



Mathematical Biology - Lecture 3 — population

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

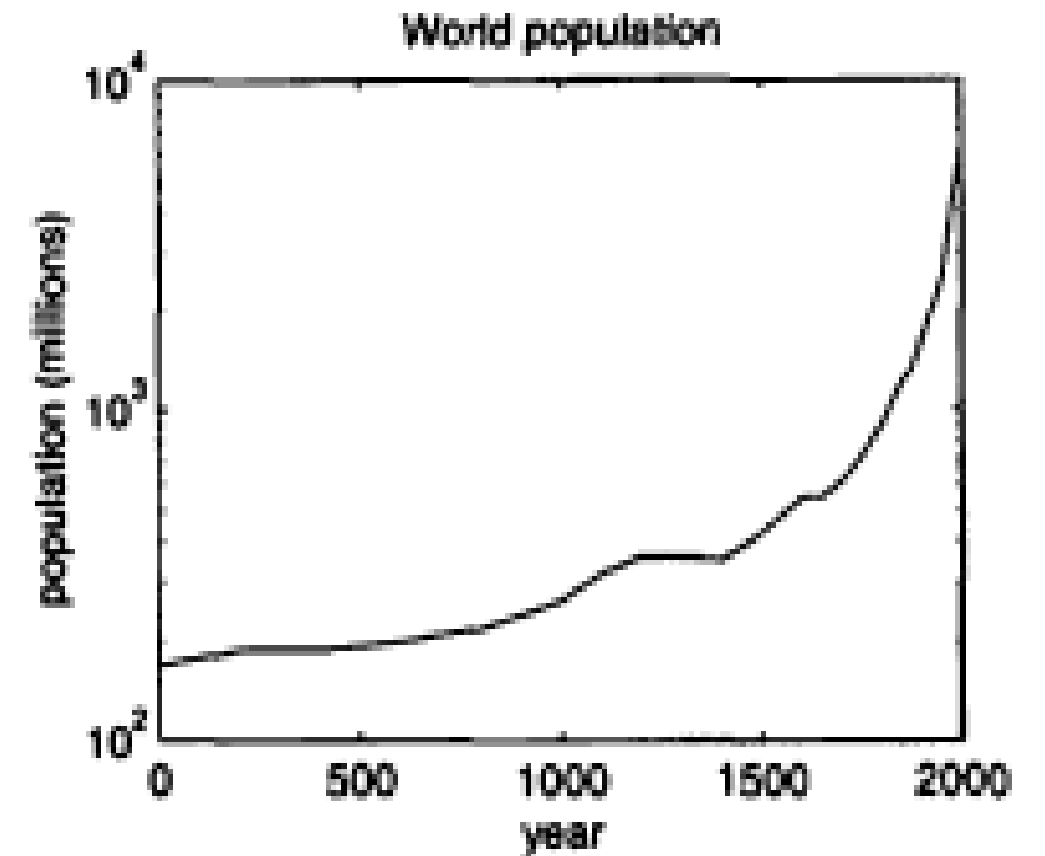
dynamics of population – how does the population change over time

generations – discrete-time or metered models

Thomas Robert Malthus – exponential growth in population limited only by 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

