Spatial Evolutionary Games
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<u>*Learning objectives*</u>: in this session you will understand (i) how to derive some basic results from an evolutionary game, (ii) the role of parameters in determining outcome to these games and (iii) the role of spatial structure on evolutionary game outcomes. The computational aspects will focus on familiarization with *for* loops, *conditional (if, else)* statements and the use of *functions*.

Standard code for each of the sections (A-C) of the practical is available in **R** and can be run in **R** or **R-studio**. These relevant **R** files are all available on CANVAS.

Section A: Evolutionary Stable Strategies (ESS) and basic Hawk-Dove (HD) game

A hawk-dove game is comprised of two players who are contesting for a limiting resource (Q). Each player can decide to play 'hawk' or 'dove'.

Simple rules determine the outcome to the game.

If two 'doves' meet the resource is shared. If two 'hawks' meet there is a costly contest for sharing the resource. If a 'hawk' and 'dove' meet the 'hawk' obtains all the resource and 'doves' do not get payoff or pay any cost in this interaction.

This basic game is symmetric – the rules and outcomes (payoffs) are the same for each player. The game can be represented in a table:

		Player 2	
Player 1		*Dove*	*Hawk*
	Dove	$Q/2$	0
	Hawk	Q	$(Q/2)-c$

The payoffs in this table are for Player 1 (Q is the resource and c is the cost of a contest). As noted, as it is a symmetric game: Player 2 has the same payoffs.

(1) Using the details below, determine evolutionary stable strategies (ESSs) outcomes for the game.

   a. For an ESS to exist, the expected payoff to a 'hawk' (E[Hawk]) must equal the expected payoff to a 'dove (E[Dove]).
   b. Say, h, is the probability of a 'hawk' strategy and remember it is a symmetric game.
   c. An expected payoff for a Player 1 strategy is the *sum* of each probability of encountering the Player 2 strategy multiplied by the payoff.

(2) In **R**, create a graph(s) to show how the ESS is influenced for variation in the cost of the contest (c). Choose a value the resource (Q). Make a sequence of c values

(what minimum value should *c* take to ensure biological relevant results). With appropriate labels, plot a graph (Example code: **HD_graph.R**)

(3) From your graph, determine the cost of the contest conditions for each pure strategies and any polymorphisms to occur.

Section B: Evolutionary outcomes for a spatially-explicit Hawk-Dove game

In order to consider evolutionary outcomes of a hawk-dove game in a spatial context, we need to define how players interact in a neighbourhood through a set of rules. We can choose these rules based on relevant biology.

In this spatial version of the hawk-dove game, we define a spatial lattice or grid and assume that a player interacts with its four nearest neighbourhoods (in a so-called von Neumman neighbourhood). Players at the edges of the grid wrap round - so the boundaries are periodic and the geometry of the grid is actually best thought of as continuous (as a sphere).

There are five rules for this game: these rules explain how individuals in neighbourhoods interact depend on whether the strategy is a ‘dove’ or a ‘hawk’.

For a ‘dove’ individual: if it surrounded by four ‘dove’ neighbours then they all equally shared the resource (*Q* /5). If the ‘dove’ individual is surrounded by at least one ‘hawk’ it gets no resource (and pays no cost).

For a ‘hawk’ individual: if it is surrounded by four ‘dove’ neighbours then it acquires all the resource (*Q*). If the ‘hawk’ individual is surrounded by all ‘hawks’, the resource is partitioned with costs (-c+*Q*/5). If the ‘hawk’ individual is surrounded by at least one but less than four ‘hawks’, the resource is partitioned amongst the individual and ‘hawk’ neighbours (*H*) with costs (-c+Q/(*H+1)*).

The **R** code (**spatial_HD_game.R**) introduces the basic code and allows you to investigate, through single fixed values:

a. Effects of grid size (*nd*) on fitness outcomes for the different strategies.
b. Effects of costs of contest (*c*).
c. Effects of initializations (*threshold*).
d. Effects of resource distributions (*rmn*).

Additional **R** code (**spatial_HD_game_function.R**) allows you to explore ranges of values by wrapping the spatial game into a *function*.

Familiarize yourself with the basics of the code (**spatial_HD_game.R**). Using these **R** scripts:

(1) Investigate pure strategy distributions - set *threshold* to 0 (for all hawks) or 1 (all doves).

(2) Adapt the **spatial_HD_game_function.R** code, to explore how hawk and/or dove fitness varies for ranges of grid sizes (*nd*) costs of contest (*c*), initial distribution (*threshold*) and resource heterogeneity (*rmn*).

(3) Payoffs are important in evolutionary games – as noted, the simple Hawk-Dove game is symmetric. Is the spatial game still symmetric? Investigate this further by exploring the assumptions for the rules.

Section C: Introduction to dynamical evolutionary games

The evolutionary games explored so far have been static; however games are more often expected to be dynamic in space and/or time. The *Game of Life* (developed by John Horton Conway in 1970: details here) is a simple spatially-dynamic game that uses simple rules to investigate the emergent properties of the evolution of diversity.

Under the *Game of Life*, evolution plays on a spatial lattice or grid with an individual interacting with its eight nearest neighbours (so-called Moore neighbourhood) and the following rules:

(a) Any live cell less than two live neighbours dies, as if through lack of support.
(b) Any live cell with two or three live neighbours lives on to the next generation.
(c) Any live cell with more than three live neighbours dies, as if by overpopulation.
(d) Any dead cell with exactly three live neighbours becomes a live cell, as if by reproduction.

The R code (**GOL_v1.R**) allows you to explore the *Game of Life*.

(1) Familiarize yourself with the rules, boundary conditions, process of initialization for this version of the *Game of Life*.

(2) One appropriate measure of fitness is the per capita population rate of change [say, (N(t+1)-Nt)/N(t)]. Adapt the code to investigate how spatial grid size affects this fitness outcome in the *Game of Life*.