and then there were many

- A **population** is all the organisms of the same group or species who live in the same geographical area and are capable of interbreeding.
- Population studies – censuses from Roman times, more elaborate modern versions, birdwatchers, pugmarks – rich statistics
- Fibonacci – one of the first models of population – rabbits that don’t die
- Euler, Laplace
- Models that explain the data through self-regulating mechanisms
- Models that look explicitly at interactions between species and environment
the population according to Malthus

dynamics of population – how does the population change over time

generations – discrete-time or metered models

Thomas Robert Malthus – exponential growth in population limited only be famine, disease etc

in discrete time,

\[ N_{n+1} = (1 + b - d)N_n = \lambda N \]

in continuous time,

\[ \frac{dN}{dt} = rN \]
beetles, bud moths and blowflies

useful in modeling insect populations etc when intra-specific competition for resources is the critical factor

\[ N_{n+1} = R_0 S(N_n)N_n = f(N_n), \text{ } R_0 - \text{ average number of offspring, } S() - \text{ survival function} \]

Contest competition – winner takes all
Scramble competition – equal shares

in real data, we see over-compensation, under-compensation not perfect compensation

Hassell equation: \[ N_{n+1} = f(N_n) = \frac{R_0 N_n}{(1+aN_n)^b} \]
How do the limiting factors to population work?

**Malthus:** \(\frac{dN}{dt} = f(N) = (b - d)N = rN\)

**Verhulst:** \(\frac{dN}{dt} = f(N) = rN(1 - \frac{N}{K})\), quadratic term inspired from physics

\(r\) – net per capita growth rate as before, \(K\) – carrying capacity of the environment
Malthus: $N(t) = N_0 e^{rt}$

Verhulst: $N(t) = \frac{N_0 e^{rt}}{K - N_0 + N_0 e^{rt}}$

the Malthusian model is the simplest and is often used when a population model has to be embedded in more complex models.

the logistic equation has been successful in explaining many populations or related effects.

Earth’s carrying capacity: 2 billion in 1924, revised to 2.6 billion in 1936.

Allee effect – depensatory growth – guillemots
what do we choose: K or r

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N}{K_1}\right), \quad \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N}{K_2}\right), \quad N = N_1 + N_2$$

A mutant competing with the original population – but does it invade?

$(K_1, 0)$ is a steady state but if it is not stable, we can say the mutant invades.

The Jacobian matrix is given by

$$\begin{bmatrix}
-r_1 & -r_1 \\
0 & r_2 \left(1 - \frac{K_1}{K_2}\right)
\end{bmatrix}$$
Fibonacci rabbits:
\[ z_{1,n+1} = [0 \ 1] z_{1,n} \]
\[ z_{2,n+1} = [1 \ 1] z_{2,n} \]

Leslie matrices: 
\[ z_{n+1} = L z_n \]
\[ L = \begin{bmatrix} s_1 m_1 & s_1 m_2 & \cdots & s_1 m_{\omega-1} & s_1 m_\omega \\ 0 & 0 & \cdots & 0 & 0 \\ s_2 & s_3 & \cdots & \vdots \\ 0 & \cdots & s_\omega & 0 \end{bmatrix} \]

\( s_i \) – survival function – probability of surviving from age \( i-1 \) to \( i \)

\( m_i \) – maternity function at age \( i \)

Euler-Lotka equations
interacting species

population of any one species depends on interactions with other species

competition – inhibitory effect for both
symbiosis or mutualism – beneficial effect for both
predation or parasitism – opposite effects for prey and predator

we look at predation: host-parasitoid interactions

Nicholson-Bailey model:
non-overlapping generations of parasitoids
parasitised host dies
$H_n, P_n$ - number of hosts, parasitoids at generation $n$

$R_0$ - basic reproductive ratio of host

$c$ – average number of parasite eggs that survive to breed

$f(H,P)$ – fraction not parasitised

Census takes place at the beginning of season before parasitism

$$H_{n+1} = R_0 H_n f(H_n, P_n), \quad P_{n+1} = cH_n (1 - f(H_n, P_n))$$

Jacobian at steady state:

$$\begin{bmatrix} R_0 (f^* + H^* f_H^*) & R_0 H^* f_P^* \\ c (1 - f^* - H^* f_H^*) & -c H^* f_P^* \end{bmatrix}$$

Jury conditions for stability: $|\text{tr}(J)| < \det(J) + 1$, $\det(J) < 1$
Nicholson-Bailey assumes parasitoids search for hosts according to a Poisson process with parameter $a$

$$f(H_n, P_n) = \exp(-aP_n)$$

Justification: Each season the parasitoids search for hosts randomly and the number of hosts changes as $\frac{dH}{dt} = -\alpha PH$

assuming parasitoid population is constant and integrating over the time of the search, $H(n + \tau) = H_n \exp(-\alpha P_n \tau)$
Lotka-Volterra

Modeling predator-prey interactions – fishing in the Mediterranean – Volterra and his son-in-law, independently Lotka

Laws of theoretical ecology

Canadian hare–lynx data

Year: 1850, 1860, 1870, 1880, 1890, 1900

- Hare (solid)
- Lynx (dashed)
Lotka-Volterra - assumptions

U – number of prey, V – number of predators

rate of change of U = net rate of growth without predation – loss due to predation
rate of change of V = net rate of growth due to predation – loss without prey

- Prey limited only by predator, otherwise grows exponentially
- Predation term linear in U
- No interference between predators in finding prey
- Without prey, predator dies off exponentially
- Every unit of prey death contributes to unit growth in predator
Lotka-Volterra - equations

\[
\frac{dU}{d\tau} = \alpha U - \gamma UV, \quad \frac{dV}{d\tau} = e\gamma UV - \beta V
\]

Steady state at (0,0)
Non-trivial steady state at \( \left( \frac{\beta}{e\gamma}, \frac{\alpha}{\gamma} \right) \)

In the Volterra fishing example, we can add catchability coefficients for predator and prey p, q and constant effort E:

\[
\frac{dU}{d\tau} = \alpha U - pEU - \gamma UV, \quad \frac{dV}{d\tau} = e\gamma UV - qEV - \beta V \quad \text{etc}
\]
Non-dimensionalising by \( u = U/U^* \), \( v = V/V^* \) and rescaling time, we get

\[
\begin{align*}
\frac{du}{dt} &= u(1 - v), \\
\frac{dv}{dt} &= av(u - 1), \\
a &= \frac{qE + \beta}{\alpha - pE}
\end{align*}
\]

We get the equation of the phase plane as

\[
\frac{dv}{du} = \frac{av(u - 1)}{u(1 - v)}
\]

This has periodic solutions:

\[
\Phi(u, v) = a(u - \log u) + v - \log v = A
\]
Lotka-Volterra - analysis

Average population is the steady state population but both prey and predator populations crash in every cycle.

Figure 2.6 Some numerical solutions of the non-dimensional Lotka-Volterra prey-predator model Equations (2.3.9) and the corresponding phase plane Equation (2.3.10).