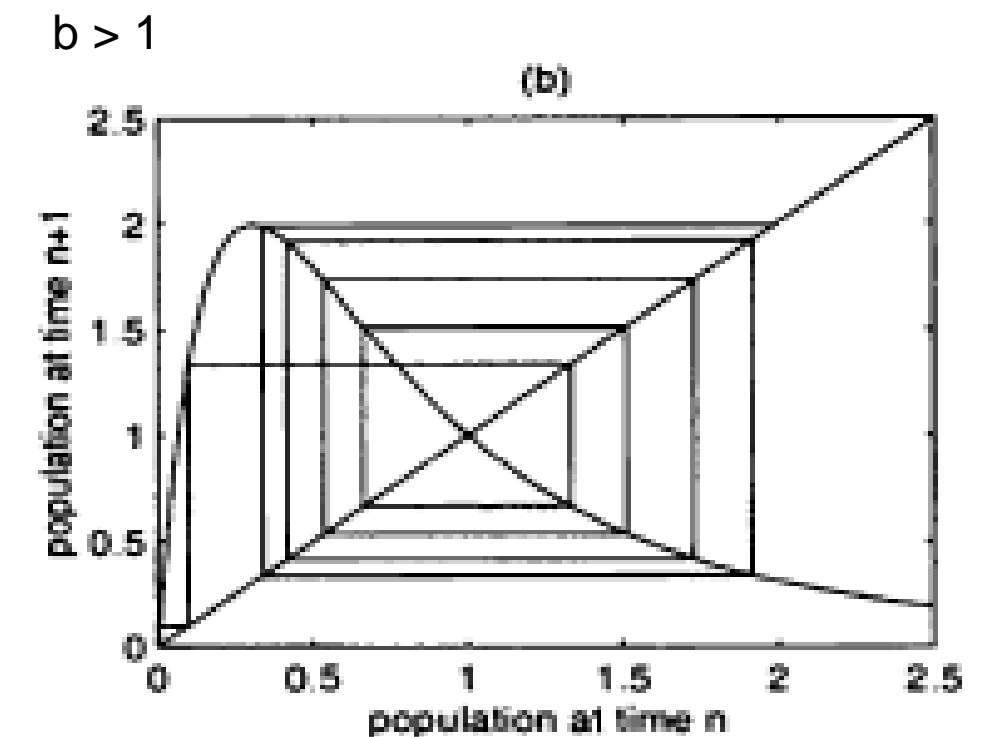
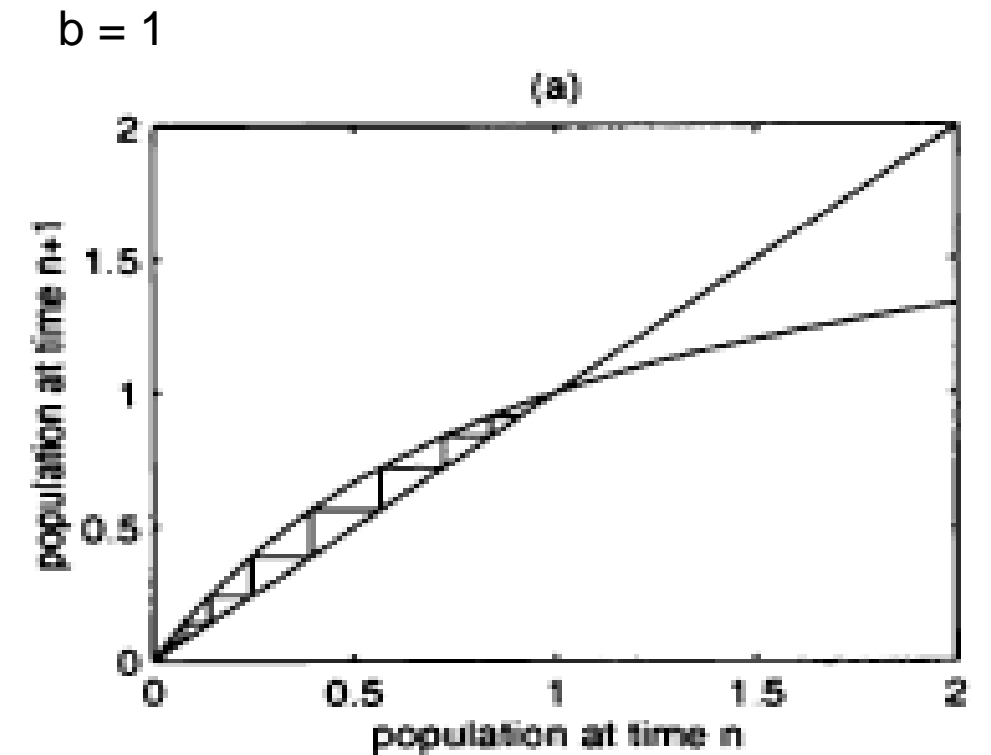
useful in modeling insect populations etc when intra-specific competition for resources is the critical factor

