Report No. 2: Predator-Prey Models
Source Summary

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1 Chauvet: A Lotka-Volterra three-species food chain

1.1 Introduction

- Volterra described interactions between two competing species
- useful models to describe population variance over time
- standard equation: a – growth rate of prey w/o predators, b – effects of predation on prey, c – death rate of predators w/o prey, d – increase of predators w/ prey; $a, b, c, d > 0$

$$\begin{cases} \dfrac{dx}{dt} = ax - bxy \quad \text{(Prey)} \\ \dfrac{dy}{dt} = -cy + dxy \quad \text{(Predators)} \end{cases}$$

- divide the second equation by the first to get a linear ODE
- $C = a \ln y - by + c \ln x - dx$, max value of C happens at $(a/d, a/b)$
- the plot moves counterclockwise because the predators lag behind the prey, which creates this movement – phase-shifted behavior
- have common period, seen in historical records
- this paper defines a three-species non-logistic system of L-V equations
- normally logistic equations are used because the prey would otherwise grow unboundedly if there are no predators
- direct generalization of the standard equations
- 3 way system is quite complicated, good teaching tool because it has degeneracies – trapping regions and other complicated shit

1.2 The model

- 3 species food chain, x is preyed on by y which is preyed on by z – mouse, snake, owl; vegetation, hare, lynx; worm, robin, falcon
- model is:

$$\begin{cases} \dfrac{dx}{dt} = ax - bxy \\ \dfrac{dy}{dt} = -cy + dxy - eyz \\ \dfrac{dz}{dt} = -fz + gyz \end{cases}$$

- $a, b, c, d, e, f, g > 0$, a, b, c, d are like in the Lotka volterra equations and e is predation of y by z, f is the death rate of z in absence of prey, g is propagation rate of z if there is prey
- populations are > 0 so we only look at positive octant

1.3 Aanlysis of the model

1.3.1 The coordinate planes

- each coordinate plane is invariant with respect to the system
- a surface is invariant to a system S if every solution starts on S and does not escape S – if species go extinct, they will not reappear
- definition of what is means to have an invariant system
- following, each of the coordinate planes is invariant
- if $z = 0$, we have classic L-V equations
- if $y = 0$ we get exponential growth for x and exponential decline for z – makes biological sense (ignoring the unbouded growth of x)
- this system has a simply found solution $z = Kx^{-f/a}$
- if x does not exist, all species go extinct eventually
- in certain cases z may grow at first by eating y but after $y = 0$ they will die out too

1.3.2 Equilibria and linear analysis

- it is often useful to investigate solutions that do not change with time, where $x_t = y_t = z_t = 0$ – called equilibria, steady-state-solutions, fixed points
- two obvious equilibria: $(0, 0, 0)$ and $(c/d, a/b, 0)$ from the L-V
- another special case $a/b = f/g$ yields ray of solutions $(s, a/b, (ds - c)/c)$ where $s \geq c/d$
- asymptotically stable if points close to equilibrium tend to it
- if an equation can be linearized, its stability often depends on the stability in the associated linearized system
- the behavior at that point is determined by the Jacobian of the matrix
- if all real parts of the eigenvalues have negative real parts the system is asymptotically stable, if not it is not stabel
- good tool for the analysis of nonlinear systems near equilibria is the Center Manifold Theorem
- each equilibrium has manifolds, one stable, one unstable, but potentially many center manifolds
- for the analysis of the system using the center manifold theorem is useful – might be interesting to use for all three cases to take up space and time

1.3.3 The case $ga = fb$

- surfaces $z = Kx^{-f/a}$ might be invariant
- on those surfaces are periodic orbits that enclose the fixed points on the ray $(s, a/b, (ds - c)/c)$
- proof that if $ga = fb$ the aforementioned surfaces are invariant to the original system of equations
- now the equation can be implicitely be solved on each surface
- for a fixed K the system becomes:

$$\begin{cases} x_t = ax - bxy \\ y_t = -cy + dxy - eyKx^{-\frac{f}{a}} \end{cases} \tag{1}$$

