On the mean age of the population of preys in a prey-predator model

Eric Deleersnijder, 2 July 2019

In the framework of the Constituent-oriented Age and Residence time Theory (CART[1]), Delhez et al. (2004[2]) showed that, in the **original Lotka-Volterra model**, the **mean age of the preys** tends to a **constant** as time progresses in spite of the oscillations of their population. This is due to the fact that **predation** is assumed to take place in a manner that **does not depend on the age of the preys**. As is seen below, **mathematical models more complex** than the original Lotka-Volterra prey-predator equations **exhibit a similar property**.

Let independent variables t and τ denote the time and the age, respectively, with $0 \le t, \tau < \infty$. Age distribution function $n(t,\tau)$ of the prey population (i.e. their age spectrum or histogram) is defined as follows: at time t, the number of preys whose age lies in the interval $[\tau, \tau + \Delta\tau]$ tends to $n(t,\tau)\Delta\tau$ as $\Delta\tau \to 0$. Obviously, the physical dimension of function $n(t,\tau)$ is time^{-1}. It is readily understood that the prey population (i.e. the number of preys) is

$$N(t) = \int_0^\infty n(t,\tau)\, d\tau \quad . \tag{1}$$

The mean age of the preys is the arithmetic mean of their ages, i.e. $a(t) = M(t)/N(t)$, where

$$M(t) = \int_0^\infty \tau\, n(t,\tau)\, d\tau \tag{2}$$

is the first-order moment of the preys' age distribution function.

The partial differential equation obeyed by $n(t,\tau)$ is obtained by studying, during time interval $[t, t+\Delta t]$, the evolution of the number of preys whose age lies in the interval $[\tau, \tau+\Delta\tau]$, leading to

$$\begin{aligned} n(t+\Delta t,\tau)\Delta\tau \sim n(t,\tau)\Delta\tau &+ \overbrace{r\, N(t)\delta(\tau)\Delta t\,\Delta\tau}^{\text{number of births}} - \overbrace{\lambda(N,P,t) n(t,\tau)\Delta t\,\Delta\tau}^{\text{number of deaths due to predation or other factors}} \\ &\underbrace{+\, n(t,\tau)\Delta t - n(t,\tau+\Delta\tau)\Delta t}_{\text{ageing terms}} \end{aligned} \tag{3}$$

where δ is the Dirac delta function. In the above relation, positive constant r is the birth rate. It assumed that the number of births is proportional to the prey population and that the age of the newly born preys is zero — so that the age of a prey is, as expected, the time elapsed since its birth. On the other hand, positive function $\lambda(N,P,t)$, which may be rather intricate (depending on the type of the prey-predator model under consideration), represents the death rate, where $P(t)$ denotes the predator population. The death rate is assumed to be independent of the age of the preys. Clearly, the physical dimension of the birth and death rates is time^{-1}.

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[1] www.climate.be/cart

[2] Delhez E.J.M., G. Lacroix and E. Deleersnijder, 2004, The age as a diagnostic of the dynamics of marine ecosystem models, *Ocean Dynamics*, 54, 221-231, http://dx.doi.org/ 10.1007/s10236-003-0075-2,

Finally, the ageing terms reflect the fact that the age of every individual increases at the same pace as time progresses.

Dividing (3) by $\Delta t\,\Delta\tau$ and rearranging the terms, one easily obtains

$$\frac{n(t+\Delta t,\tau)-n(t,\tau)}{\Delta\tau} \sim rN(t)\delta(\tau) - \lambda(N,P,t)n(t,\tau) - \frac{n(t,\tau+\Delta\tau)-n(t,\tau)}{\Delta\tau} \quad . \tag{4}$$

Then, taking the limit $\Delta t,\Delta\tau \to 0$ yields

$$\frac{\partial n}{\partial t} = rN\delta(\tau) - \lambda n - \frac{\partial n}{\partial\tau} \tag{5}$$