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

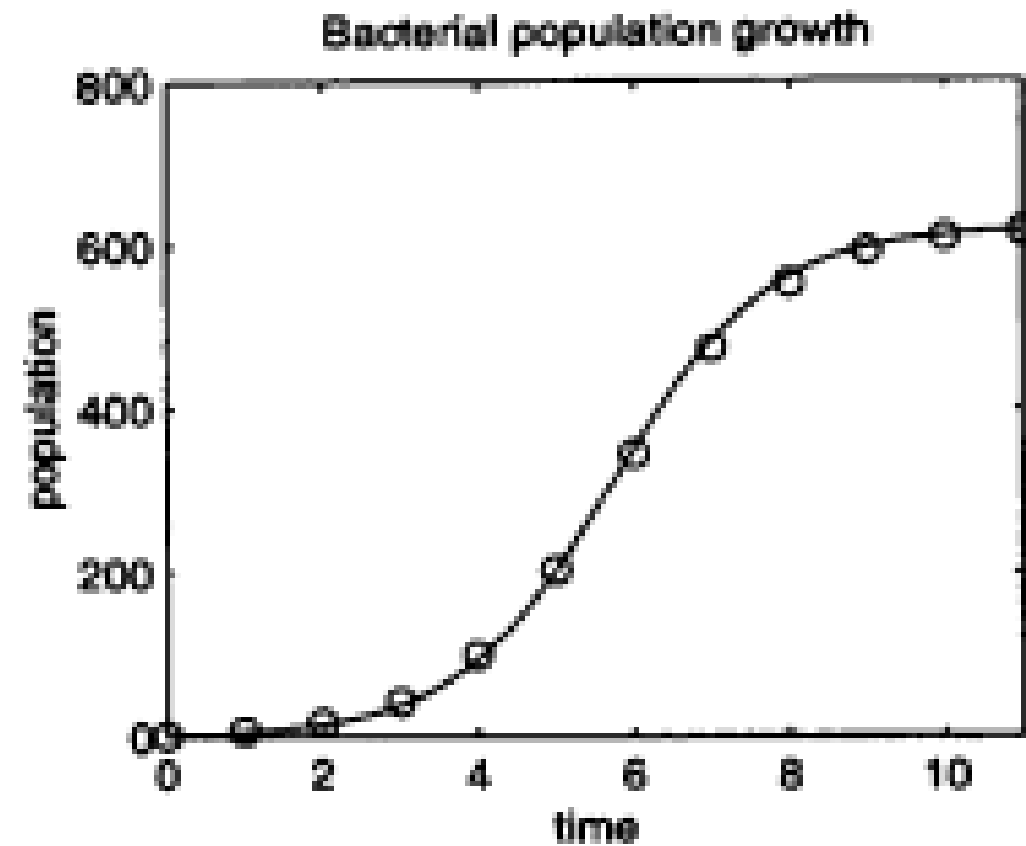
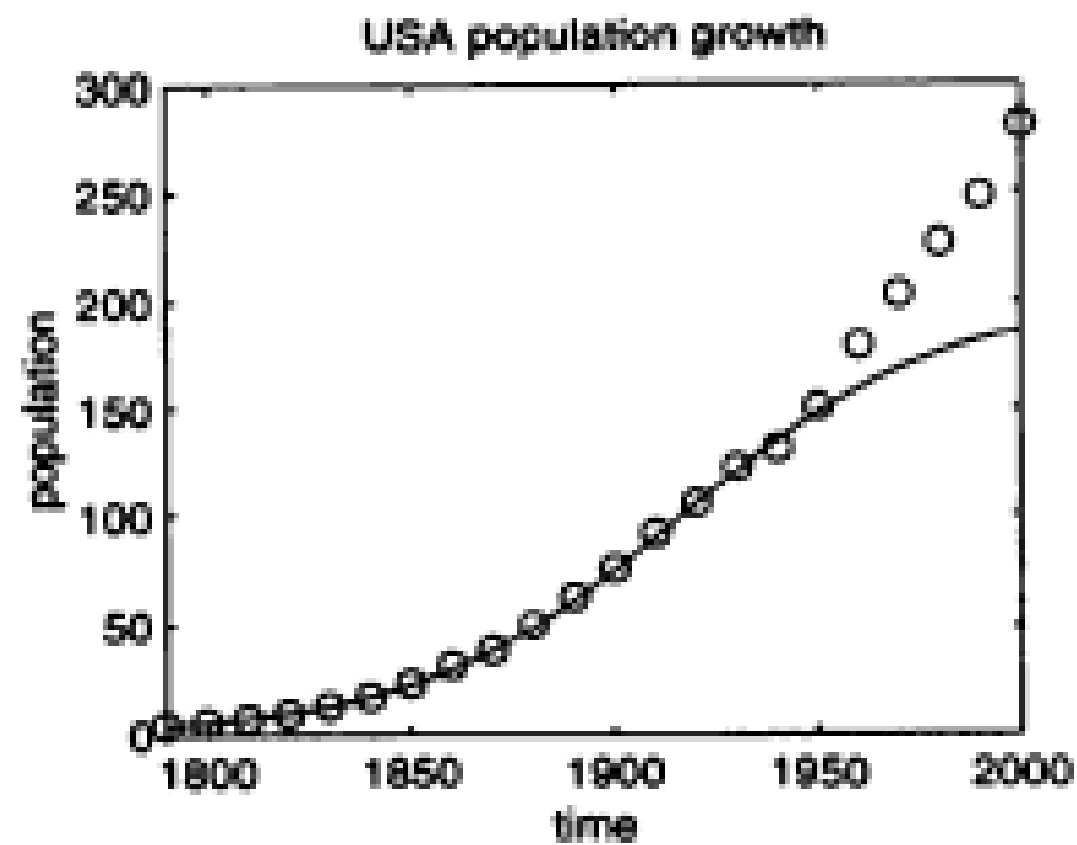
Contest competition – winner takes all
Scramble competition – equal shares

