Project 3 (Part I): Discrete Model of the Evolution of a Lizard Population

Sinervo and Lively reported in *Nature* [4] about the mating strategies of side-blotched lizards that live on mounds in Los Baños Grandes, Merced County, California. For this project, you will model the lizards' mating strategies using both difference and differential equations and compare the two models.

Female side-blotched lizards are slightly smaller than male lizards and exhibit yellow throat colorations. There are three types of male lizards and their mating strategies are perfectly correlated with their throat color; the three throat colors are yellow, blue, and orange. The three types of lizards are in competition with one another to mate with as many female lizards as possible.

Yellow throated male lizards are called "sneakers" in that they mimic female behavior. These yellow-throated males pretend to be disinterested females and reject orange-throated males. The orange-throated males tend to have many mates and cover a lot of territory. By pretending to be a female, the yellow-throated males can mate with female lizards in an orange-throated lizards territory. This approach does not work against blue-throated lizards that tend to have a smaller territory and actively challenge yellow-throated lizards, preventing them from mating in their territory.

Because blue-throated males are not fooled by the female impersonation of the yellow-throated male lizards, blue-throated lizards thrive when the proportion of the population of yellow-throated male lizards is high. Blue males challenge other lizards in an effort to have the males assess one another (and thereby, the females assess the males). The high-testosterone orange-throated males attack blue-throated males, often with little advance warning, not following the show and display that blue-throated males engage in. For this reason, blue-throated males lizards are not successful at mating when a large percentage of the male population consists of orange-throated males.

As described above, the aggressive orange-throated male that covers a large territory is not successful in competition with the "sneakers," yet is successful versus blue-throated males. Each strategy has a strength and a weakness due to the strong asymmetries in the mating behavior. Each strategy becomes more successful when another strategy becomes more frequent in the population. However, mating contests between lizards with the same throat colors exhibit symmetric behavior as their strategies do not benefit or are hindered by one another.

a) The mating strategies have been described as a real-life scenario in which the lizards are playing rock-paper-scissors or roshambo. Explain why this is the case. Which strategies correspond to the strategies of playing rock, paper, or scissors?

Because the male lizards with different colored throats pass their mating strategies to their similarly colored male offspring, the number of male lizards with a particular coloring in a generation depends on how successful the lizards with the same coloring were in the previous generation or time period. To model how the distribution of different male lizards changes over time, assign variables to represent the percentage of the three types of lizards at a given time period. Assume that the percentage of the population of the yellow-throated lizards in the next mating season is proportional to the sum of twice the percentage of the population of the orange-throated lizards and the percentage of the population of the yellow-throated lizards in the current mating season. Similarly, the percentage of the population of the blue-throated lizards in the next mating season is proportional to the sum of twice the percentage of the population of the yellow-throated and the percentage of blue-throated lizards in the current mating season. And, finally, the percentage of the population of the orange-throated lizards in the next mating season is proportional to the sum of twice the percentage of the population of the blue-throated lizards and the percentage of the population of orange-throated lizards in the current mating season. Additionally, all of the proportionality coefficients are the same.

b) Assign variables and represent the evolutionary process as a linear system of difference equations.

c) Consider at least 5 different initial conditions for the percentages of the population. Plot how the distribution of male lizards changes over time for the next 25 time periods.

d) Find the general solution to the system of difference equations you found in part *b*). Discuss the long-term behavior. Does this matter what the initial conditions are? (What if there are only blue-throated lizards in the population?)

For the record, the above depiction of evolution of the lizard population where the percentage of the population in one period depends on the percentages in the previous period is called replicator dynamics. This is a common technique to model population changes in evolutionary biology or evolutionary game theory. See, for example, Weibull's book on evolutionary game theory [5] that our library has. Alternately, the evolutionary process can be viewed as a Markov chain (meaning that rows of your matrix sum to 1). You can learn more about Markov chains in Operations Research II or in [1]. Finally, learn more about the side-blotched lizards by visiting the website [3]. The article [2] provides a good overview. Recall that early in the term, a post-doctoral researcher from Sinervo's lab interviewed for a position at Montclair. She gave a talk about more recent research on the physiology of side-blotched lizards.

References

[1] D.L. Isaacson and R.W. Madsen, *Markov Chains: Theory and Applications*, Robert E. Krieger Publishing Company, Inc., Malabar, FL, 1985.

[2] "It's only a game," *The Economist*, April 13, 1996.

[3] B. Sinervo, *http://www.biology.ucsc.edu/∼barrylab/#lizardland*, 2003.

[4] B. Sinervo and C.M. Lively, "The rock-scissors-paper game and the evolution of alternative male strategies," *Nature*, 340 (1996) 240-246.

[5] J.W. Weibull, *Evolutionary Game Theory,* M.I.T. Press, Cambridge, MA, 1995.

Project 3 (Part II): Continuous Models of the Evolution of a Lizard Population

a) A naive way to take a discrete model and change it to a continuous model is to think of the difference between successive terms in the difference equation as a derivative. From Calculus I, we know that

$$f'(t) = \lim_{h \to 0} \frac{f(t+h) - f(t)}{(t+h) - t}.$$

Although it is not the case that $f' = f(n+1) - f(n)$, consider the system of linear differential equations derived from the proportionality equations that generated your system of difference equations where $f' = f(n+1) - f(n)$ for the three equations in the discrete model. You will have to modify things a little to get "$f(n+1) - f(n)$." Graph the solutions for $t = 0$ to 30 to determine the long-term behavior. Is this a reasonable assumption? How has time changed? Or has it? Explain.

b) An alternate way to model the evolution of the lizard populations is with the system of nonlinear differential equations given below:

$$\begin{aligned} y' &= (y + 2o - 1)y = (y-1)y + 2ao \\ b' &= (b + 2y - 1)b = (b-1)b + 2yb \\ o' &= (o + 2b - 1)o = (c-1)c + 2bo \end{aligned}$$

where y, b, and o represent the precentage of yellow-, blue-, and orange-throated lizards in the population at time t.
Graph the solutions for $t = 0$ to 30 to determine the long-term behavior. Does this seem reasonable? Explain.

c) The system of differential equations in *b*) look like the logistic equation with another term. Explain why it looks like the logistic equation and what this means. Also, what effect do the extra terms have? Can you give an explanation for the additional terms?

The system of differential equations that describe the lizard population is one type of generalization of the rock-paper-scissors game to continuous time. Variations appear in Weibull [1].

References

[1] J.W. Weibull, *Evolutionary Game Theory,* M.I.T. Press, Cambridge, MA, 1995.