Integrating this partial differential equation over the age under "boundary" conditions $n(t,0)=0=n(t,\infty)$ leads to

$$\underbrace{\frac{d}{dt}\int_0^\infty n(t,\tau)\,d\tau}_{=N(t),\text{ see (1)}} = rN\underbrace{\int_0^\infty \delta(\tau)\,d\tau}_{=1} - \lambda\underbrace{\int_0^\infty n(t,\tau)\,d\tau}_{=N(t),\text{ see (1)}} - \underbrace{\int_0^\infty \frac{\partial n}{\partial\tau}\,d\tau}_{=\underbrace{n(t,\infty)}_{=0}-\underbrace{n(t,0)}_{=0}} \tag{6a}$$

which simplifies to the classical formulation of the equation governing the prey population, i.e.

$$\frac{dN}{dt} = rN - \lambda N \quad . \tag{6b}$$

Multiplying (5) by τ, integrating over the age and assuming that

$$\lim_{\tau\to\infty} \tau\, n(t,\tau) = 0 \quad , \tag{7}$$

the following relation is arrived at

$$\underbrace{\frac{d}{dt}\int_0^\infty \tau\, n(t,\tau)\,d\tau}_{=M(t),\text{ see (2)}} = rN\underbrace{\int_0^\infty \tau\,\delta(\tau)\,d\tau}_{=0} - \lambda\underbrace{\int_0^\infty \tau\, n(t,\tau)\,d\tau}_{=M(t),\text{ see (2)}} - \int_0^\infty \tau\frac{\partial n}{\partial\tau}\,d\tau \quad . \tag{8}$$

Integrating by parts, the last term in the right-hand side of (8) transforms to

$$\int_0^\infty \tau\frac{\partial n}{\partial\tau}\,d\tau = \int_0^\infty \left(\frac{\partial(\tau n)}{\partial\tau} - n\right)d\tau = \underbrace{[\tau n]_{\tau=0}^{\tau=\infty}}_{=0,\text{ see (7)}} - \underbrace{\int_0^\infty n\,d\tau}_{=N,\text{ see (1)}} = N \quad . \tag{9}$$

Substituting (9) into (8) yields the equation for the first-order moment of the age distribution function:

$$\frac{dM}{dt} = -\lambda M + N \tag{10}$$

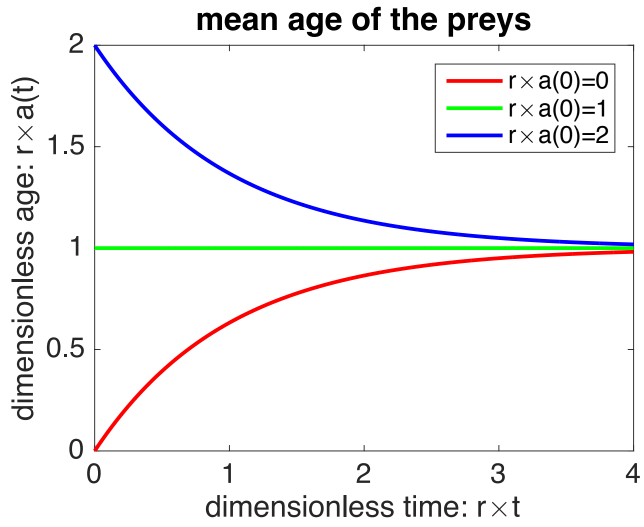
Combining (6b) and (10), one obtains after some manipulations the equation for the mean age of the prey population, $a(t)=M(t)/N(t)$, i.e.

$$\frac{da}{dt} = -ra + 1 \quad . \tag{11}$$

Finally, the mean age of the prey population is readily seen to be

$$a(t) = [a(0)-r^{-1}]\,e^{-rt} + r^{-1} \tag{12}$$

Thus, irrespective of the initial value of the age and the oscillations of the prey population, the mean age of the preys tends to r^{-1} as time progresses. See figure below.



The key **takeaway** of the above developments is as follows:

Under the commonly-used assumptions that the birth rate is constant and the death rate (due to predation or other processes) is independent of the age of the preys, the mean age of the prey population tends to the inverse of the birth rate as time progresses irrespective of the initial value of the mean age of the preys and the oscillations of the prey population.