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

Hassell equation: $N_{n+1} = f(N_n) = \frac{R_0 N_n}{(1 + a N_n)^b}$



the population according to Verhulst



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

how many people on earth

$$\text{Malthus: } N(t) = N_0 e^{rt}$$

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

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

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

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 $\begin{bmatrix} -r_1 & -r_1 \\ 0 & r_2 \left(1 - \frac{K_1}{K_2}\right) \end{bmatrix}$

age-structure

Fibonacci rabbits:

$$\begin{matrix} z_{1,n+1} \\ z_{2,n+1} \end{matrix} = \begin{bmatrix} 0 & 1 \\ 1 & 1 \end{bmatrix} \begin{matrix} z_{1,n} \\ z_{2,n} \end{matrix}$$

Leslie matrices: $z_{n+1} = Lz_n$

$$L = \begin{bmatrix} s_1 m_1 & s_1 m_2 & \cdots & s_1 m_{\omega-1} & s_1 m_{\omega} \\ & 0 & & 0 & 0 \\ s_2 & & & & \\ & s_3 & \ddots & & \vdots \\ 0 & & & & \\ & \cdots & & s_{\omega} & 0 \\ 0 & & & & \end{bmatrix}$$

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

Nicholson-Bailey

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

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

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

Nicholson-Bailey assumes parasitoids search for hosts according to a Poisson process with parameter a

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

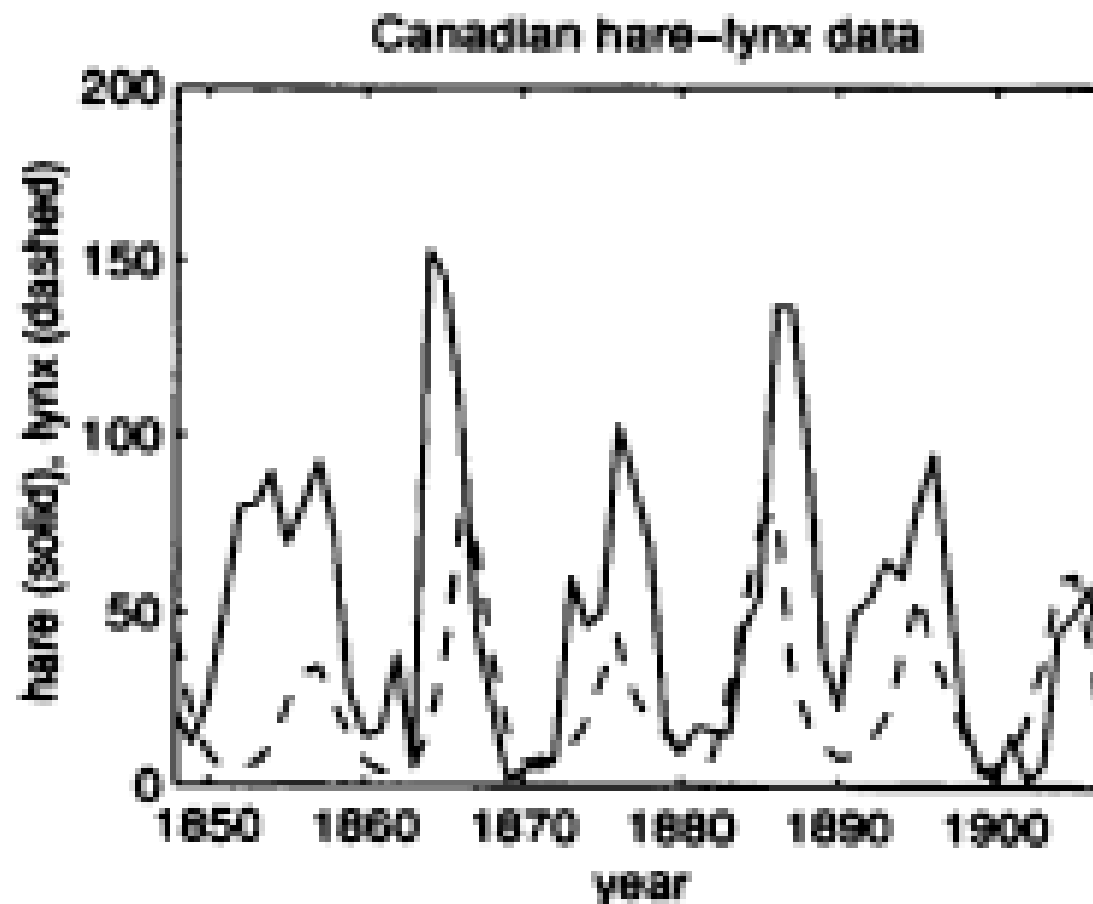
Justification: Each season the parasitoids search for hosts randomly and the number of hosts changes as $\frac{dH}{dt} = -\alpha PH$

