously described
- annual migratory cycle that includes movement between temperate foraging areas and tropical breeding areas

James, Eckert and Myers Marine Biology (in press)


## Filtered Data

0 Raw data
State estimates


## 




## A Switching SSM

Switching model, estimates switches b/w 2 behavioural states




Lewison et al. 2004 Ecology Letters




Swordfishing fleot at anchor. Neils Harhour, Cape Breton. 13.

Mike James
Andrea Ottensmeyer


Identification of high-use areas and threats to leatherback sea turtles in northern waters

James, Ottensmeyer and Myers Ecology Letters (2005)


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tience as some line got fouled in the rapid hauling, or an obstreperous fellow in the depths below made off with the best part of a valuable line. To an unsophisticated observer our crew,

Fish, like women, are a very uncertain institution, and their tastes are equally unaccountable. When you least expect it, off they sail and leave you in the lurch when the prize is almost within your grasp; at least such has proved my sailor's experience with them. Thus it was that, while we were merrily hauling up the denizens of Whale Deep, the supply suddenly gave out-either our bait had cloyed on their palates, or, what is quite as likely, they began to smell a submarine rat, and regarded the sudden upward movement of their companions with wellgrounded suspicion. As if by simultaneous agreement they suddenly ceased to bite, and afte: wooing them in vain for a couple of days, we resolved to weigh and head for the northward.


## Questions?

- What are the fundamental changes in a community that occur after the apex predators are removed?
- Have lower trophic levels responded?
- How can we carry our a meta-analysis in different communities that may not be independent?


## Major shrimp stocks in the North Atlantic



## Cod and shrimp biomass in the North Atlantic:

 time seriesLabrador


Northern Newfoundland




Flemish Cap




Worm and Myers, Ecology 2003

## Step 2: Random-effects metaanalysis






Labrador and N.E. Newfoundland



E. Scotian Shelf

S.W. Scotian Shelf


Central Baltic


Spawners (tonnes/km^2)


## There is much less than $10 \%$ of cod left -



Proportion of virgin biomass

Source: Myers and Worm 2005.
Proc. R. Soc. Lond. B

Fitting a simple model to crazy data can yield reliable, and very powerful conclusions

Newspaper reports of sharks in Croatia


## With training, "experts" can ignore the most obvious of data:

1872 - Man's head and leg and dolphin in stomach 1872 - 8 Great White Sharks reported caught 1888 - Woman's body and lamb in stomach 1894 - Preserved at Zagreb Nat. Hist. Mus. 1926 - Woman's shoes, laundry in stomach 1946 - Pig of 10 kg in stomach 1950 - Encounter during eating a dead calf 1954 - Attack on boat 1975+ -No sightings.

Newspaper reports of sharks in Croatia



Myers and Worm 2003 Nature


## Spatial Loss of Cod History




Fig. 21.-Recaptures to October, 1934, of cod tagged in the Jeddore Rock to Egg Island area, N.S., in May, 1934.


Fig. 18.-Recaptures in May to October, 1934, 1935, 1936 and 1937, of cod tagged near Halifax in June, 1934.


Fig. 15.-Recaptures during "summers" of 1927, 1928, 1929 and 1930 of cod tagged off Shelburne, N.S., during September and the first day of October, 1926.

Identification of high-use areas and threats to leatherback sea turtles in northern waters

James, Ottensmeyer and Myers Ecology Letters (2005)


## Global changes in species

 diversityjoint work with Boris Worm
Dalhousie University