- from quotients we can find separable equations and solve them
- **read from section (5) onwards to understand**
- this completely characterizes the case $ga = fb$
- all three species have populations that vary over time with common periods
- peak follow: x, then y, then z

1.3.4 The cases $ga \neq fb$

First $ga < fb$

- all solutions seem to spiral down to the xy-plane towards a periodic solution
- solutions move down across surfaces $z = Kx^{-f/a}$ from higher to lower values of K
- next proof shows that solutions travel down a set and bounded path in **proposition 4**
- thus for $ga < fb$ all solutions tend towards the xy-plane or $z = 0$
- thus the apex predator always goes extinct in these circumstances and the two lower species exhibit standard L-V behavior

Second $ga > fb$

- analogous in solution, all trajectories in the positive first octant escape to $+\infty$ as t increases – the trajectories travel up the surfaces
- this means that populations x, z tend to ∞ and that y experiences larger and larger fluctuations
- all are non-monotonic though

1.4 Conclusion and comments

- survival of z only depends on a, b, f, g: if $ag < fb$ z dies out, if $ag \geq fb$ z survives and grow without bound if $ag > fb$
- fits our intuition about larger values of a, g and their advantages for z
- larger values of b, f are inhibitive for z
- c, d, e who are most directly influencing y don't have an effect on whether z goes extinct
- y is basically a conduit from x to y
- y cannot go extinct if x remains
- this is an excellent model for learning etc because it features a lot of good things that generally don't come up

2 Hoppensteadt: Predator-prey model

2.1 Introduction

- ppm are the building blocks of bio- and ecosystems
- biomasses are grown out of their resource masses
- resource-consumer, plant-herbivore, parasite-host, disease-immune system, susceptible-infectous ...
- general loss-win interactions found outside ecology

2.2 A General Predator-Prey Model

- two populations
- size at time t is $x(t), y(t)$, population numbers, concentrations, both are continuous
- changes of population over time are the time derivatives $\dot{x}, \dot{y}$, equivalent to $dx/dt, dy/dt$
- general system, f, g are the *per capita growth rates* of the species, $f_y < 0, g_x > 0$, f is prey, g is predator

$$\dot{x} = xf(x, y)$$
$$\dot{y} = yg(x, y)$$

2.3 Lotka-Volterra Model

- 1926 Vito Volterra proposed a differential equation to describe increase in predator fish and decrease in prey fish in the Adriatic sea during WWI
- 1925 in the US Alfred Lotka described a hypothetical chemical reaction with oscillating concentrations
- Lotka-Volterra model is the simplest predator-prey model
- based on linear, per-capita growth rates; prey: $f = b - py$, predators: $g = rx - d$; b – prey (x) growth rate with no predators, p – impact of predation on $\dot{x}$ of prey, d – decline of predators with no prey, r – growth of predator population depending on prey numbers

- full predator-prey model

$$\begin{cases} \dot{x} = (b - py)x & \text{(Prey)} \\ \dot{y} = (rx - d)y & \text{(Predators)} \end{cases}$$

- system can be integrated directly, any solution of the system $(x(t), y(t))$ satisfies $C = b \ln y(t) - py(t) - rx(t) + d \ln x(t)$ for all t
- $C = b \ln y(0) - py(0) - rx(s) + d \ln x(0)$
- for phase plots with contour plot: $z = b \ln y - py - rx + d \ln x$
- the curves describe solutions of the system – because the curves are closed we have periodic oscillations
- **if** $b > 0$ **– prey multiplies on its own** you have $(0, 0)$ and $(d/r, b/p)$ as equilibria, the latter one has single peak in z

2.4 Lotka and Volterra

2.4.1 Alfred James Lotka

- 1880–1949
- chemist, demographer, ecologist, mathematician
- born in Lviv, Ukraine (then Lemberg, Austria)
- to US in 1902, wrote papers about chemical oscillations, theoretical biology
- then worked at insurance company
- eventually became president on Population Association of America