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



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

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

Steady state at (0,0)

Non-trivial steady state at $(\frac{\beta}{e\gamma}, \frac{\alpha}{\gamma})$

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

$$\frac{dU}{d\tau} = \alpha U - pEU - \gamma UV, \frac{dV}{d\tau} = e\gamma UV - qEV - \beta V \text{ etc}$$

Lotka-Volterra - analysis

Non-dimensionalising by $u = U/U^*$, $v = V/V^*$ and rescaling time, we get

$$\frac{du}{dt} = u(1 - v), \quad \frac{dv}{dt} = av(u - 1), \quad a = \frac{qE + \beta}{\alpha - pE}$$

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

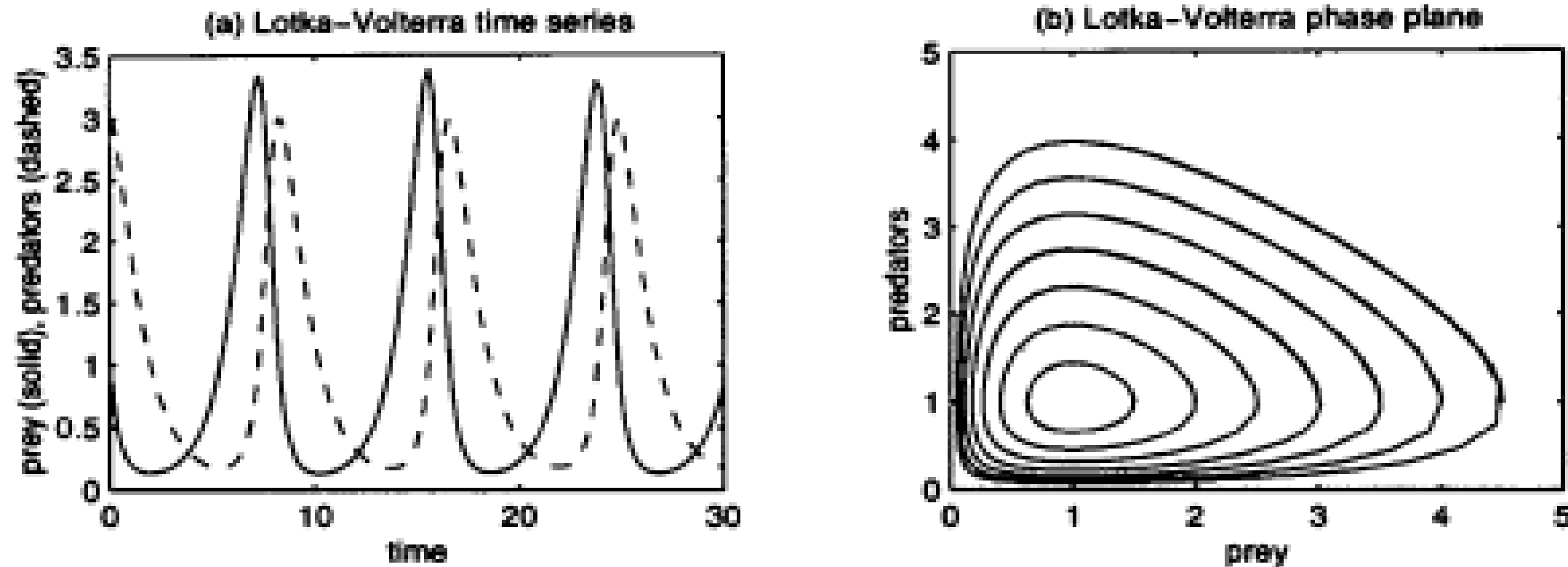


Figure 2.6 Some numerical solutions of the non-dimensional Lotka-Volterra prey-predator model Equations (2.3.9) and the corresponding phase plane Equation (2.3.10).

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