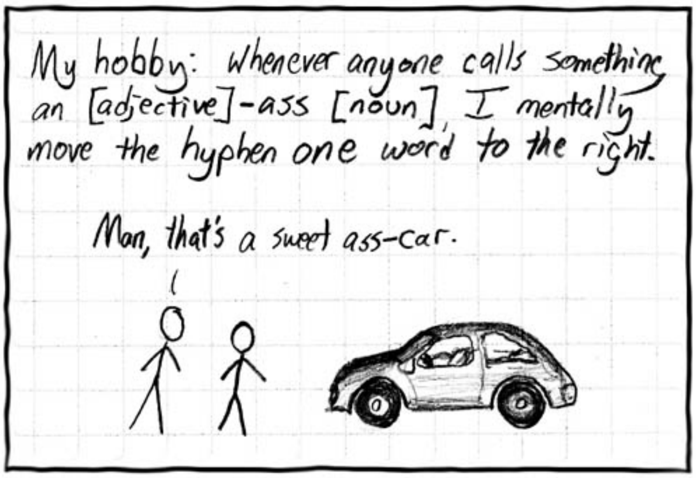
*

Allee effect and multiple stable states



In the logistic model of population growth, every population that starts greater than zero will eventually reach the carrying capacity. However, many natural populations are not viable below a minimum threshold. That can happen because that species depends on social interactions, or because the mere aggregation in space raises the chance of individual survival.

In this tutorial, you will see how a simple adaptation of the logistic equation creates a model that describes the Allee effect. You will also see that this new model has one more stable equilibrium point.

The model

The logistic equation for population growth is normally expressed as:

\begin{equation} \label{eq:logistica} \frac{dN}{dt} ~ = ~ rN \left(1- \frac{N}{K} \right) \end{equation}

Where * N = population size at time t * r = intrinsic growth rate * K = carrying capacity

The Allee effect can be included as one more term of the logistic growth:

\begin{equation} \label{eq:allee} \frac{dN}{dt} ~ = ~ rN \left(1- \frac{N}{K} \right) \left(\frac{N-a}{K}\right) \end{equation}

Here, a is the minimum viable population size.

Equilibrium points

Here we will see an interactive graph[1)] of the population growth speed ($V=dN/dt$) as a function of the population size, considering the Allee effect (equation $\ref{eq:allee}$).

Click `Evaluate` and you will see a menu in which you can change the model parameters. The option `Evaluation point` defines the tangency point of the speed velocity curve as a function of N. The tangent line in this point is the derivative of the speed as a function of the population size (that is, dV/dN, not to be confounded with dN/dt), evaluated at this point.

The population sizes that are in equilibrium are those in which the growth speed is zero. These points are stable if the derivative dV/dt in this point is negative[2].

Question

- Which are the equilibrium points? - Which of the equilibrium points are stable? - What is the difference, regarding equilibria and stability, in relation to the simple logistic model?

Local stability and resilience

The derivative of the growth speed in the equilibrium points indicate which points are locally stable[3]. But this analysis don't tell us about resilience, which is the capacity of the system to return to the equilibrium after a non-infinitesimal perturbation.

Let's use the numerical simulation of the equation $\ref{eq:allee}$ to assess the local stability and the resilience of the equilibrium points. Click the `Evaluate` button to begin. An option menu will open up, and you can change the model parameters and also add perturbation to the population, adding or subtracting as much as 20 individuals. The option `Disturb` defined the size of the disturbance, and the option `Disturb time` the moment in which it occurs.

Questions

1. Assess whether each equilibrium point is stable: use the equilibrium value as the initial population size (N_0) and make small perturbations[4].
2. Assess the resilience of the locally stable equilibrium points. Use the equilibrium value as the starting population and make larger positive and negative perturbations.

- Which parameters affect the resilience of each stable point? Is it possible to increase both points resiliences at the same time?

Alternative states and abrupt changes

Our model has locally stable equilibrium points that are separated by an unstable point. Thus, the system has **alternative states**. These states have a certain resilience, because they resist to a certain amount of perturbation.

Because of these model features, a population following this model is subject to **abrupt changes of state*. A large enough perturbation may abruptly change the system state from one of the equilibrium points to the other. That is somewhat expected, as it is an abrupt change caused by an abrupt cause.

Much more disturbing[5] is the possibility that a small, gradual alteration of the system may cause an abrupt transition. In other words, these systems have a *threshold*, or a non-linear response to environmental changes.

In our model, a gradual environmental shift that changes the value of the unstable equilibrium - that is, the minimum viable population - may trigger an abrupt change in the population. For example, it may happen that the environmental conditions slowly degrade, up to a point where populations that once were viable are now too small to persist. In our model, that corresponds to an increase in the value of a.

Exercise

Click `Evaluate` to open the interactive graphs. The graph to the right show the variation in population size (N) over time (t). The graph to the left shows the growth speed (V) as a function of population size (N).

Use the interactive graphs to simulate an environmental shift that increases the minimum viable population size. The graph simulates a population that is already at the carrying capacity. Slowly increase the value of a and observe the changes in the graphs. Take note of the changes that happen in both graphs as the system gets near the state transition.

To learn more

* Allee W. C. 1931. Animal aggregations, a study in general sociology. Chicago University Press. * Drake, J. M. & Kramer, A. M. (2011) Allee Effects. Nature Education Knowledge 3(10):2. *A complete review on the subject*. * Dai L, Vorselen D, Korolev KS, Gore J. 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. Science. Jun 1;336(6085):1175-7. *An ingenious experiment to show the Allee effect in yeast*.

[1]
using the Sage notebook, which is running remotely on the Sage Cell Server.
[2]
see details in the equilibrium and stability analysis tutorial
[3]
that is, resistant to a small perturbation, as you can see here
[4]
the program allows for perturbations of magnitude 0.5, which will work for this exercise, even if the perturbation rigorously should be infinitesimal
[5]
pun intended