2.4.2 Vito Volterra

- 1860–1940
- mathematician, physicist
- born in Italy
- attended university of Pisa, wrote a book on integral and integro-differential equations
- after WWI he returned to applications of maths in biology
- joined opposition to Mussolini in 1922, refused oath in 1931 and left the country to live abroad

2.5 Kermack-McKendrick Model

- in epidemiology we can use these equations too
- prey $\rightarrow$ susceptibles; predators $\rightarrow$ infectives
- susceptibles can become infectives and infectives can become ineffective
- critical value / tipping point: $R \equiv rx(0)/d = 1$ is the tipping point
- some suceptibles will always survive – herd immunity

2.6 Jacob-Monod Model

- this model accounts for limited uptake rates (e.g. bacteria)
- x is population of feeders, they feed on chemical species of concentration y
- V – uptake velocity, K – saturation constant, Y – yield of x per unit of y taken up

$$\begin{cases} \dot{x} = \dfrac{Vy}{K+y}x & \text{(Feeders / species } x\text{)} \\ \dot{y} = -\dfrac{1}{Y}\dfrac{Vy}{K+y}y & \text{(Food / nutrient)} \end{cases}$$

- if $y = K$ uptake velocity is $V/2$; $y = K$ is taken as a tipping point: if $y < K$ the uptake is ignored
- this stuff underlines a lot of biology, microbiology, food engineering
- as $t \to \infty$ the nutrients are depleted
- some of the terms can be replaced by other ones to account for different environments

2.7 Logistic Equation

- V and YK can be very large compared to the other data but the ratio is of moderate size $V/(KY) \approx r$

$$\dot{x} = \frac{V(C-x)}{YK + (C-x)}x$$

- if we have $V/(KY) \approx r$ and get $\dot{x} = r(C-x)x$
- this has kind of the same results as Jacob-Monod

2.8 Predation with Time Delays: Chaos in Ricker's Reproduction Equation

- accurate time delays and stuff
- **goes into too much detail, not relevant**

3 Israel: On the contribution of Volterra and Lotka to the development of modern biomathematics

- birth of modern biomathematics took place in 1920s – maths not as mere aid but as conceptual tool and application of determinist and mechanist conceptions to biology
- now all of mathematical analysis was used in biology
- classical mathematical and physical methods and concepts now used in maths
- 1925 – Lotka publishes famous treatise, 1926 Volterra publishes first paper on population dynamics:

$$\begin{cases} \dfrac{dx}{dt} = Ax - Bxy \\ \dfrac{dy}{dt} = Cxy - Dy \end{cases}$$

- which of them takes priority? always and important question when these things are independently and at the same time discovered, seems like is was supposed to happen
- 1926 Volterra got published, Lotka had stuff published before and written about it in 1920 and 1910
- Lotka used an analogy between the chemical system and the biological system to derive his predator prey equations which is interesting
- only reason that Lotka didn't claim priority based on those previous papers is because he did not see the relevant concepts in his paper
- both the biology and chemistry examples can be called isomorphisms of each other – they are fundamentally equivalent, both are non-linear oscillators
- both of their approaches are rooted in empirical analysis as was normal back then, they didn't use analogy like one might today
- Volterra was in favor the mathematicalization of biology – differential equations are the obvious results of this
- Volterra started because his son-in-law sent him a paper about fish in the Adriatic sea
- he took a very physical approach, using friction between members of species and energy derivations

4 Kingsland: Alfred J. Lotka and the origins of theoretical population ecology

- ecology has borrowed from many disciplines, but phtsical chemistry is one of the more unlikely candidates
- somewhat stimulated the development of population ecology
- Alfred James Lotka is responsible for this
- his real goal was to create *physical biology*, applying physical principles to biological systems
- Lotka started papers by discussing chemical systems and then moving to biological examples
- first systems were undamped and later damped
- L-V showed that even just 2 populations could regulate each other while ecologists at the time were thinking of 5 species food chains

5 Keyszig: Chapter 4

5.1 Chapter 4.5: Qualitative Methods for Nonlinear Systems

- qualitative methods are methods of finding qualitative information on solutions without actually solving the equations
- assumptions: autonomous system, t does not occur explicitly
- talk about families of solutions

5.1.1 Lotka-Volterra Population Model – Example 3

- prey has unlimited food, exponential growth without foxes
- prey is killed at a rate proportional to both population numbers
- predators die exponentially if there is no prey, if there is prey they grow exponentially to both population numbers
- typical system
- critical points: factor out population numbers and set one of the factors to 0, get the linearization and see that this is a saddle point, which is
- second critical point is also linearized, we get a family of ellipses that has the critical point at it's center
- if the non-linear system is analyzed, we see it has the same center but closed trajectories and not ellipses

6 Terman: State Space

- state space: set of all possible states of a dynamic system
- each state of the system corresponds to a point in state space
- in pendulum: pairs of "(angle, velocity)" which forms a cylinder
- can be finite – just some points
- finite-dimensional – infinite number of points forming a smooth manifold, for ODEs and mapping – often called **phase space**
- infinite-dimensional – for PDEs and delay differential equations
- degrees of freedom is the number of variables needed to completely describe a system

6.1 Phase portrait

- dynamical things make curves or points in phase space
- change of a dynamical system corresponds to a trajectory in phase space
- set of all trajectories forms the phase portrait
- because actual solution of nonlinear equations are often not possible phase portraits are often used to study them

6.2 Phase Line

- if the system can be described by one variable we have this case
- line is partitioned by equilibria etc.
- one can study the equation simply with this line

6.3 Phase plane

- arise in 2D autonomous ODEs, like the L-V equations
- if $(x(t), y(t))$ is a solution to the system, then at $t = p$, $(x(p), y(p))$ is a point in phase plane, point changes over time and traces a trajectory in the phase plane
- solution trajectories have their velocity vector given, vector field assigns stuff, see p. 3 beginnig
- equilibrium points are where both f and g are 0, these points are constant with respect to time
- some elements or solutions are periodic and have periods of time when they repeat – they are closed curves in the phase plane
- periodic solutions are stable if solutions near it remain near it through time

6.4 Higher Dimensional and Abstract state spaces

- n-dimensional explanation
- abstract spaces
- random examples and pendulum example

7 Wangersky: Lotka-Volterra population models

7.1 Introduction

- tension between theorists and experimentalists
- math. modeling in biology is often neglected because both sides don't really know about the other and thus make errors
- modeling is misunderstood, only see as predictors and called useless if they aren't 100% accurate
- only very special models have any chance of being accurate – normal models are used to find forms of solutions and not future states of systems
- descriptive model: best-fit curves based on data, simple and good fit
- analytical model: considers mechanisms of the system, mostly logic, little data, very complex, can predict with changing circumstances, theoretical ecology, often based on assumptions
- most models are a mix, problem: fitting constants might be misinterpreted
- assumptions are made, sometimes unaware

7.2 Growth of a single species population

- exponential growth of species like $dx/dt = rx$, x population, r constant of growth
- not best assumption but ok in labs, if just taken to fit data it's ok, if we take it as birthrate - deathrate and take is as intrinsic rate of natural increase that's not ok
- can add a proportion of the max growth rate that is achieved
- population density tends to be a factor too, it's ignored here
- if it's incorporated, we get $dx/dt - rx[1 - (x/K)]$, K is number of supported organisms in an environment
- today logistic equations are generally used for this
- model only works for species of long or short lifetimes where changes in environment are negligible
- oscillations often occur, even in lab conditions where there is no scarcity – L-V models have that
- time lag is generally introduced here to fit reality better

7.3 Prey-Predator Equations

- typical model, x number of prey, y number of predators, a prey mortality liked to predator and prey numbers, b predator growth linked to predator and prey numbers, d mortality constant of predators
- models and their periodic behavior is well known, but few examples of oscillations are known that conclusively depends on predator prey cycles – not even snowshoe hare-lynx in (50) and brown lemming-grass (206)
- there are some examples of well-fitting lab populations, mostly bacteria
- first step is to introduce dampening into prey population and then time delay to the predators
- **mostly irrelevant stuff**

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